Chapter 2
The Microbiology of Natural Soils

Teri C. Balser, Devin Wixon, Lindsey K. Moritz, and Laura Lipps

Introduction

Soil microorganisms, such as bacteria and fungi, control ecosystem functioning through decomposition and nutrient cycling and may serve as indicators of land-use change and ecosystem health (Doran and Zeiss 2000; Waldrop et al. 2000; Yao et al. 2000). However, the study of soil microorganisms is difficult and our current understanding limited. The sheer number, astonishing diversity and small size of these communities become more apparent as our technologies to explore them have improved in recent years (Cardon and Gage 2006). With the rapid rise of molecular techniques, microbial ecologists are now able to walk through the world with the equivalent of the naturalist's "field notebook," cataloguing and classifying species. However, we often do not know what they do functionally or ecologically, or why they are found in some soils and not others (Balser et al. 2006). What we do know is that soil microbial communities are dynamic and diverse (Sylvia et al. 2005) almost beyond measure (Schloss and Handelsman 2006), and that some patterns seem to hold on a global scale.

In this chapter we survey a variety of ecosystems and summarize what we know about their underground microscopic inhabitants. Our knowledge is limited by the

T.C. Balser (✉) and L.K. Moritz
Department of Soil Science, University of Wisconsin-Madison, 1525 Observatory Drive, Madison, WI 53706, USA
e-mail: tcbalser@wisc.edu

D. Wixon
Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA
e-mail: dwixon@gmail.com

L. Lipps
Gaylord Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, WI 53706, USA
e-mail: laalipps@yahoo.com

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relative lack of studies and the particular challenge of linking microbial function with identity. However, trends such as astounding belowground diversity in the tropics, and the importance of fungi in forest soils, are gaining wider attention.

Methods of Study

Any treatment of microbial communities or ecology must include consideration of how we study them. More than most areas of endeavour, the study of soil microbiology is methodologically constrained: the size and fantastic diversity of microorganisms have long been a challenge to researchers. Historically, most techniques have relied on growing the organisms in a laboratory (culturing), but we now know that less than 1% of bacteria and an estimated 17% of fungi are culturable (Torsvik et al. 1990; Amann et al. 1995; Bridge and Spooner 2001; Horner-Devine et al. 2004). Currently we have many new tools for biochemical and molecular analysis of microorganisms, including phospholipid fatty acid (PLFA) analysis and genetic sequencing. These tools allow the targeting of the entire microbial community, rather than just those that grow in culture (Zelles 1999; Nannipieri et al. 2003; Kirk et al. 2004; Leckie 2005). In PLFA (lipid biomarker) analysis, soil microbial community members are identified based on the structure of fatty acids in the microbial cell membrane (Vestal and White 1989). Cell membranes of microorganisms degrade rapidly upon cell death and thus the fatty acids extracted from a soil sample provide an estimate of viable microbial community biomass and composition (Balser 2000; White et al. 1979). Amino sugar analysis instead assesses compounds from cell walls that persist for a very long time after cell death in the soil (Liang et al. 2008). In contrast to lipid biomarker analysis, molecular methods use DNA or RNA sequencing to identify genes unique to microorganism groups, potentially providing a higher level of resolution of the soil microbial community (Nannipieri et al. 2003). New molecular methods attempt to consider the entire community genome rather than that of particular inhabitants (metagenomics, Handelsman 2005).

Regardless of what biochemical or molecular method is used to examine the structure of a microbial community, they usually have the same shortcoming: they primarily provide information about what groups of microorganisms are present, rather than allowing insight into the functionality, or what the microorganisms are *doing* in the soil (Zelles 1999; Nannipieri et al. 2003; Kirk et al. 2004; Leckie 2005). Other methods do allow determination of functionality, i.e., we know what they consume based on how rapidly they consume food (substrate-induced respiration, or SIR), community-level physiological profiling (CLPP), or the enzymes microbes produce (extracellular enzyme assays). However, while these methods can assess the potential and actual activities of the soil biota, they don't tell us exactly who is doing what. In other words – using a given method we can determine *who* is there, but not what they are doing, or we can determine what they are doing, but not who it is. Currently, key studies often combine identification-based methods with activity-based methods. Future research will depend on finding better ways to do both simultaneously.

Soil as a Habitat

Soil microbial community structure and activity depend to a large extent on the status of their soil habitat. Within this habitat, soil organisms are eating, respiring, competing, cooperating, and responding to changes in their immediate environment. Indeed, the majority of the microbial community may be dormant at any given time in most soils, ready to respond as conditions for a particular group become favorable (Stenström et al. 2001). The soil habitat is perhaps best envisioned as a complex matrix with pores and soil aggregates of differing sizes (Sylvia et al. 2005). Certain bacteria and fungi tend to congregate in the soil immediately adjacent to plant roots (the rhizosphere), where they may feed off the sugars that plant roots exude or actually physically associate with the plant root system and exchange sugars and nutrients in a (usually) mutualistic relationship (mycorrhizas). The soil community and its habitat are influenced by an interconnected web of variables that differ among ecosystems, making each ecosystem somewhat unique in its microbial community (Wixon and Balser 2009). Across the globe, as with vegetation, community structure is perhaps most influenced by soil temperature and moisture (Sylvia et al. 2005), though it changes with the seasons (e.g. Lipson 2007), and is strongly affected by soil acidity or alkalinity (pH).

Within a given ecosystem, depth in soil is a primary consideration for microbial habitat, and many key habitat characteristics (e.g. oxygen levels, availability of food and nutrients) change through the soil profile. Carbon availability (and often quality) declines, as does overall microbial biomass (Fig. 1). Soil structure, such as particle size fractions and stable aggregates also change with depth and impact the soil biological habitat (Van Gestel et al. 1996; Ranjard et al. 2000; Sessitsch et al. 2001; Poll et al. 2003). Few studies have considered, however, the importance of both soil parent material and resultant soil texture (Ulrich and Becker 2006; Rasmussen et al. 2007).

Soil organic carbon (SOC) is the largest terrestrial component of the global carbon budget (Jobbágy and Jackson 2000). Worldwide, the top 1 m of soil contains two to three times more carbon than the amount stored in all aboveground vegetation (Brady and Weil 2002). Studies of soil carbon and microbial communities often concentrate on the upper 20–30 cm of soil, as this is considered to be the most biologically active portion of the soil profile (Fierer et al. 2007; Jobbágy and Jackson 2000; Veldkamp et al. 2003; Baisden and Parfitt 2007; Goberna et al. 2006). However, the majority of carbon in soil occurs below 20 cm, and thus by discounting lower depths we are missing up to 50–65% of the carbon (Jobbágy and Jackson 2000). As a result, many current ecosystem models of land-use and climate change inadequately model carbon turnover and microbial communities because they disregard the carbon stocks and biological activities of deeper soil horizons (Baisden and Parfitt 2007). Generally, most microbial community studies down the soil profile have occurred in grasslands and agricultural lands (Fierer et al. 2007; Lavahun et al. 1996; Blume et al. 2002; Taylor et al. 2002; Allison et al. 2007), with fewer studies in boreal and temperate forests (Goberna et al. 2005; 2006;

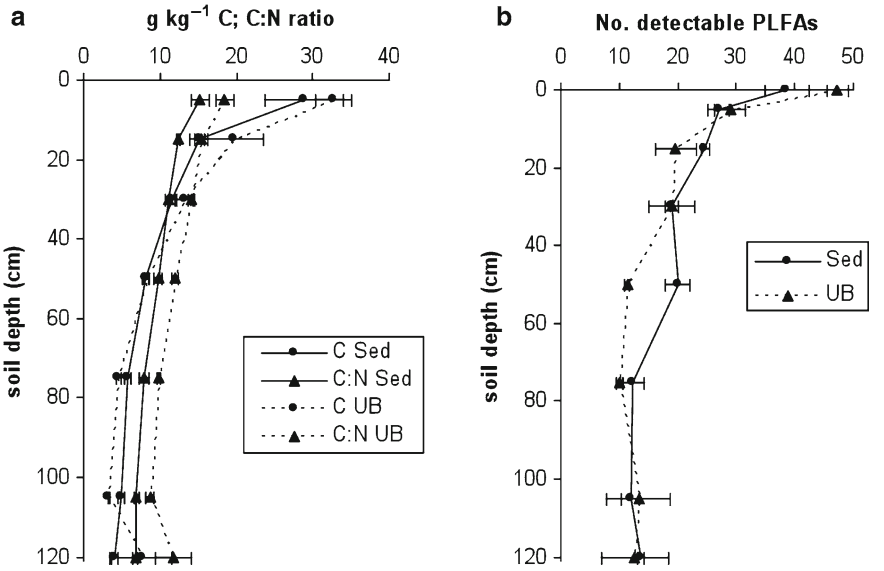

Fig. 1 Microbial and soil properties vary with depth. Depth profile graphs from Sedimentary and Ultrabasic sites in Borneo (See Moritz, 2008). (**a**) Total soil C and carbon:nitrogen (C/N) ratios with depth. Soil C/N differed significantly ($p < 0.05$) between sites under the conditions of two-way ANOVA. (**b**) The number of identified lipid peaks (detectable PLFAs) at each soil sampling depth, representing PLFA richness. Error bars are ± 1 SEM and $N = 3$. Error bars are ± 1 standard error of the mean (SEM) and $N = 3$

Ekelund et al. 2001), and even fewer in tropical forests (Veldkamp et al. 2003). In general, studies demonstrate that fungal-to-bacterial ratios decline with depth, as does overall microbial biomass. Deeper soils become more dominated by bacteria, particularly the slower growing Gram-positive types. In exceptionally deep soils bacterial diversity declines, though organisms are still capable of living at great depths.

Survey of Ecosystems

Soil formation is generally considered to be driven by five factors: parent material, climate, biota, topography and time (Brady and Weil 2002). As we saw briefly above, parent material provides the framework for soil 'architecture', which provides habitable space for microorganisms. Parent material and climate influence weathering rates, which influence soil chemical properties. Over time soils evolve and change and develop in accordance with their environmental and biological factors. The resulting global mix of soil-ecosystems differs in many ways that impact microbial communities. Tropical, temperate, agricultural and wetland ecosystems each have distinct soils, and pose strikingly different challenges for soil microbial life. For example, tropical systems often have low levels of nutrients in the soil, and generally constant warm,

moist temperatures, while high-latitude systems store massive amounts of carbon and can experience dramatic temperature shifts (Brady and Weil 2002). Finally, human land use can also greatly alter ecosystems and thus soil life and its functioning.

Although some generalization by ecosystem is possible, the diversity of factors impacting microbial community habitats implies some caution is needed. Even in adjacent areas, the microbial community of soils of differing types can be strikingly different. For example, two studies in the Pacific Northwest of the United States have compared microbial communities between adjacent soils of differing types (serpentine and non-serpentine) and found that microbial communities in the former were more similar to each other than non-serpentine communities (Oline 2006). The serpentine soils had reduced microbial biomass (DeGrood et al. 2005), suggesting that these offer an inferior environment for microbial growth.

Among the least well understood areas in terms of soils and their microbial community structure and function are the tropical and wetland ecosystems. The vast majority of studies are focused on temperate grasslands and forests, with some emphasis on taiga or boreal forest communities. However, tropical forest and wetland soils are some of the most endangered in the world. They are critical in their potential response to current and future climate change, and as potential sites for agriculture in a world with ever increasing human population size. Below we review some of what is known about the microbiology of these soils.

Tropical Forests

Tropical forests are complex natural ecosystems endowed with unrivaled biodiversity. Located between the Tropics of Cancer and Capricorn, and comprising only 7–12% of the earth's total landmass, tropical forests contain approximately 50% of all known species (Laurance 1999; FAO 2001). In addition to supporting these high levels of biodiversity, tropical forests offer a multitude of ecosystem services including: human habitat, pharmaceuticals, food, and other natural products; watershed stability, flood amelioration, and soil conservation; control of regional climate patterns through evapotranspiration; and regulation of global carbon and nutrient budgets (Laurance 1999; Reiners et al. 1994; Serrão et al. 1996; Bawa et al. 2004; Davidson and Artaxo 2004; Fearnside 2005).

The importance of tropical forests has recently taken on greater importance as the scale of global climate change becomes appreciated. The tropics are at the forefront of concerns for the risks posed by global change because of the high levels of de-forestation and rapid rates of land conversion to cropping, with subsequent loss of biodiversity and capacities for carbon sequestration. From 1981 to 2000, 21% of the area occupied by tropical forests was de-forested (FAO 2001; Bawa et al. 2004) and these rates have not slowed (FAO 2005); if anything they have accelerated. Efforts are being made to catalogue the enormous species diversity in tropical forests and assess what ecosystem characteristics are altered by land-use changes in order to assess the implications of their loss. In 2001, tropical biologists convened in

Bangalore, India, to establish research priorities for the tropics and refined these objectives and directions over subsequent years by additional meetings, workshops, and retreats (Bawa et al. 2004). A primary broad ecological research goal that emerged from these efforts aimed to achieve a better understanding of the structure and function of tropical ecosystems. Emphasis was placed on studies of soil microbial communities and belowground ecosystem structure and function including specifically: describing genetic and species diversity in poorly known regions, groups, and habitats of the tropics. This included defining the fungi and other microorganisms in soil; exploring relationships between components of soil biodiversity, nutrient cycling, and productivity; and predicting the functional response of tropical ecosystems to naturally and anthropogenically induced change.

The tropics are an especially understudied microbial ecosystem. Those studies which do exist have focused on tropical soil microbial communities in the Neotropics, primarily in the Amazon, Costa Rica, and Hawaii, with infrequent scattered studies in other locations (Veldkamp et al. 2003; Borneman and Triplett 1997; Nüsslein and Tiedje 1999; Burke et al. 2003; Carney and Matson 2006; Gomez-Alvarez et al. 2007; Kim et al. 2007; Cleveland et al. 2003). There has been little research on soil microorganisms in the Tropics of Africa, Southeast Asia, and Oceania (Waldrop et al. 2000; Amir and Pineau 1998; Krave et al. 2002; Bossio et al. 2005; Venkatesan and Senthurpandian 2006), with no studies of microbial communities yet published for tropical Australia. The majority of these studies have examined shifts in microbial community composition and function when tropical forest is converted to other land uses, such as pasture, plantations, and agriculture (e.g. Waldrop et al. 2000; Borneman and Triplett 1997; Burke et al. 2003). Other studies have examined seasonal influences of tropical wet and dry seasons (Carney and Matson 2006; Krave et al. 2002), and the effects of plant species and aboveground diversity on soil microbial communities (Carney and Matson 2005; 2006). Below we consider several studies from around the world that have investigated soil microbial communities in the tropics using culture-independent methods (Table 1).

Neotropics: Amazonia, Costa Rica, Hawaii

Amazonia. The Amazon Basin is the largest area of contiguous primary rainforest in the world (Davidson and Artaxo 2004; FAO 2005; Rudel 2005). Amazonia is four times larger than the world's second major expanse of rainforest in the African Congo Basin, and spans nine countries across the northern portion of South America (FAO 2005). Brazil contains nearly two thirds of Amazonian tropical forests and is home to an estimated 7,780 native tree species (FAO 2001; 2005; Rudel 2005). From 2000 to 2005, Brazil had the largest annual net loss of forested area worldwide with 3.1 million hectares lost per year (FAO 2005). The dominant land-use change is conversion to pasture, accounting for approximately 50–70% of the de-forestation, with broadacre cropping and logging being the other major forms of land-use change (Serrão et al. 1996; Fearnside 2005).

Table 1 Summary of tropical soil microbiology studies included in review

Authors	Location	Study scheme	Sampling depth	Microbiological methods
Borneman and Triplett 1997	Eastern Amazon (Para, Brazil)	Mature forest; Pasture	0–10 cm	SSU rDNA
Kim et al. 2007	Western Amazon (Rondonia, Brazil)	Pristine forest; Terra preta soils	0–10 cm	16S rRNA
Cleveland et al. 2003	Costa Rica	Oxisol forest and pasture; Mollisol forest and pasture	0–10 cm	Chloroform fumigation-extraction; phosphatase enzyme assay; substrate-induced growth response
Veldkamp et al. 2003	Costa Rica (La Selva)	Alluvial forest and pasture; residual forest and pasture	0–3 m (alluvial) 0–4 m (residual)	Basal respiration; substrate-induced respiration
Carney and Matson 2005; 2006	Costa Rica (La Selva)	Plant diversity gradient of 1, 3, 5, or >25 species	0–10 cm	Phospholipid fatty acid analysis (PLFA)
Nüsslein and Tiedje 1998	Hawaii (Big island of Hawaii)	200 year old volcanic ash deposit with low plant diversity	0–7.5 cm	Guanine-plus-Cytosine (G+C)of DNA; SSU rDNA; denaturing gradient gel electrophoresis (DGGE)
Nüsslein and Tiedje 1999	Hawaii (Big island of Hawaii)	Pristine forest; Pasture	0–10 cm	G+C of DNA; SSU rDNA
Gomez-Alvarez et al. 2007	Hawaii (Big island of Hawaii)	Volcanic deposits of four different ages	Litter + 1 cm mineral soil	16S rRNA
Burke et al. 2003	Hawaii	Pasture; sugarcane	0–20 cm	PLFA
	Brazil	Forest; sugarcane	0–20 cm	
	Ecuador	Forest; pasture; SC	0–10 cm	
Bossio et al. 2005	Western Kenya	Range of soil textures; forest, woodlot, or agriculture land use; improved fallow, traditional ag., or tea	0–5 cm	Chloroform fumigation-extraction; five enzyme assays; BIOLOG; PLFA; 16S rRNA DGGE

(continued)

Table 1 (continued)

Authors	Location	Study scheme	Sampling depth	Microbiological methods
Venkatesan and Senthurpandian 2006	Western Ghats, India	Pristine forest; tea plantations	0–200 cm	Five enzyme assays
Amir and Pineau 1998	New Caledonia	Five ultrabasic soils of varying plant cover	0–20 cm	Dilute plate count; fluorescein diacetate hydrolysis
Waldrop et al. 2000	Tahiti, French Polynesia	Forest; pineapple plantations of varying ages	0–12.5 cm	Chloroform fumigation-extraction; seven enzyme assays; BIOLOG; PLFA
Krave et al. 2002	Java, Indonesia	Seasonal effects (wet and dry season)	Litter + 0–10 cm mineral soil	16S rRNA DGGE
Moritz 2008	Borneo (Mt. Kinabalu, Sabah, Malaysia)	Pristine forest on ultrabasic or meta-sedimentary bedrock	0–120 cm	Two lignocellulose degrading enzyme assays; PLFA; amino sugar analysis

The traditional first step in conversion of primary forest to some other land-use is to slash and burn, which may or may not be preceded by selective logging (Hölscher et al. 1997; Fearnside and Imbrozio Barbosa 1998; Desjardins et al. 2004). The slash and burn process results in a rapid redistribution of nutrients because of the substantial removal of aboveground biomass. Large amounts of carbon are removed from the system during burning while other nutrients, including phosphorus, potassium, calcium, magnesium, and sometimes ammonium-nitrogen, are concentrated in the ash layer. These nutrients are deposited on top of the soil and incorporated throughout the surface layer, resulting in a temporary influx of basic nutrients and an increase in alkalinity (Reiners et al. 1994; de Moraes et al. 1996; Müller et al. 2004). This temporary enrichment of soil nutrients allows alternate land uses on the otherwise nutrient-poor soils of the tropics (Hölscher et al. 1997; Müller et al. 2004). Over time, the conversion from primary tropical forest to pasture decreases the bulk density and porosity of the soil (Reiners et al. 1994; Eden et al. 1991), and has varying effects on carbon content (Fearnside and Imbrozio Barbosa 1998). Some studies in Amazonia have quantified increases in soil carbon under pasture management (Desjardins et al. 2004; de Moraes et al. 1996; Trumbore et al. 1995; Neill et al. 1996); others report decreases in soil carbon (Desjardins et al. 2004; Eden et al. 1991). Some studies document the absence of changes to soil carbon after conversion (Müller et al. 2004; Buschbacher et al. 1988). These conflicting results appear to be related to forms of pasture management and age of pasture, though there may be an as-yet unspecified role for microorganisms in carbon cycling in such changes to land-use (Balser and Firestone 2005).

While the effects of conversion of primary tropical forest to pasture on soil properties have been relatively well documented in Amazonia, comparatively very little is known about the effects of conversion and anthropogenic influences on soil microbial communities in the Region. Few enough studies have examined soil microorganisms in the tropics at all, while even fewer have been conducted using culture-independent techniques (Borneman and Triplett 1997; Kim et al. 2007). In the first published study using molecular methods which surveyed Amazonian soils, Borneman and Triplett (1997) analyzed 100 small-subunit rRNA gene sequences (SSU rDNA) from northeastern Pará, Brazil, from active pasture and mature forest (50 clones from each land-use). They found 98 bacterial and two archaeal sequences that were unique (with no duplicate sequences), and all were novel sequences that had not been previously documented. Representative major bacterial phyla included *Planctomyces*, *Clostridium*, *Fibrobacterium*, and *Proteobacteria*. Phylogenetic analysis of the sequences indicated that in general, most clones were distinct from other organisms that had been previously described in sequence libraries and 18% of the sequences could not be placed into a known bacterial kingdom. Accordingly, Borneman and Triplett (1997) suggested that these tropical soils contained high levels of microbial diversity composed of some unusual microorganisms. The authors then used rRNA intergenic spacer analysis (RISA) to investigate the effects of vegetative cover and land-use changes on microbial communities and found different banding patterns for the mature forest and pasture soils, indicating that distinct microbial communities were present under

each form of land-use. This study made a major impact in soil and tropical microbiology by providing evidence of novel soil microorganisms and vast microbial diversity. Further, this study showed that de-forestation in the tropics and subsequent conversion to pasture resulted in changes in the composition of the bacterial community, which may also indicate or result in altered nutrient cycling and ecosystem functioning. Unfortunately, the authors did not assay microbial activity together with the community composition. The influence of de-forestation on the role of microbial communities in ecosystem processes (such as nutrient cycling) under each land-use remains unknown.

The next molecular survey of Amazonian soils was published a decade later by Kim et al. (2007). In this work, the authors used oligonucleotide fingerprint groupings (OFRG) to sort through 1,500 16S rRNA clone libraries and DNA sequencing to compare bacterial communities of pristine tropical forest soils and 'terra preta' forest soils in Rondonia, Brazil, in Western Amazonia. Terra preta soils were anthropogenically created by disturbance during pre-Colombian times by the indigenous practice of "slash and char" agriculture. This alternative to slash and burn involves converting the biomass to charcoal, or charring, rather than burning, and results in a lower impact on the environment. Today these soils contain thick epipedons (e.g. the 'A' horizon was 1 m thick at the study site of Kim et al.) with high organic matter contents (Lima et al. 2002; Mann 2002). There is interest in terra preta soils for their ability to stabilize large amounts of organic matter and maintain high fertility in spite of the presence of favorable conditions for rapid organic matter decomposition (Amundson 2001; Lehmann et al. 2003). Kim et al. (2007) found that terra preta soils had greater bacterial diversity and were significantly different from pristine forest soils, with approximately 25% greater species richness. This is particularly interesting given that both soils had similar aboveground species composition and structure, and indicates that the legacy effect from past land-use and the alteration of soil properties remained apparent in the extant microbial community, regardless of subsequent vegetational cover. Phylogenetic analysis showed 14 major bacterial groups were present on terra preta, compared with nine in the pristine forest soil. Phyla common to both soils included the predominant *Acidobacterium*, *Proteobacteria*, *Actinobacteria*, *Planctomycetes*, and *Verrucomicrobia*. Similarly, Borneman and Triplett (1997) found *Planctomycetes* and *Proteobacteria* dominated in eastern Amazonian soils. An important difference between this study by Kim et al. (2007) and Borneman and Triplett (1997) was that the methodology and technology for clone analysis had greatly improved in a decade, thereby facilitating a more comprehensive survey using 1,500 clones in 2007 versus the 100 sequenced by Borneman and Triplet in 1997. In the same way, the sequence databases were much larger following 10 years of additional research, and consequently, fewer novel sequences were found in the study by Kim et al. (2007), although they did identify three potential new subgroups of *Acidobacterium*. A similarity between the two studies was that neither employed a functional measure of the microbial community alongside their molecular analysis and therefore the role of each microbial community remained unknown. The taxonomic information generated using molecular methods only allows us to quantify the diversity of soil microorganisms and facilitates comparison, but cannot currently give information about ecological functions (Fierer et al. 2007).

Nevertheless, both studies showed that soil microbial communities in Amazonia changed alongside anthropogenic disturbance, be it a soil legacy effect from hundreds of years ago or recent de-forestation and pasture conversion. Further, both studies indicated that Amazonian tropical soils harbour distinct microbial communities belowground, paralleling the distinctness found in aboveground biodiversity.

Costa Rica. Central America contains approximately 4.5% of the world's tropical forests and houses an estimated 7% of the world's biodiversity (FAO 2001). From 1990 to 2005, Central America experienced one of the highest rates of de-forestation in the world (FAO 2001; 2005). As in Amazonia, cattle ranching and broadacre cropping have generally been the forces driving land-use change, with urban expansion playing a lesser but still important role (FAO 2001; Rudel 2005). Costa Rica contains just over 2.5% of Central American tropical forests and has the lowest rate of de-forestation in the region (FAO 2001). Costa Rica is one of the pre-eminent locations for tropical forest research in Central America and the world. In the 1960s, pristine tropical forest was set aside in northeastern Costa Rica for ecological research and named La Selva Biological Station of the Organization for Tropical Studies (Veldkamp et al. 2003). Three studies have focused on soil microbial activities and communities at La Selva (Veldkamp et al. 2003; Carney and Matson 2005; 2006), with one additional study of soil microbial dynamics located elsewhere in Costa Rica (Cleveland et al. 2003).

At La Selva Biological Station in 1991, an abandoned cacao plantation was cleared, the merchantable trees extracted, and then the area was slash burned (Haggar and Ewel 1995). Subsequently, plant communities with gradients of diversity were established, including plots planted with one, three and five species, and >25 species (natural regeneration). Carney and Matson (2005; 2006) utilized these experimental plots to investigate the influence of aboveground diversity on belowground soil microbial communities using PLFA (Carney and Matson 2005; 2006), catabolic potential and litter decomposition assays (Carney and Matson 2005). They found that microbial communities shifted in composition with each level of plant diversity and bacterial communities (not fungal) were primarily responsible for these differences (Carney and Matson 2005). Catabolic and litter decomposition assays suggested that each microbial community under different levels of plant diversity harboured distinct functional characteristics. The authors suggested that these shifts were related to the diversity of secondary compounds available for microorganisms to use in their metabolism; for example, a monoculture that produces a carbon source of uniform composition results in a microbial community with lower enzyme diversity. Thus, a reduction in aboveground diversity may affect the catabolic capacity of a belowground microbial community, thereby altering carbon and nutrient cycling and ecosystem functioning. This could indicate an important linkage between aboveground and belowground biodiversity. This finding is particularly relevant to de-forestation issues in the tropics, where primary forest is often cut down and replaced with monocultural plantations (e.g. Waldrop et al. 2000; Krave et al. 2002; Venkatesan and Senthurpandian 2006).

In 2006, Carney and Matson published a follow-up to their 2005 study, where they presented comparisons among different monocultures and focal members in the three species combinations and ranges of sampling dates (representative of wet and

dry seasons). They found that microbial community composition differed significantly among different monocultures and focal species, further supporting the suggested influence of individual plant species in shaping microbial communities. Examination of the microbial communities from different sampling dates showed no significant effect of season relating to community composition. Taking the results of both studies together, it may be concluded that land-use change that alters plant species diversity and composition affects soil microbial communities and their functional roles in ecosystems. These are notable studies because Carney and Matson (2005; 2006) successfully utilized functional and compositional measures of the microbial community to provide an insight into altered ecosystem functioning under land-use change (an important goal of tropical ecology [Bawa et al. 2004]).

At La Selva, in addition to the experimental set-up for studies of aboveground and belowground diversity used by Carney and Matson (2005; 2006), there is primary forest that lies adjacent to de-forested areas cleared for pasture during the 1970s (Veldkamp et al. 2003). Thus, an existing system is in place to study the ecological effects of pasture conversion on native tropical forests. Veldkamp et al. (2003) used the pristine forest and adjacent pasture to look at microbial activity throughout the profile (0–3 m) using basal respiration (BR) and substrate-induced respiration (SIR). Both BR and SIR measure the carbon dioxide production of a soil sample over a period of time, but SIR adds a labile substrate (e.g. glucose) to maximize the respiration rate (representative of the "potential" of the soil microbial community), while BR represents the capacity of the microbial community in situ. Soil profiles in the tropics are highly weathered and often many metres deep, containing substantial stores of soil carbon (Veldkamp et al. 2003; Trumbore et al. 1995; Nepstad et al. 1994). Thus, an energy source is available for microorganisms at depth, but very little is known about their activities in the subsoil. Veldkamp et al. (2003) detected both BR and SIR down to 3 m depth in both forest and pasture. The pasture had 30–50% higher SIR than the forest above 2 m, below which there was no significant difference between land-use cover types. By contrast, BR was higher in the forest than the pasture in surface sampling depths (10–50 cm), with no significant difference below 50 cm. It is interesting that the potential community activity under pasture was greater than under forest cover, but the actual activity of the community was greater under forest cover than pasture. However, the focus of the Veldkamp et al. (2003) study was primarily to assess the existence of substantial carbon pools and microbial activity at depth in tropical soils and therefore soil microbial communities and the ecology of microorganisms were not generally addressed.

A final study in Costa Rica was located outside of La Selva on the Osa Peninsula, and also examined soil microorganisms under forest and pasture (Cleveland et al. 2003). In contrast to the depth study by Veldkamp et al. (2003), the focus of Cleveland et al. (2003) was to investigate how land conversion to pasture affects soil microbial communities using two contrasting soil types, Oxisols and Mollisols. (Oxisols are highly weathered, low-nutrient tropical soils, while Mollisols are generally higher-nutrient grassland soils) (Brady and Weil 2002). Cleveland et al. (2003) used chloroform fumigation-extraction to quantify microbial biomass, and phosphatase enzyme assays and substrate-induced growth response (SIGR) to measure

microbial activities. They found that both soil carbon and microbial biomass decreased upon conversion to pasture, with a more pronounced effect on Oxisols. The authors suggested that low fertility soils (e.g. Oxisols and Ultisols; also the most common in the tropics) are more susceptible to reductions in microbial biomass than soils of higher fertility (e.g. Mollisols). Analysis of microbial activities between pasture and forest showed different physiological capacities, with forest communities being more responsive to changes in resource availability. Further, forest communities appeared to be better adapted to decompose recalcitrant carbon compounds (as evidenced by SIGR using salicylate) than pasture soils. This indicates alterations in microbial community composition after land-use conversion from high biodiversity forest vegetation to less diverse pasture vegetation, and supports the conclusions of Carney and Matson (2005) who suggested shifts in microbial communities under different levels of plant diversity were related to the diversity of carbon sources. However, Carney and Matson (2005) used both compositional and functional measures of the microbial community, while Cleveland et al. (2003) did not use a compositional measure of the microbial community, but rather inferred it from shifts in the microbial activity with different types of cover.

Hawaii. The Hawaiian Islands are the most secluded archipelago in the world (Gomez-Alvarez et al. 2007), formed in the Pacific Ocean over millions of years from basaltic magma that originated from a "hotspot" in the earth's crust, creating a chain of volcanic islands that migrate outward from the centre, activity that continues today (Crews et al. 1995). The geographic isolation and continuing volcanic activity of the Hawaiian Islands make the archipelago an attractive system for ecological studies (Gomez-Alvarez et al. 2007; Crews et al. 1995; Nüsslein and Tiedje 1998). Several studies of soil microbial communities have taken place in the Hawaiian Islands, including examination of soil bacteria in volcanic deposits (Gomez-Alvarez et al. 2007; Nüsslein and Tiedje 1998) and the effects of land-use change on soil microorganisms (Nüsslein and Tiedje 1999; Burke et al. 2003).

Nüsslein and Tiedje (1998) were the first to study soil microbial communities in Hawaii using molecular methods. For their study site, they selected a 200 year-old volcanic ash deposit with low plant diversity and used genetic nucletotide guanine-plus-cytosine (G+C) content to distinguish members of the community. An advantage of G+C content is that it is comprehensive for all DNA and not subject to methodological bias (Kirk et al. 2004; Nüsslein and Tiedje 1999). Prior to the study, they hypothesized there would also be a low level of bacterial diversity on the parent material because of its youth and lack of aboveground diversity. By contrast, they found such high bacterial diversity that they could not determine the community structure using G+C content, as this measure of microbial diversity has relatively coarse resolution. To attempt to reduce the diversity to more manageable levels, they fractionated the G+C content into 63% and 35% (indicative of certain bacterial groups), but still found few duplicates and high diversity. The 63% fraction represented the dominant bacterial biomass and consisted of fewer bacterial taxa, including *Pseudomonas*, *Rhizobium-Agrobacterium*, and *Rhodospirillum*, while the 35% fraction was not dominant but had higher bacterial diversity. The authors

suggested that this reflects the ecological paradigm (Levine 1976) where the most successful competitors consist of fewer species, while the less competitive minority consists of more diverse organisms that occupy smaller, more defined niches. This initial study of microbial communities in Hawaii identified high levels of bacterial diversity, even on a young substrate.

The next study of bacterial diversity in Hawaii, by Gomez-Alvarez et al. (2007) was conducted nearly a decade later. The authors used molecular methods with higher resolution and compared soil bacterial communities on three volcanic deposits ranging in age and included an established old-growth tropical forest (Gomez-Alvarez et al. 2007). The study sites ranged in vegetative cover from a complete absence of vegetation to mature forest. The sequencing and phylogenetic analysis of 16S rRNA showed 56% of the sequences were unclassified and largely distinct. The three volcanic deposits had 60–80% of sequences unclassified, while the mature forest had only 6% unclassified. The oldest volcanic deposit had the greatest bacterial diversity, while the intermediate-age volcanic deposit with an absence of vegetative cover showed the least. Only *Acidobacteria* and *Actinobacteria* were common to all four study sites and no phylotype showed >97% homology among sites. The results of Gomez-Alvarez et al. (2007) indicated a high diversity of soil bacteria within a relatively small area of the Kilauea volcano caldera and found a large number of previously un-described clone sequences in Hawaiian Andisols. Similar to the study of Nüsslein and Tiedje (1998), the work of Gomez-Alvarez et al. (2007) emphasized the diverse and ubiquitous abilities of bacteria to colonize young, even un-vegetated soil, while providing more detailed genetic sequencing of the microbial community.

Another study in Hawaii by Nüsslein and Tiedje (1999) used G+C content fractionation to compare soil bacterial communities under land conversion from native tropical forest to pasture. Similar to other studies in other tropical areas, they found a significant G+C shift (49%) in microbial community structure with the change in vegetative cover (Veldkamp et al. 2003; Borneman and Triplett 1997; Cleveland et al. 2003). *Fibrobacter*, an organism that specializes in cellulose degradation, dominated the 63% G+C content in the forest, with a shift to *Proteobacteria* (general Gram-negative type bacteria) dominance in the pasture. This shift in dominance may indicate that the physiological capacity of the soil bacterial community also changed upon land-use conversion, but there was no quantitative or qualitative measure of microbial function in this study. Thus, while Nüsslein and Tiedje (1999) described genetic diversity of the soil bacterial community, the inter-relationships between bacterial community structure and ecosystem functioning were not addressed.

The final study we consider in the Hawaii and Neotropics section used of phospholipid fatty acid (PLFA) analysis to examine shifts in microbial community composition in forest, pasture, and sugarcane soils in Hawaii, Brazil, and Ecuador (Burke et al. 2003). Lipid analysis provides a more general perspective of microbial community structure; rather than genetic information, it provides information on ecological functional groups, such as Gram-positive bacteria, Gram-negative bacteria, actinomycetes, and saprophytic fungi (Vestal and White 1989). Generally, Burke et al. (2003) found that soil type (e.g. Hawaiian Andisols versus Brazilian Oxisols) was most closely related to the relative abundances of Gram-positive and Gram-negative bacteria.

Conversely, land-use was the major determinant of fungal, actinomycete, and protozoal abundance. Overall, biomass and more specifically, Gram-negative biomarkers, declined upon conversion from forest to sugarcane in Hawaii and Brazil. Gram-positive bacteria were more abundant in agricultural soils, most likely reflecting the less labile carbon substrate that is available on cropland without continuous additions of fresh litter. The study by Burke et al. (2003) reaffirmed that land-use conversion affects the structure of soil microbial communities and introduced the concept that these changes show some regional variability (i.e. Hawaii versus Ecuador versus Brazil) but can be broadly applied to a range of tropical soils.

Conclusions: Neotropics

The majority of tropical soil microbiology studies have had sites in the Neotropics and have concentrated on the effects of land-use conversion on soil microbial communities. These studies have utilized a wide range of methods for the study of soil microorganisms, including PLFA, DNA-based methods, and measures of microbial function. However, we can collectively use the results from these studies to conclude that the effects of land-use change on vegetative cover type and plant species diversity changes the structure and function of the soil microbial communities (Veldkamp et al. 2003; Borneman and Triplett 1997; Nüsslein and Tiedje 1999; Burke et al. 2003; Cleveland et al. 2003; Carney and Matson 2005; 2006). There is indication that the conversion to pasture reduces microbial activity and biomass (Veldkamp et al. 2003; Burke et al. 2003; Cleveland et al. 2003) and that microbial communities have a less diverse physiological response as aboveground biodiversity decreases (Cleveland et al. 2003; Carney and Matson 2005). Other studies have indicated there is an immense diversity of soil microorganisms in the tropics, with many previously unclassified organisms (Borneman and Triplett 1997; Kim et al. 2007; Nüsslein and Tiedje 1998). The majority of studies restricted soil sampling to the upper 10 cm of soil, and given the substantial carbon pools at depth in tropical soils, further studies of microbial activity in tropical subsoils are much needed (Veldkamp et al. 2003). In addition, more studies that use both compositional and functional measures of tropical soil microbial communities are needed to help understand what changes in ecosystem functioning occur under land-use changes.

Tropics of Africa, Southeast Asia, and Oceania

Africa. In 2000, Africa was estimated to contain approximately 33% of global tropical forests (FAO 2001). The Congo Basin, located in the heart of Africa, is the second largest expanse of primary rainforest in the world (FAO 2001; 2005). From 2000 to 2005, six out of the top ten countries with the highest de-forestation rates in the world

were located in Africa (Congo, Nigeria, Sudan, Tanzania, Zambia and Zimbabwe), making tropical African forests a rapidly diminishing resource. Although it is difficult to generalize for the whole of Africa, the major force behind de-forestation is often conversion to small-scale subsistence agriculture (FAO 2001; Rudel 2005). While much is unknown about the tropics, the tropical forests of Africa are perhaps the most understudied of all tropical areas, with little known about the structure and function of these systems and the effects of de-forestation and land-use conversion.

A single study by Bossio et al. (2005) investigated tropical soil microbial communities in Western Kenya under a variety of land uses and employed a consortium of microbiological analyses. This study included comparisons among forest, woodlot, and agriculture land-use types; agriculture practices of traditional maize cropping (two crops per year), management with improved fallow (alternating maize with a species of nitrogen-fixing tree, *Tephrosia candida*), and perennial tea cultivation; and a range in soil textures from sandy (5% clay) to clay (60% clay). To assess microbial community activity, Bossio et al. (2005) used BIOLOG and enzyme assays, and used PLFA and genetic analysis (DGGE analysis of 16S rRNA) to determine microbial community structure. This is the only study that used such a comprehensive assemblage of microbial characterization techniques (Table 1). Molecular methods showed that soil type (such as sandy, clay) appeared to induce the primary differentiation among soil microbial communities, while land-use (wooded or agriculture) was the secondary determinant. The DGGE analyses showed there was no significant difference in bacterial diversity between wooded and agricultural soils. While PLFA data showed greater relative abundance of Gram-negative bacterial indicators in wooded soils than agricultural soils, and agricultural soils had higher proportions of actinomycetes and Gram-positive bacteria. These same shifts in lipid biomarkers under land-use change were reported in the Neotropics by Cleveland et al. (2003) and are likely to be linked with varying availabilities of carbon sources under different land-uses. Bossio et al. (2005) found that soil microbial communities from wooded sites had the most diverse abilities for substrate utilization, a finding also reported by Cleveland et al. (2003). Finally, the authors found substantially lower soil carbon, microbial biomass, and total enzyme activities under traditional maize cultivation, all of which generally increased under improved fallow management. Using a complex suite of methods and study sites, Bossio et al. (2005) found that the microbial community shifted with different soil types and land-uses, but overall levels of microbial diversity were similar among land uses. Shifts in activity or functions of the microbial community were closely linked to management practices, but showed less specificity than measures of microbial community structure. This study reiterates the important influences of land-use change and management practices on soil microbial communities in the tropics. This study by Bossio et al. (2005) is the only study we are aware of that focused on soil microbial communities in tropical Africa. Clearly, there is a need for more studies on this continent with its vast tropical forest reserves and rapid de-forestation.

India. India is unique among the other tropical regions examined in this literature review in that it has had a high population density exerting pressure on the land since at least the nineteenth century (Rudel 2005). While pristine tropical forests

are being newly encroached upon and exploited in Amazonia, Africa, and parts of Southeast Asia, tropical forests in India have been de-aforested and fragmented in response to poverty and anthropogenic pressures for over a century. As a result, in the 1980s, only 2% of India's land area contained primary forest, with much of the remaining land consisting of cutover and degraded forests. The government responded by establishing forestry management plans and intensive re-forestation efforts, resulting in a slight increase (38 ha $year^{-1}$) in forested area from 1990 to 2000 with 72% of India's forests under management plans. Not surprisingly, the majority of soil microbiology studies in the tropical forested regions of India have examined the effects of land conversion and management practices on soil microorganism populations. Changes in microbial biomass under different land uses have been researched intensively in India and studies have generally shown that microbial biomass declines upon conversion from primary forest (Srivastava and Singh 1991; Basu and Behera 1993; Singh and Singh 1995; Behera and Sahani 2003). However, no studies in India were found that explored shifts in microbial community structure upon land-use changes using culture-independent methods (PLFA or molecular methods), while one study was found that investigated differences in microbial enzyme activities between pristine forest and land converted to tea plantations (Venkatesan and Senthurpandian 2006).

In the middle of the nineteenth century, the Western Ghats, a region in Southern India, was covered with native tropical wet evergreen forests (FAO 2001; Kumara et al. 2004). In the 1880s, private landowners cleared large tracts of this rainforest and established tea plantations on the deeply weathered tropical soils, creating a mosaic of plantations and primary forest (Venkatesan and Senthurpandian 2006; Kumara et al. 2004). A study by Venkatesan and Senthurpandian (2006) examined differences in microbial enzyme activities between these two land uses in the Western Ghats. They sampled every 25 cm down the soil profile to 200 cm depth in an effort to quantify microbial activities throughout the typical rooting zone of tea. All enzyme activities (with the exception of protease) were detectable in the deepest sampling depths, indicating an active microbial community in the subsoil. Veldkamp et al. (2003) reported a similar result with measurable microbial respiration at 3 m depth in tropical pasture and forest soils in Costa Rica. Venkatesan and Senthurpandian (2006) found that acid phosphatase activities were highest in both tea and forest soils, followed by alkaline phosphatase activities. At any given depth, urease activity was higher under tea plantations than under forest, and showed no significant decline with depth under tea crops. The authors attributed this result to the continuous application of urea used in plantation management. Aryl sulfatase activity was considerably higher in the top 50 cm of the tea plantation than the forest, below which the forest had consistently higher aryl sulfatase activity. Generally, Venkatesan and Senthurpandian (2006) summarized their findings of enzyme activities and attributed observed patterns to organic matter content and beyond this provided little insight into their results. Thus, data are presented, but lack an ecological context, which is a common shortcoming in soil microbiology. The enzymatic patterns observed by Venkatesan and Senthurpandian (2006) were generally irregular with no distinct conclusion to be drawn between types of cover. However, they overlooked

that all enzyme activities were greater below 150 cm in the forest than the tea plantations (with the exception of urease). This may be attributed to the deeper rooting patterns of tropical wet evergreen forests that extend well below the 2 m zone of tea plantations. This study is important because of its focus on microbial activity with depth in the tropics, a relatively unknown realm of study (Veldkamp et al. 2003). However, further studies of depth that include determinations of microbial community structure along with measures of activity are needed in order to arrive at ecologically meaningful interpretations of ecosystem functioning.

Pacific Southeast Asia and Oceania. The tropical forests of the Southeast Asian Pacific and Oceania have some of the highest reported levels of biodiversity in the world (FAO 2001; 2005; Myers and Mittermeier 2000). However, recent estimates have shown that Pacific Southeast Asia retains only 3–15% of its primary vegetation, while Oceania, including New Caledonia and Polynesia/Micronesia, preserves 22–28% of its original vegetation (Myers and Mittermeier 2000). Indonesia lost almost 1.9 million hectares per year from 2000 to 2005, the second largest annual net loss of forest behind Brazil (FAO 2005). Conversely, from 1990 to 2000, New Caledonia and French Polynesia, two countries considered in this review, had no net loss of tropical forests. De-forestation in Southeast Asia results primarily from logging and the timber trade (Laurance 1999; FAO 2001). Similar to the tropical forests in Africa, the forests of Southeast Asia and Oceania have few studies of soil microorganisms and ecosystem functioning (Waldrop et al. 2000; Amir and Pineau 1998; Krave et al. 2002).

On the island of Java, Indonesia, nearly all primary tropical forests have been harvested and today approximately 50% of the forest is has been converted to pine plantations (Krave et al. 2002). A study by Krave et al. (2002) investigated seasonal influences (wet and dry season) on soil bacterial communities in Javanese *Pinus merkusii* plantations. Their objective was to achieve a better understanding of nutrient cycling and so improve plantation management. They sampled litter, duff,[1] and mineral soil samples during successive dry and rainy seasons and then used DGGE analysis of 16S rRNA to assess bacterial community structure. They found that each layer of forest floor and mineral soil had significantly different physical and chemical properties, including organic matter content, and the bacterial communities were stratified accordingly. Moisture content, pH, and nitrogen levels of the three forest layers changed significantly with season, but bacterial communities in the duff and mineral soil were not influenced. Only the litter microbial communities varied with season. Similarly, Carney and Matson (2006) found that season did not influence the composition of soil microbial communities in Costa Rica. Krave et al. (2002) constructed a clone library for one litter sample taken in the wet season and found that it contained high levels of bacterial diversity. *Proteobacteria* (specifically *Rhizobium-Agrobacterium*) and Gram-positive bacteria with high G+C content dominated the profiles. *Rhizobium-Agrobacterium* was reported in the study of Hawaiian soils by Nüsslein and Tiedje (1998) and Gomez-Alvarez et al. (2007),

[1]Duff: the layer of partially and fully decomposed organic materials lying below the forest flar litter and immediately above the mineral soil.

but was not documented in phylogenetic analyses of tropical soils by Borneman and Triplett (1997) and Nüsslein and Tiedje (1999). Overall, this study suggests that microbial communities in duff and mineral soil are better buffered from seasonal changes than litter microbial communities, and each layer harbours a distinct community of considerable diversity.

Another study of tropical soil microbial communities in the Southeast Asian Pacific was conducted by Amir and Pineau (1998) in New Caledonia using culture-dependent methods to identify microbial community structure and culture-independent methods to assay microbial activity. Approximately one third of New Caledonia is underlain by ultramafic outcrops. Soils weathered from ultramafic rock, often also referred to as ultrabasic or serpentine soils, pose special challenges for plant growth and survival. These rocks and their resulting soils are characterized by high levels of metals (e.g. nickel, cobalt); low levels of nitrogen, phosphorus, and potassium; high levels of magnesium with low calcium; and low soil moisture (Walker 1954; Proctor 1999; Brady et al. 2005). Ultrabasic outcrops often have poor productivity and contain many endemic species that are specially adapted to the potentially toxic levels of magnesium and other metals (Walker 1954). Most ultramafic outcrops are exposed in orogeny (mountain-building) zones and are rare, occupying approximately 1% of the Earth's surface (Proctor 1999). In New Caledonia, many ultramafic outcrops have been mined for nickel and revegetation efforts are underway to reclaim land degraded by mining activities (Amir and Pineau 1998). Amir and Pineau (1998) examined soil microorganisms in a series of ultrabasic soils that varied in vegetative cover (e.g. bare ground, cluster of vegetation and crop cover) to investigate methods for improving soil fertility on reclaimed lands. Soil microbial populations were estimated using dilution plate counts (a culture dependent method) and microbial activity was estimated using the fluorescein diacetate (FDA) hydrolysis test (a culture-independent method). The authors found that microbial populations and activity in New Caledonian ultrabasic soils were lower than other estimates reported in studies of nonserpentine soils. These low numbers were attributed to minimal organic matter contents in the ultrabasic soils. Actinomycetes were the predominant bacteria, accounting for 70–90% of the total culturable microorganisms, and two very common culturable fungal families, *Tubercularіaceae* and *Dematiaceae*, were absent. The authors suggest these results may be related to the metal tolerance of these microbial groups. The ultrabasic soils varied widely in microbial characteristics depending on the level of root colonization of soil, with the highest biomass and activity under vegetation and the lowest values on bare uncolonised ground. Cropping appeared to affect microbial communities positively, as bacterial and fungal diversity increased under cultivation. The authors caution that their results are difficult to compare with other soils because of the uniquely extreme conditions of ultramafic outcrops. Amir and Pineau (1998) provided preliminary information about soil microbial communities in tropical ultrabasic soils, but more comprehensive studies using culture-independent methods are needed along with further studies of microbial function.

A further study in Oceanic tropical soils used enzyme activity assays and BIOLOG along with PLFA to investigate responses of the soil microbial community

to land-use conversion from primary forest to pineapple plantations in Tahiti (Waldrop et al. 2000). Researchers found that conversion to plantation agriculture increased soil acidity and decreased carbon content, and accordingly soils had one quarter of the microbial biomass of forest soils. Soil microbial communities were significantly different between primary forest and plantations, with greater relative abundances of fungi and actinomycetes in plantation soils. BIOLOG did not show differences between forest and plantation treatments. This contrasts with the hypothesis presented by Carney and Matson (2005) in their study of the effects of plant diversity on soil microbial communities in Costa Rica where they suggested that under less diverse vegetative cover (e.g. plantation) soils have lower diversity in their degradative abilities. Waldrop et al. (2000) further found that enzyme activities were similar between forest and plantation soils, with the exception of β-glucosidase and sulphatase enzymes. However, the pineapple plantations are managed distinctly from other crops and every 5 years the entire pineapple crop is cut down and incorporated into the soil, 'resetting' the system with organic matter input. Thus, pineapple plantations may have carbon inputs comparable to natural forests, resulting in similar microbial community enzyme activities between forest and plantation soils. Similarly, Venkatesan and Senthurpandian (2006) found no discernible differences in enzymatic patterns (with the exception of urease) between tea plantations and tropical forest soils in India. Relating microbial community composition to function, Waldrop et al. (2000) were able to correlate specific enzyme activities (total activity divided by microbial biomass) and relative abundance of specific indicator lipids. They found β-glucosidase and β-xylosidase, enzymes used to degrade simple carbon compounds, were correlated with Gm–, fast-growing bacteria that metabolize simple sugars. Thus, the authors successfully deduced the function of a member of the soil microbial community, lending insight into its role in ecosystem functioning. This study by Waldrop et al. (2000) confirmed that land-use change in the tropics alters soil properties and soil microbial communities. Further, it provided a successful interpretation of microbial structure and function, achieving a major goal of tropical ecology (Bawa et al. 2004).

Conclusions: Old World Tropics

These studies of soil microbial communities were as varied as their locations. They examined the effects of soil type and land-use in Africa (Bossio et al. 2005); microbial activity through depth in tea plantations and tropical forests in India; wet and dry seasons on litter and mineral soil in Java (Krave et al. 2002); vegetative cover in New Caledonia (Amir and Pineau 1998); and conversion from primary forest to pineapple plantations in Tahiti (Waldrop et al. 2000). Perhaps the best collective conclusion from these five studies of the tropics is that little research has been done in this vast region of the world concerning soil microbial communities and ecosystem functioning. Clearly, there is a huge range of diversity of soils and land uses in the tropics, and many questions concerning ecosystem functioning remain to be answered.

Wetlands

Wetlands are transient or permanently saturated terrestrial habitats. The term wetland has been applied to freshwater marshes, bogs, peatlands and swamps (EPA 2004). It also encompasses coastal areas such as salt marshes and mangroves (Shaw and Fredine 1956). This excessively broad definition has long hampered our understanding of these ecosystems and its inhabitants. Overall wetland ecosystems comprise a small proportion of the earth surface (at least 9% by some estimates [Ramsar Convention Secretariat 2007]), yet their contribution to biochemical cycles, water cycle (as source and filter), and the maintenance of species richness overshadow that of other larger terrestrial environments (Basu and Behera 1993). Additionally, wetlands are used by humans for water, flood control, fiber, food, and recreation. The services delivered by wetlands have been arguably valued at US$14 trillion annually (Ramsar Convention Secretariat 2007). Worldwide, wetlands have long been underappreciated and drained. Wetland loss and degradation has primarily been driven by land conversion for agriculture, infrastructure development, water extraction for irrigation or drinking water, eutrophication and pollution and over-exploitation (Ramsar Convention Secretariat 2007). Climate change is expected to exacerbate the loss and degradation of wetlands, both through drying out and resulting shifts in precipitation (Ramsar Convention Secretariat 2007).

Wetland ecosystems link terrestrial, aquatic, and biosphere level processes through their contribution to biogeochemical cycles and global climate change (Fig. 2). This includes interactions between environmental, hydrological and biotic processes. Among these the physical processes, e.g. hydrology, have been studied in more detail than the biotic processes. A recent review of wetland microbial communities by Gutknecht et al. (2006) notes that research in wetland biogeochemistry has most often been focused on microbially-mediated processes (e.g., methanogenesis, denitrification and methanotrophy), and less often on microbial communities or on populations of specific microorganisms of interest (Fig. 3). Work to date indicates an important process level role for hydrology and soil nutrient status. The impact of plant species composition on processes is potentially critical, but is as yet poorly understood.

Research on microbial communities in wetland soils has primarily focused on anaerobic bacteria responsible for methanogenesis (production of methane gas), denitrification and sulfate reduction (Gutknecht et al. 2006). There has been less work on taxonomic groups such as those responsible for nitrogen fixation, or aerobic processes such as nitrification. While less well known, it is also possible that aerobic organisms such as nitrifiers and methanotrophs may play an important role in wetland ecosystem functioning.

Work on general community composition and on wetland mycorrhizal fungi is particularly sparse. Despite longstanding conventional wisdom that says fungi are not abundant or important in wet systems, it has now been demonstrated that mycorrhizal fungi are often abundant in wetlands (Mentzer et al. 2006) and may play a significant role, and mycorrhizal association was the focus of a recent review (Anupam 2003).

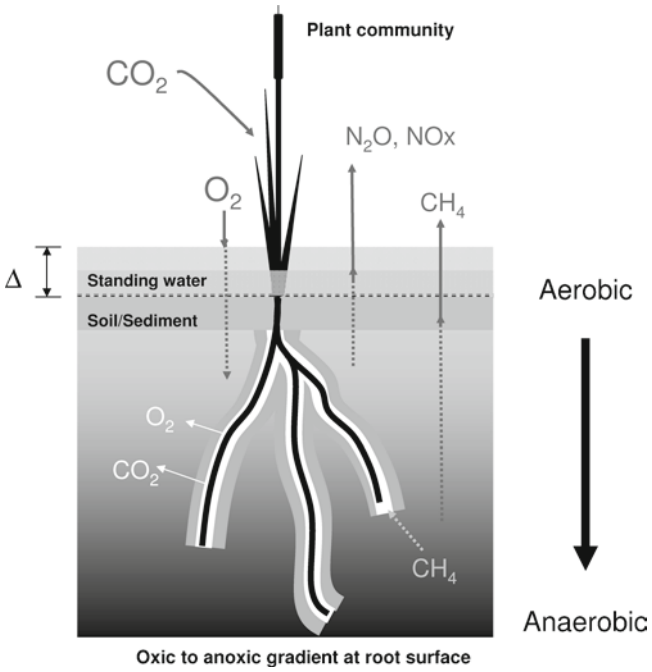

Fig. 2 Wetland structure. Water table height, depth from surface, and distance from plant roots create oxic to anoxic gradients. The result is a complex interplay between anaerobic and aerobic conditions that allows for a wide range in processes to occur in wetland soils

While arbuscular mycorrhizas (AMF) can be found at all levels along moisture gradients from dry to excessive moisture, abundance may decrease under very high water content (Miller and Bever 1999). In particular, AMF species accustomed to dry environments may be very sensitive to high water levels, indicating that water level is an important factor in AMF colonization. Mycorhizzal community composition is also likely sensitive to plant community structure (Gutknecht et al. 2006).

The most conspicuous effect of alterations to a wetland habitat is perhaps the drastic change in vegetation composition and structure. Wetlands habitats receive high levels of pollution (i.e. nitrogen, phosphorus and pesticides) as runoff and ground water from agricultural activities and human settlements, which has contributed to their high susceptibility to invasive species (Zedler and Kercher 2004), and a high proportion of local extinctions. Invasions alone could bring in drastic changes in vegetation composition and litter chemistry, which ultimately influence soil processes. Over a span of decade to centuries, changes at plant and microbial levels would influence ecosystem properties such as geomorphology, hydrology, biochemistry and disturbance regime (Gordon 1998). Although invasive species are spreading rapidly in wetland habitats at local and global levels (Zedler and Kercher 2004), their current impact in nutrient cycling and soils processes are not well

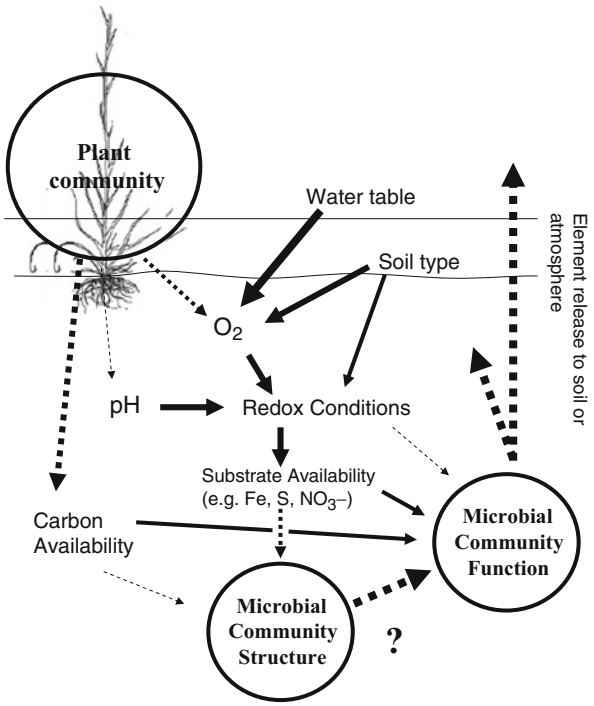

Fig. 3 Relationships among controls over wetland ecosystem microbial communities and element cycling. Arrows indicate relationships, and width of arrows indicates relative importance of relationship for ecosystem functioning. Dashed arrows represent interactions that are poorly understood, even though they may be important

understood (Windham and Ehrenfeld 2003). One study has shown that different levels of an aggressive wetland invader (reed canary grass, *Phalaris arundinacea*) do differentially impact the microbial community, affecting both biomass and the structure of the biota (Kao-Kniffin and Balser 2007).

In recent years the value of wetlands has been increasingly recognized. The cost associated with constructing and restoring wetlands contributes to this appreciation.

Soil Microbial Communities and Changing Agricultural Management Regimes

Humans have converted one-quarter of the Earth's surface to cultivated systems, largely by changing native ecosystems to arable lands within the past 50 years (Millennium Ecosystem Assessment 2005). Agricultural expansion and intensification is likely to accelerate as the world human population grows, and soil functions

at all levels will be affected, including the structure and functions of soil microbial communities. An important area of study is community-level responses to land-use changes rather than effects particular species or groups such as arbuscular mycorrhizal fungi or nitrogen-fixing bacteria, which are well known to play key roles in agroecosystems.

It is well established that the conversion of native ecosystems to agricultural uses can strongly affect microbial community structure, composition and diversity. For example, conversions of tropical forest to plantations (Waldrop et al. 2000) have been found to engender distinct soil microbial community structures, and agricultural intensification has been reported to decrease microbial diversity (Steenwerth et al. 2006). Additionally, the type of land management practices used in agroecosystems also affects microbial community structure and function through a variety of different mechanisms. Numerous studies have documented changes in microbial community structure resulting from physical disturbance, especially tillage (Frey et al. 1999; Guggenberger et al. 1999). Tillage represents a severe disturbance to fungi by severing hyphal connections. However, no-till systems favour the development of fungi as compared with bacterial community components (Minoshima et al. 2007; Kennedy and Schillinger 2006). Conversions to agriculture and attendant cultivation practices also alter microbial communities through changes to temperature, soil moisture (through irrigation and alteration of soil structure), and other physical parameters.

Land-use changes alter soil microbial community structure through changes in carbon availability and quality, pH (Cookson et al. 2007), nutrient availability, or other chemical parameters. For example, studies comparing agroecosystems and natural systems report that adding nitrogen decreases the relative abundance of fungi by comparison to bacteria (Bradley et al. 2006; Bardgett et al. 1999). Seghers et al. (2004) found that nitrogen fertilizers decreased populations of methanotrophs and root endophytes in the bulk soil microbial community. They also found differential effects of organic fertilizers versus inorganic, which was consistent with other studies. For example, Wander et al. (1995) (Cookson et al. 2007) reported that manure-amended plots showed less diverse populations of microorganisms than cover cropped soil, but that microbial biomass was more metabolically active (Wander et al. 1995). Ulrich et al. (2008) found that manure applications led to an increase in the population densities of cellulytic bacteria within the soil microbial community (see chapters elsewhere in this book). Fungal-to-bacterial ratios are commonly measured as indicators of microbial community structure, and the relative proportions of fungi are increased by no-till practices, crop rotations, and use of cover crops (Six et al. 2006).

In addition to physical disturbance effects, alterations in vegetation, plant diversity and species-specific plant traits can cause changes in aboveground litter quantity and quality, and belowground root dynamics. However, alterations in vegetation tend to cause idiosyncratic effects of particular plant species or particular functional traits, and it is difficult to draw more generalized patterns (Porazinska et al. 2003). The effects on plant litter quality and quantity, in

particular, become limiting factors to microorganisms, and thus species-specific differences in plant litter can affect microbial community structure and function (Wardle et al. 2004).

Effects may persist for many years and decades after a given land-use has stopped (Steenwerth et al. 2006). For example, Fraterrigo et al. (2006) (Ulrich et al. 2008) found long-term microbial alteration in forest stands that had been cultivated but not logged. Fungal markers, especially, were lower in previously cultivated sites, suggesting that fungi may need extensive periods of time to recover from agriculture (Fraterrigo et al. 2006). Spiegelberger et al. (2006) found changes in the microbial community due to lasting pH changes resulting from liming 70 years after agricultural abandonment (Spiegelberger et al. 2006). Evidence is beginning to accumulate that the history of land-use can leave significant legacies in the soil microbial community, ultimately influencing successional dynamics of future plant communities (Kardol et al. 2007) and hence, providing a mechanism by which changes due to agricultural management practices may persist.

Conclusion

This chapter has discussed studies of soil microbial communities in the tropics, highlighted the importance of wetland communities, and reviewed potential agricultural impacts on soil microbial communities. We have explored general patterns in microbial communities, and within communities in these systems in particular. Overall, the complexity of soil microbial communities pose a challenge that has limited the number and power of studies. The recent emergence of new methods is beginning to supply much-needed information, but connecting the function and identity of microbes remains a key research area. Major human impacts have altered both wetland and tropical ecosystems, which are rapidly diminishing. Studies have focused on pasture conversion effects in the tropics and reveal a diversity of microbial life underground, and the functional and structural changes brought with such conversion. Wetland systems experience strong fluctuations in environmental and biotic conditions. Recent research points to the sensitivity of the microbial community to both hydrology and plant structure. Finally, agricultural regimes strongly impact the soil microbial community and its functions, in particular decreasing fungal biomass and overall microbial diversity. These changes in belowground community can be persist on the order of decades, even when the aboveground community shifts.

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References

Allison V, Yermakov Z, Miller R, Jastrow J, Matamala R (2007) Using landscape and depth gradients to decouple the impact of correlated environmental variables on soil microbial community composition. Soil Biol Biochem 39(2):505–516

Amann R, Ludwig W, Schleifer K (1995) Phylogenetic identification and in situ detection of individual microbial cells without cultivation. Microbiol Rev 59(1):143–169

Amir H, Pineau R (1998) Influence of plants and cropping on microbiological characteristics of some New Caledonian ultramafic soils. Aust J Soil Res 36(3):457

Amundson R (2001) The carbon budget in soils. Annu Rev Earth Planet Sci 29(1):535–562

Anupam B (2003) Mycorrhizae in wetlands: a review. Int J Forest Manage 4:34–40

Baisden W, Parfitt R (2007) Bomb ^{14}C enrichment indicates decadal C pool in deep soil? Biogeochemistry 85(1):59–68

Balser TC (2000) Linking soil microbial communities and ecosystem functioning. PhD dissertation, University of California-Berkeley, Berkeley, CA

Balser TC, Firestone MK (2005) Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. Biogeochemistry 73(2):395–415

Balser T, McMahon K, Bart D, Bronson D, Coyle D, Craig N et al (2006) Bridging the gap between micro – and macro-scale perspectives on the role of microbial communities in global change ecology. Plant Soil 289(1):59–70

Bardgett RD, Mawdsley JL, Edwards S, Hobbs PJ, Rodwell JS, Davies WJ (1999) Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. Funct Ecol 13(5):650–660

Basu S, Behera N (1993) The effect of tropical forest conversion on soil microbial biomass. Biol Fertil Soils 16(4):302–304

Bawa KS, Kress WJ, Nadkarni NM, Lele S (2004) Beyond paradise – meeting the challenges in tropical biology in the 21st century. Biotropica 36(4):437–446

Behera N, Sahani U (2003) Soil microbial biomass and activity in response to Eucalyptus plantation and natural regeneration on tropical soil. For Ecol Manage 174(1–3):1–11

Blume E, Bischoff M, Reichert JM, Moorman T, Konopka A, Turco RF (2002) Surface and subsurface microbial biomass, community structure and metabolic activity as a function of soil depth and season. Appl Soil Ecol 20(3):171–181

Borneman J, Triplett E (1997) Molecular microbial diversity in soils from eastern Amazonia: evidence for unusual microorganisms and microbial population shifts associated with deforestation. Appl Environ Microbiol 63(7):2647–2653

Bossio D, Girvan M, Verchot L, Bullimore J, Borelli T, Albrecht A et al (2005) Soil microbial community response to land use change in an agricultural landscape of western Kenya. Microb Ecol 49(1):50–62

Bradley K, Drijber R, Knops J (2006) Increased N availability in grassland soils modifies their microbial communities and decreases the abundance of arbuscular mycorrhizal fungi. Soil Biol Biochem 38(7):1583–1595

Brady NC, Weil RR (2002) The nature and properties of soils, 13th edn. Prentice Hall, Upper Saddle River, NJ

Brady KU, Kruckeberg AR, Bradshaw H Jr (2005) Evolutionary ecology of plant adaptation to serpentine soils. Annu Rev Ecol Evol Syst 36(1):243–266

Bridge P, Spooner B (2001) Soil fungi: diversity and detection. Plant Soil 232(1):147–154

Burke RA, Molina M, Cox JE, Osher LJ, Piccolo MC (2003) Stable carbon isotope ratio and composition of microbial fatty acids in tropical soils. J Environ Qual 32(1):198–206

Buschbacher R, Uhl C, Serrao EAS (1988) Abandoned pastures in Eastern Amazonia. II. Nutrient stocks in the soil and vegetation. J Ecol 76(3):682–699

Cardon ZG, Gage DJ (2006) Resource exchange in the rhizosphere: molecular tools and the microbial perspective. Annu Rev Ecol Evol Syst 37(1):459–488

Carney K, Matson P (2005) Plant communities, soil microorganisms, and soil carbon cycling: does altering the world belowground matter to ecosystem functioning? Ecosystems 8(8):928–940
Carney K, Matson P (2006) The influence of tropical plant diversity and composition on soil microbial communities. Microb Ecol 52(2):226–238
Cleveland CC, Townsend AR, Schmidt SK, Constance BC (2003) Soil microbial dynamics and biogeochemistry in tropical forests and pastures, southwestern Costa Rica. Ecol Appl 13(2):314–326
Cookson W, Osman M, Marschner P, Abaye D, Clark I, Murphy D et al (2007) Controls on soil nitrogen cycling and microbial community composition across land use and incubation temperature. Soil Biol Biochem 39(3):744–756
Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D et al (1995) Changes in soil-phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76(5):1407
Davidson EA, Artaxo P (2004) Globally significant changes in biological processes of the Amazon basin: results of the large-scale biosphere-atmosphere experiment. Glob Change Biol 10(5):519–529
de Moraes JFL, Volkoff B, Cerri CC, Bernoux M (1996) Soil properties under Amazon forest and changes due to pasture installation in Rondônia, Brazil. Geoderma 70(1):63–81
DeGrood SH, Claassen VP, Scow KM (2005) Microbial community composition on native and drastically disturbed serpentine soils. Soil Biol Biochem 37(8):1427–1435
Desjardins T, Barros E, Sarrazin M, Girardin C, Mariotti A (2004) Effects of forest conversion to pasture on soil carbon content and dynamics in Brazilian Amazonia. Agric Ecosyst Environ 103(2):365–373
Doran JW, Zeiss MR (2000) Soil health and sustainability: managing the biotic component of soil quality. Appl Soil Ecol 15(1):3–11
Eden MJ, Furley PA, Mcgregor DFM, Milliken W, Ratter JA (1991) Effect of forest clearance and burning on soil properties in northern Roraima, Brazil. For Ecol Manage 38:283–290
Ekelund F, Rønn R, Christensen S (2001) Distribution with depth of protozoa, bacteria and fungi in soil profiles from three Danish forest sites. Soil Biol Biochem 33(4–5):475–481
EPA (2004) Wetlands overview, EPA 843-F-04-011a [Internet]. http://www.epa.gov/owow/wetlands/pdf/overview.pdf
FAO (2001) Global forest resources assessment 2000 – main report. Forestry Paper 140. Rep. 140
FAO (2005) Global forest resources assessment 2005. Forestry paper 147. Rep. 147
Fearnside PM (2005) Deforestation in Brazilian Amazonia: history, rates, and consequences. Conserv Biol 19(3):680–688
Fearnside PM, Imbrozio Barbosa R (1998) Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. For Ecol Manage 108(1–2):147–166
Fierer N, Bradford MA, Jackson RB (2007) Toward an ecological classification of soil bacteria. Ecology 88(6):1354–1364
Fraterrigo JM, Balser TC, Turner MG (2006) Microbial community variation and its relationship with nitrogen mineralization in historically altered forests. Ecology 87(3):570–579
Frey S, Elliott E, Paustian K (1999) Bacterial and fungal abundance and biomass in conventional and no-tillage agroecosystems along two climatic gradients. Soil Biol Biochem 31(4):573–585
Goberna M, Insam H, Pascual J, Sánchez J (2005) Storage effects on the community level physiological profiles of Mediterranean forest soils. Soil Biol Biochem 37(1):173–178
Goberna M, Sánchez J, Pascual J, García C (2006) Surface and subsurface organic carbon, microbial biomass and activity in a forest soil sequence. Soil Biol Biochem 38(8):2233–2243
Gomez-Alvarez V, King GM, Nüsslein K (2007) Comparative bacterial diversity in recent Hawaiian volcanic deposits of different ages. FEMS Microbiol Ecol 60(1):60–73
Gordon D (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecol Appl 8(4):975–989

Guggenberger G, Frey SD, Six J, Paustian K, Elliott ET (1999) Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. Soil Sci Soc Am J 63(5):1188–1198
Gutknecht J, Goodman R, Balser T (2006) Linking soil process and microbial ecology in freshwater wetland ecosystems. Plant Soil 289(1–2):17–34
Haggar JP, Ewel JJ (1995) Establishment, resource acquisition, and early productivity as determined by biomass allocation patterns of three tropical tree species. Forest Sci 41:689–708
Handelsman J (2005) Metagenomics or megagenomics? Nat Rev Microbiol 3(6):457–458
Hölscher D, Ludwig B, Möller RF, Fölster H (1997) Dynamic of soil chemical parameters in shifting agriculture in the Eastern Amazon. Agric Ecosyst Environ 66(2):153–163
Horner-Devine MC, Carney KM, Bohannan BJM (2004) An ecological perspective on bacterial biodiversity. Proc R Soc Lond B Biol Sci 271(1535):113–122
Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10(2):423–436
Kao-Kniffin J, Balser T (2007) Elevated CO_2 differentially alters belowground plant and soil microbial community structure in reed canary grass-invaded experimental wetlands. Soil Biol Biochem 39(2):517–525
Kardol P, Cornips N, van Kempen M, Bakx-Schotman J, van der Putten W (2007) Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecol Monogr 77(2):147–162
Kennedy A, Schillinger W (2006) Soil quality and water intake in traditional-till vs. no-till paired farms in Washington's Palouse region. Soil Sci Soc Am J 70(3):940–949
Kim J, Sparovek G, Longo RM, De Melo WJ, Crowley D (2007) Bacterial diversity of terra preta and pristine forest soil from the Western Amazon. Soil Biol Biochem 39(2):684–690
Kirk JL, Beaudette LA, Hart M, Moutoglis P, Klironomos JN, Lee H et al (2004) Methods of studying soil microbial diversity. J Microbiol Meth 58(2):169–188
Krave AS, Lin B, Braster M, Laverman AM, Straalen NMV, Röling WFM et al (2002) Stratification and seasonal stability of diverse bacterial communities in a *Pinus merkusii* (pine) forest soil in central Java, Indonesia. Environ Microbiol 4(6):361–373
Kumara HN, Kumar MA, Sharma AK, Sushma HS, Singh M, Singh M (2004) Diversity and management of wild mammals in tea gardens in the rainforest regions of the Western Ghats, India: a case study from a tea estate in the Anaimalai Hills. Curr Sci 87:1282–1287
Laurance WF (1999) Reflections on the tropical deforestation crisis. Biol Conserv 91(2–3): 109–117
Lavahun MFE, Joergensen RG, Meyer B (1996) Activity and biomass of soil microorganisms at different depths. Biol Fertil Soils 23(1):38–42
Leckie SE (2005) Methods of microbial community profiling and their application to forest soils. For Ecol Manage 220(1–3):88–106
Lehmann J, Pereira da Silva J, Steiner C, Nehls T, Zech W, Glaser B (2003) Nutrient availability and leaching in an archaeological Anthrosol and a Ferralsol of the Central Amazon basin: fertilizer, manure and charcoal amendments. Plant Soil 249(2):343–357
Levine SH (1976) Competitive interactions in ecosystems. Am Nat 110(976):903
Liang C, Fujinuma R, Balser T (2008) Comparing PLFA and amino sugars for microbial analysis in an Upper Michigan old growth forest. Soil Biol Biochem 40(8):2063–2065
Lima HN, Schaefer CER, Mello JWV, Gilkes RJ, Ker JC (2002) Pedogenesis and pre-Colombian land use of "Terra Preta Anthrosols" ("Indian black earth") of Western Amazonia. Geoderma 110(1–2):1–17
Lipson DA (2007) Relationships between temperature responses and bacterial community structure along seasonal and altitudinal gradients. FEMS Microbiol Ecol 59(2):418–427
Mann CC (2002) Agriculture: the real dirt on rainforest fertility. Science 297(5583):920–923
Mentzer J, Goodman R, Balser T (2006 June) Microbial response over time to hydrologic and fertilization treatments in a simulated wet prairie. Plant Soil 284(1–2):85–100
Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis [Internet]. http://www.millenniumassessment.org/documents/document.356.aspx.pdf

Miller SP, Bever JD (1999) Distribution of arbuscular mycorrhizal fungi in stands of the wetland grass Panicum hemitomon along a wide hydrologic gradient. Oecologia 119(4): 586–592
Minoshima H, Jackson L, Cavagnaro T, Sanchez-Moreno S, Ferris H, Temple S et al (2007) Soil food webs and carbon dynamics in response to conservation tillage in California. Soil Sci Soc Am J 71(3):952–963
Moritz LK (2008) Soil habitat and microbial communities on Mount Kinabalu, Borneo. MS thesis, University of Wisconsin-Madison, Madison, WI
Müller MML, Guimarães MF, Desjardins T, Mitja D (2004) The relationship between pasture degradation and soil properties in the Brazilian amazon: a case study. Agric Ecosyst Environ 103(2):279–288
Myers N, Mittermeier RA (2000) Biodiversity hotspots for conservation priorities. (Cover story). Nature 403(6772):853
Nannipieri P, Ascher J, Ceccherini MT, Lan Dl L, Pietramellar G, Renell G (2003) Microbial diversity and soil functions. Eur J Soil Sci 54(4):655
Neill C, Fry B, Melillo JM, Steudler PA, Moraes JFL, Cerri CC (1996) Forest- and pasture-derived carbon contributions to carbon stocks and microbial respiration of tropical pasture soils. Oecologia 107(1):113–119
Nepstad DC, de Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH et al (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372(6507):666–669
Nüsslein K, Tiedje JM (1998) Characterization of the dominant and rare members of a young Hawaiian soil bacterial community with small-subunit ribosomal DNA amplified from DNA fractionated on the basis of its guanine and cytosine composition. Appl Environ Microbiol 64(4):1283–1289
Nüsslein K, Tiedje JM (1999) Soil bacterial community shift correlated with change from forest to pasture vegetation in a tropical soil. Appl Environ Microbiol 65(8):3622–3626
Oline D (2006) Phylogenetic comparisons of bacterial communities from serpentine and nonserpentine soils. Appl Environ Microbiol 72(11):6965–6971
Poll C, Thiede A, Wermbter N, Sessitsch A, Kandeler E (2003) Micro-scale distribution of microorganisms and microbial enzyme activities in a soil with long-term organic amendment. Eur J Soil Sci 54(4):715–724
Porazinska DL, Bardgett RD, Blaauw MB, Hunt HW, Parsons AN, Seastedt TR et al (2003) Relationships at the aboveground-belowground interface: plants, soil biota and soil processes. Ecol Monogr 73(3):377–395
Proctor J (1999) Toxins, nutrient shortages and droughts: the serpentine challenge. Trends Ecol Evol 14(9):334–335
Ramsar Convention Secretariat (2007) Wise use of wetlands: a conceptual framework for the wise use of wetlands. Ramsar handbooks for the wise use of wetlands, 3rd edn, vol 1 [Internet]. http://www.ramsar.org/pdf/lib/lib_handbooks2006_e01.pdf
Ranjard L, Poly F, Nazaret S (2000) Monitoring complex bacterial communities using culture-independent molecular techniques: application to soil environment. Res Microbiol 151(3): 167–177
Rasmussen C, Southard RJ, Horwath WR (2007) Soil mineralogy affects conifer forest soil carbon source utilization and microbial priming. Soil Sci Soc Am J 71(4):1141–1150
Reiners WA, Bouwman AF, Parsons WFJ, Keller M (1994) Tropical rain-forest conversion to pasture – changes in vegetation and soil properties. Ecol Appl 4(2):363
Rudel TK (2005) Tropical forests regional paths of destruction and regeneration in the late twentieth century. Columbia University Press, New York
Schloss PD, Handelsman J (2006) Toward a census of bacteria in soil. PLoS Comput Biol 2(7):e92
Seghers D, Wittebolle L, Top E, Verstraete W, Siciliano S (2004) Impact of agricultural practices on the *Zea mays* L. endophytic community. Appl Environ Microbiol 70(3):1475–1482
Serrão EAS, Nepstad D, Walker R (1996) Upland agricultural and forestry development in the Amazon: sustainability, criticality and resilience. Ecol Econ 18(1):3–13

Sessitsch A, Weilharter A, Gerzabek MH, Kirchmann H, Kandeler E (2001) Microbial population structures in soil particle size fractions of a long-term fertilizer field experiment. Appl Environ Microbiol 67(9):4215–4224

Shaw SP, Fredine CG (1956) Wetlands of the United States – their extent and their value to waterfowl and other wildlife. Version 05JAN99 [Internet]. http://www.npwrc.usgs.gov/resource/wetlands/uswetlan/index.htm

Singh S, Singh JS (1995) Microbial biomass associated with water-stable aggregates in forest, savanna and cropland soils of a seasonally dry tropical region, India. Soil Biol Biochem 27(8):1027–1033

Six J, Frey SD, Thiet RK, Batten KM (2006) Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Sci Soc Am J 70(2):555–569

Spiegelberger T, Hegg O, Matthies D, Hedlund K, Schaffner U (2006) Long-term effects of short-term perturbation in a subalpine grassland. Ecology 87(8):1939–1944

Srivastava S, Singh J (1991) Microbial C, N and P in dry tropical forest soils: effects of alternate land-uses and nutrient flux. Soil Biol Biochem 23(2):117–124

Steenwerth K, Jackson L, Carlisle E, Scow K (2006) Microbial communities of a native perennial bunchgrass do not respond consistently across a gradient of land-use intensification. Soil Biol Biochem 38(7):1797–1811

Stenström J, Svensson K, Johansson M (2001) Reversible transition between active and dormant microbial states in soil. FEMS Microbiol Ecol 36(2–3):93–104

Sylvia DM, Fuhrmann JJ, Hartel PG, Zuberer DA (2005) Principles and applications of soil microbiology, 2nd edn. Prentice Hall, Upper Saddle River, NJ

Taylor JP, Wilson B, Mills MS, Burns RG (2002) Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. Soil Biol Biochem 34(3):387–401

Torsvik V, Goksoyr J, Daae FL (1990) High diversity in DNA of soil bacteria. Appl Environ Microbiol 56(3):782–787

Trumbore SE, Davidson EA, Camargo PBD, Nepstad DC, Martinelli LA (1995) Belowground cycling of carbon in forests and pastures of eastern Amazonia. Glob Biogeochem Cycles 9(4):515–528

Ulrich A, Becker R (2006) Soil parent material is a key determinant of the bacterial community structure in arable soils. FEMS Microbiol Ecol 56(3):430–443

Ulrich A, Klimke G, Wirth S (2008) Diversity and activity of cellulose-decomposing bacteria, isolated from a sandy and a loamy soil after long-term manure application. Microb Ecol 55(3):512–522

Van Gestel M, Merckx R, Vlassak K (1996) Spatial distribution of microbial biomass in microaggregates of a silty-loam soil and the relation with the resistance of microorganisms to soil drying. Soil Biol Biochem 28(4–5):503–510

Veldkamp E, Becker A, Schwendenmann L, Clark DA, Schulte-Bisping H (2003) Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest. Glob Change Biol 9(8):1171–1184

Venkatesan S, Senthurpandian VK (2006) Comparison of enzyme activity with depth under tea plantations and forested sites in south India. Geoderma 137(1–2):212–216

Vestal JR, White DC (1989) Lipid analysis in microbial ecology. Bioscience 39(8):535–541

Waldrop MP, Balser TC, Firestone MK (2000) Linking microbial community composition to function in a tropical soil. Soil Biol Biochem 32(13):1837–1846

Walker RB (1954) The ecology of serpentine soils: a symposium. II. factors affecting plant growth on serpentine soils. Ecology 35:259–266

Wander M, Hedrick D, Kaufman D, Traina S, Stinner B, Kehrmeyer S et al (1995) The functional significance of the microbial biomass in organic and conventionally managed soils. Plant Soil 170(1):87–97

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304(5677):1629–1633

White DC, Davis WM, Nickels JS, King JD, Bobbie RJ (1979) Determination of the sedimentary microbial biomass by extractible lipid phosphate. Oecologia 40(1):51–62

Windham L, Ehrenfeld J (2003) Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. Ecol Appl 13(4):883–896

Wixon D, Balser T (2009) Complexity, climate change and soil carbon: a systems approach to microbial temperature response. Syst Res Behav Sci 26(5):601–620

Yao H, He Z, Wilson MJ, Campbell CD (2000) Microbial biomass and community structure in a sequence of soils with increasing fertility and changing land use. Microb Ecol 40(3): 223–237

Zedler J, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Crit Rev Plant Sci 23(5):431–452

Zelles L (1999) Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biol Fertil Soils 29(2):111–129[1]Duff: the