Chapter 3
Impacts of Forest Conversion to Agriculture on Microbial Communities and Microbial Function

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3.1 Introduction

Over the past century, humans have dramatically altered the structure and function of ecosystems across the globe. The expansion of agriculture is one of the most significant of these changes. According to the Food and Agriculture Organization of the United Nations (FAO), agricultural land now occupies around 4.7 million km^2, which is about 40% of the Earth's land surface (Foley et al. 2005), and these cultivated lands are expanding. Most agricultural land is under pasture (~70%), and only a small percentage (<3%) is under permanent crops such as cacao, coffee and tea. The remaining 27% is under arable crops. For the last four decades, global agricultural production has been increasing steadily, at a rate averaging 2.3% per year (FAO 2007), and on average, 6 million ha of forest and grassland have been converted to agriculture annually. Increasing population, technological change, public policies, increasing food and oil prices, and economic growth drive this conversion. Given that projections for population growth indicate a global population of between 9 and 10 billion by 2050, and if the experiences of the Green Revolution are a guide for future expectations, agricultural land could expand to 10 million km^2 (Tilman et al. 2001).

Conversion of land to agriculture is largely a tropical phenomenon at the moment (Fig. 3.1), whereas the area occupied by agricultural land is decreasing in developed countries. Land under row crops and permanent crops has increased since 1965 in sub-Saharan Africa (37%), West Asia and North Africa (28%), East, South and Southeast Asia (23%), and Latin America and the Caribbean (48%). Recent trends suggest that land area for cropping is leveling off only in Latin America. Likewise, the area under meadow and pasture is increasing in West

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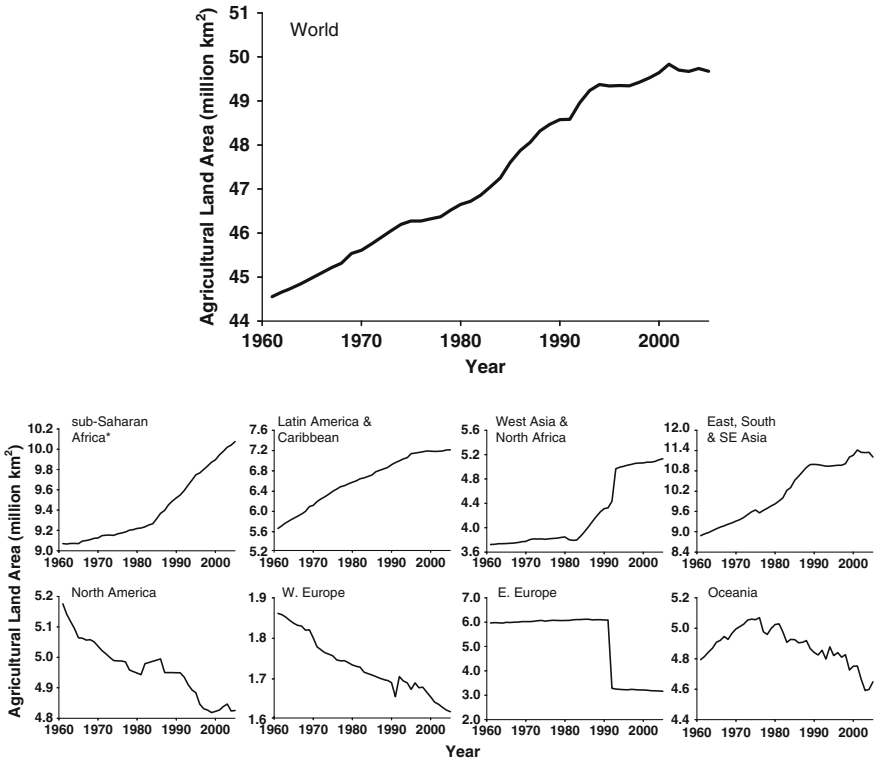

Fig. 3.1 Global and regional land-use change to agricultural land (cropland + pasture land). Ethiopia was not included in Africa panel as there were significant reporting discrepancies following the separation with Eritrea. (Source of data: http:// faostat.fao.org)
Note: different *Y* axis scales for each graph

Asia and North Africa (40%), East, South and Southeast Asia (24%), and Latin America and the Caribbean (48%). Short-term trends suggest that growth in pasture area may be leveling off in all regions, with the exception of sub-Saharan Africa.

A major focus of ecological research has been to understand how structural alterations such as land-use change affect the biological functioning of ecosystems. This concern is driven in part by the perception that land-use change results in degradation of natural ecosystems and particularly of the soil. Oldeman (1994) estimated that soil degradation is extensive, covering about 1,780 million ha across the world, and indicated that land-use change is a major driver of degradation. Soil biological processes respond directly to modifications of ecosystems and provide feedbacks that alter larger scale ecosystem processes, such as productivity, decomposition, and production and consumption of greenhouse gases (GHGs). In turn, these biotic changes alter the state of the world's ecosystems and the services they provide to humanity. For example, in many smallholder-farming systems, inorganic nutrient inputs are non-existent following conversion to agriculture, and only small

amounts of organic nutrients are added as manure or green manures. Consequently, soil degradation is an important problem throughout the tropics and is an important driver in decreasing food security in Africa (Sanchez 2002).

Biological research in soils and land-use change has primarily focused on macrobiota. This work has shown how organisms such as earthworms and termites regulate carbon turnover and nutrient cycling (Black and Okwakol 1997; Fragoso et al. 1997; Jimenez et al. 1996; Brussaard et al. 1993). In this chapter, we will look at the current state of our understanding of the impacts of land-use change on microbial communities and how these impacts alter biogeochemical cycles. The literature on this topic is much more fragmentary than that concerning macrobiota. Nevertheless, a significant amount of work has been done in this area, and our knowledge is advancing, particularly with the advent and application of novel biotechnological approaches to understanding belowground biodiversity.

3.2 Soil Organic Matter and Microbial Biomass

Understanding the dynamics of soil organic matter (see Chap. 2) following land-use change is the starting point for understanding how microbial communities respond to the change. The simplest models of SOM dynamics distinguish between organic inputs and stabilized organic matter (van Noordwijk et al. 1997). Between 50 and 90% of the organic inputs are lost from the soil in the first year. By contrast, stabilized organic matter decomposes at rates of 1–5% per year (Nye and Greenland 1960; van Faasen and Smilde 1985; Young 1989). More recent models subdivide soil organic carbon (SOC) into functional pools with different turnover times (Parton et al. 1989; van Noordwijk and Lusiana 1999; Zimmermann et al. 2007). These models recognize that factors associated with the nature of the soil (Fig. 3.2)

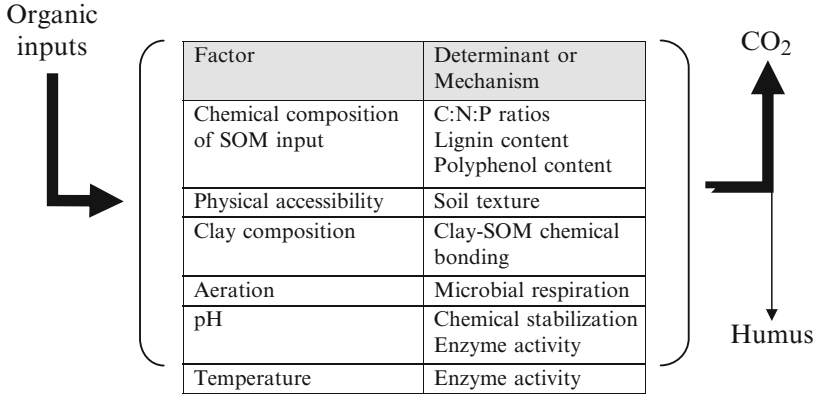

Fig. 3.2 Factors and their determinants or mechanisms affecting decomposition of organic inputs and providing partial or temporary protection from decomposing organisms; SOM: soil organic matter

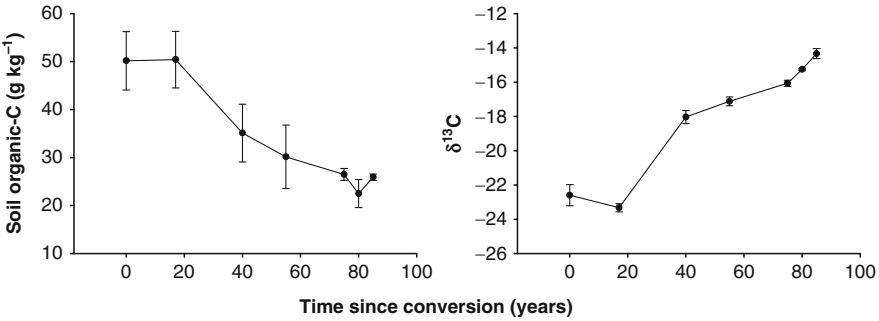

Fig. 3.3 Changes in soil C following land-use change in a landscape in Western Kenya (Verchot et al. unpublished) and change in δ^{13}C composition of the soil organic carbon (SOC). Time = 0 are forested conditions. Soil organic matter (SOM) remains relatively constant during an initial phase following conversion and decreases as soil is continuously cultivated. SOM initially maintains a high proportion of forest derived C as shown by the δ^{3}C signature of the SOM, but as carbon content decreases, the SOC becomes dominated by agricultural C (as shown by an increase in the δ^{13}C signature)

and management practices (e.g., cultivation intensity) play important roles in determining how fast carbon is lost from the system. For example, soil aggregation in medium- to fine-textured soils protects carbon from mineralization, and these soils maintain high carbon stocks for a number of years following conversion. Sandy soils provide little protection for organic matter decomposition, and lose carbon more quickly.

Following conversion from indigenous ecosystems to arable or permanent cropping systems, SOC decreases over time (Davidson and Ackerman 1993) and nutrient availability declines (Fig. 3.3). Carbon stocks are generally high in soils under forest vegetation. As carbon inputs decline following conversion, and tillage exposes protected carbon to mineralization, SOC declines. Forest-derived carbon persists, as the isotope data show, and even after 90 years following conversion, forest-derived carbon makes up a small percentage of SOM. A new equilibrium SOC level is reached between 30 and 80 years following conversion (Solomon et al. 2007; Awiti et al. 2008). Intensification of agriculture, particularly if it involves organic matter management, can stem the losses and stabilize SOC at higher levels (Mitchell et al. 2008); however, this is not the case in many parts of the tropics where subsistence agriculture is practiced. The story is different and perhaps less clear with regard to conversion of forests to pastures. A comprehensive literature review showed that conversion of forest to pasture can lead to either carbon stock increases or decreases (Murty et al. 2002). The authors reviewed 109 studies, and found that about half reported carbon gains and half reported losses.

As forestland is converted to pasture or cropland, microbial biomass follows a trend parallel to that of SOC. Basu and Behera (1993) characterized this relationship in the Eastern Ghat mountain range of Orissa. They used the $CHCl_3$ fumigation–incubation method to assess microbial biomass C, and they measured basal respiration in soils from forest, savanna and agricultural fields. Basal respiration is

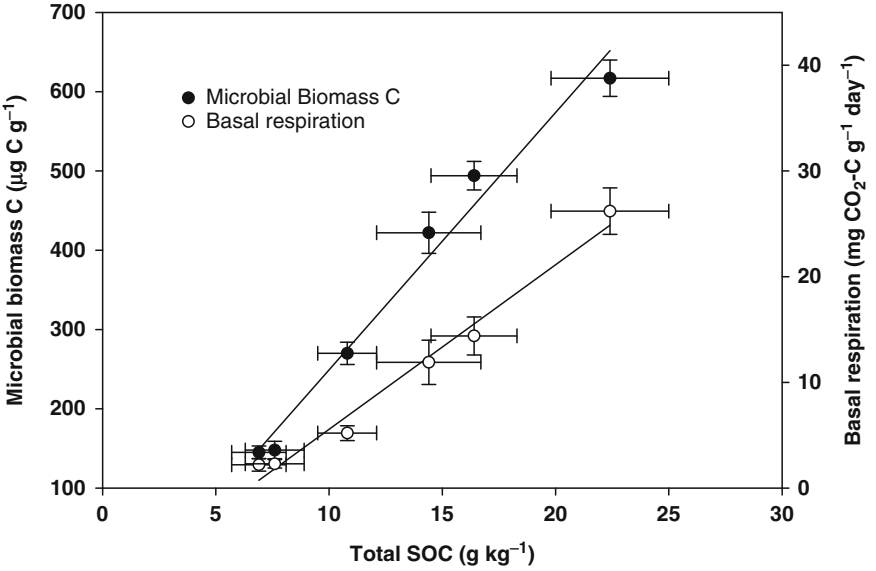

Fig. 3.4 Relationships between total soil organic carbon (SOC) and microbial biomass, and between SOC and basal respiration in an Inceptisol in Southern India. Microbial community size and activity show linear relationships across a gradient of indigenous ecosystems and permanent cropping systems with total SOC
Source: Dinesh et al. (2004)

an operationally defined parameter that integrates microbial activity and carbon availability in the laboratory and can be used to compare soil samples. As SOC declined by 40% in the land converted to agriculture or savanna, microbial biomass declined by 46–52% and basal respiration also declined. Dinesh et al. (2004) showed similar decreases when forests in southern India were replaced with permanent cropping systems (Fig. 3.4). Total SOC decreased by 69% with the conversion of moist deciduous forest to coconut plantation. Microbial biomass C decreased by 77% and basal respiration decreased by 91%. Linear relationships existed between SOC and the size of the microbial biomass, and between SOC and microbial activity measured in terms of basal respiration.

3.3 Microbial Communities

With the advent of novel techniques, it is now possible to study the effects of land-use change and management on entire microbial communities. There are several approaches based on the extraction of "signature" lipid biomarkers (Table 3.1) from the cell membrane and wall of micro-organisms (White and Ringelberg 1998). Short-chain phospholipids (C10–C20) derive from microbes, while longer-chain phospholipids derive from plants. Two approaches look at either fatty-acid

Table 3.1 Signature PLFA markers for different components of the soil microbial community

Community component	PLFA markers
General bacteria	15:0 anteiso, 17:0 anteiso, 17:0 iso, 14:0, 16:1 ω7c, 19:0 cyclo
Gram-positive bacteria	15:0 iso, 16:0 iso
Gram-negative bacteria	17:0 cyclo, 18:1ω7c
Actinomycetes	16:0 10 methyl, 17:0 10 methyl, tbsa 10me18:0
Fungi	18:2ω6c, 18:1ω9c
Arbuscular mycorrhizal fungi	16:1ω5c
Protozoa	20:2ω6,9c, 20:4ω6,9,12,15c

methyl esters (FAME) or phospholipid fatty acids (PLFA). The two measures differ in that FAME examines all phospholipids, while PLFA considers only the polar phospholipids. Because these fatty acids decompose rapidly in the soil following microbial death, FAME and PLFA analyses give a profile of the active microbial community. These methods offer opportunities to quantify the biomass of several groups such as the Gram-negative bacteria, the Gram-positive bacteria, actinomycetes, fungi, arbuscular mycorrhizal fungi (AMF), protozoa, and even some functional groups (e.g., methane oxidizers, sulfur reducers). Thus, these methods offer relatively easy means for quantitative assessment of the structure of microbial communities, although the presence of a large number of background unspecific fatty acids may mask differences in community structure (Marschner 2007). The major disadvantage of these methods is that they provide no information at the species level.

There are also several community "fingerprinting" techniques based on extraction and analysis of 16S ribosomal DNA (rDNA) fragments. Two analytical techniques, denaturing gel gradient electrophoresis (DGGE) and terminal restriction fragment length polymorphism (TRFLP), are popular for soil studies. These techniques involve extraction of rDNA from the soil, and specific amplification of this DNA through a polymerase chain reaction (PCR). There are some problems with these methods. Martin-Laurent et al. (2001) showed that the rDNA extraction method affected the results of observations on abundance and composition of phylotypes from bacterial communities of agricultural soils in France. They also showed that both the extraction method and the soil matrix introduce biases that affect the amplification efficiency of the PCR reaction, making comparisons across studies and sites difficult. There are also unknown biases in the PCR reaction, and the products of these reactions do not truly reflect community composition because of the selectivity of the primers (Marschner 2007). Thus, it is essential to consider these limitations when drawing conclusions from studies on the relative abundance of microbial phylotypes in soils.

One important limitation of the rDNA approaches is that we cannot look at the whole community, nor ascribe changes in community structure to particular functional groups. Primers are selective for either bacteria or fungi or for subgroups within these kingdoms, and we have only had adequate fungal primers for environmental

samples since 2000 (Hawksworth 2001; Borneman and Hartin 2000). Thus, most of the rDNA work on microbial communities has focused on their bacterial components. However, we know that fungi play a major role in ecosystem processes, and fungal species remain largely undescribed (Hawksworth and Rossman 1997). Because of the selectivity of the primers for important genes, DNA-based techniques are particularly well suited for studies that seek to link the microbial population with biogeochemical or enzymatic functions in the soil.

Several authors have suggested that community structure and biochemical function should be related, but the experimental results to date are ambiguous (Lucas et al. 2007; Manefield et al. 2002; Torsvik and Øvreås 2002). Advanced molecular and biochemical ecological approaches have only been used to study micro-organisms in a limited number of tropical systems (Bossio et al. 2005; Gomes et al. 2003; Waldrop et al. 2000; Nusslein and Tiedje 1999; Borneman and Triplett 1997). Most of these studies focus on cataloging diversity of soil bacteria, profiling communities, and documenting how these communities are affected by disturbance or by some form of environmental change. However, most of this work has been site-specific.

The emerging picture is that different constituents of the microbial community respond differently to changes in the quality of organic matter inputs associated with land-use change. De Ruiter et al. (1995) showed that both top-down and bottom-up processes drive food webs in grassland soils. Organisms at high trophic levels were more subject to bottom-up drivers (e.g., resource quality and quantity), whereas top-down forces (e.g., consumers) regulated organisms at lower trophic levels. This work identified stabilizing feedbacks in these systems that maintain either states of low or high productivity (Wardle et al. 2004; Moore et al. 2003; De Ruiter et al. 1995). Plant species that are adapted to fertile conditions return high quality litter (characterized by low C:N ratios, low phenolics, low lignin and structural carbohydrates) and support soil food webs in which energy transfers are accomplished through bacterial channels. Low quality organic matter inputs from the plant community condition food webs on infertile soils, where fungal energy channels predominate. Thus, there is a tight linkage between the trajectories of the microbial community and the aboveground vegetation, which bears direct relevance to the effect of land-use change.

We have a very limited understanding of the factors that structure soil microbial communities, the effects of disturbance on structure, and how this disturbance plays out in larger-scale biogeochemical cycles. The results of the few studies that have looked at the effects of land-use change on the structure of microbial communities are consistent. Changes in vegetation in young Hawaiian soils led to dramatic changes in microbial community structure (Nusslein and Tiedje 1999), and conversion of forest to agriculture decreased microbial biomass and produced compositionally distinct microbial communities in Tahiti (Waldrop et al. 2000); Borneman and Triplett (1997) demonstrated significant differences between soil microbial populations in a mature forest and adjacent pasture in eastern Amazonia. Bossio et al. (2005) found similar results in eastern Kenya. In addition, they found that a regenerating secondary forest on one site was more similar to an indigenous forest

at another site than it was to nearby agricultural sites. Many of these studies are anecdotal and are not based on replicated field trials. Therefore, little is known about how agricultural practices or land-use change affect microbial communities.

The legacy of land-use change has been appreciated from the point of view of biogeochemical function (Verchot et al. 2001), but the effects on microbial community structure is underappreciated in the literature. Fraterrigo et al. (2006) used PLFA and FAME analyses to determine that community composition varied significantly with past land use in the Appalachian region of western North Carolina, USA. They studied forest stands on sites that had been farmed in the 1930s and other sites that had been logged and regenerated in the 1950s. Microbial communities in forest stands that had previously been farmed had a higher relative abundance of markers for Gram-negative bacteria and a lower abundance of markers for fungi compared with previously logged and undisturbed stands. This lasting effect of land-use history on microbial community structure affected N mineralization rates, which were negatively correlated with fungal and Gram-negative bacteria markers. These results indicate that contrary to expectations of microbial community resilience, there is a persistent legacy of disturbance on microbial communities and the nutrient cycling processes they mediate.

3.4 Effects of Land-Use Change on Mycorrhizal Fungi

Mycorrhizal fungi warrant particular attention, as they are keystone species in the microbial community because of their importance in regulating the aboveground plant community (Wardle et al. 2004; Matson et al. 1997; Grime et al. 1987; see Chap. 9). There has been a considerable amount of effort in improving our understanding of the effects of land-use change and management on mycorrhizal fungi, because of their importance to ecosystem health. Because of the symbiotic relationships with plants in the ecosystem, where each plant benefits from a unique fungal isolate (Klironomos 2003), mycorrhizae can affect the composition of the aboveground plant community (Gange et al. 2003; Grime et al. 1987). This in turn can feed back to the microbial community through effects on quality and quantity of organic matter inputs to the soil from the plant community. Thus, changes to the composition of the mycorrhizal component of the soil microbial community may influence ecosystem productivity, standing biomass, nutrient cycling, carbon allocation, and relative abundance of plants (Stampe and Daehler 2003; van der Heijden et al. 1998). For example, increasing diversity of ectomycorrhizal fungi has been found to promote tree seedling productivity in low-fertility but not high-fertility substrates (Jonsson et al. 2001). These effects, in turn, can control the aboveground consumers associated with individual plant species (Vicari et al. 2002; Goverde et al. 2000; Gange and Nice 1997).

The effect of land-use change on mycorrhizae in general, and on AMF in particular, has been difficult to study because of the lack of adequate indicators of AMF activity. Determination of spore counts and infection rates are tedious and

give poor indication of the biomass of mycorrhizae. However, these methods can help understand shifts in community structure. Studies employing these approaches generally show that land-use change results in decreased AMF abundance. Ling-Fei et al. (2007) measured AMF colonization and spore density in a landscape in southwest China and found that both parameters were lower in fallow and cropped agricultural land compared to native forest.

Mathimaran et al. (2007) showed that management and crop rotation have a significant effect on the AMF, particularly through alterations of the plant community present in the agroecosystem. The mycorrhizal communities in soils planted with a tree (Crotolaria) or a cereal crop (maize) were very different from the community in soils under sunflower or leeks. This specificity between mycorrhizae and the plant host sets up a positive feedback within the ecosystem (Wardle et al. 2004). AMF are associated with fertile soils, while intermediate- and low-fertility soils are associated with ectomycorrhizal and ericoid mycorrhizal fungi, respectively (Cornelissen et al. 2001). Because plants that are associated with AMF have high N content, and also low lignin and low phenol content, they return high quality organic materials to the soil, thus maintaining rapid nutrient cycling and high productivity. Plants associated with ectomycorrhizal and ericoid mycorrhizal fungi have lower N and higher phenol and lignin content. Thus, they return a lower quality litter to the soil, which reinforces low production on the site. We see that land-use change and management following conversion of forest to agriculture represents a phase change for the mycorrhizal community that alters the function of the ecosystem and has the potential to set up a new dynamic between the detrital and plant communities.

3.5 Microbial Community Activity

The microbial community regulates nutrient cycles by its effects on the decomposition process, and affects nutrient acquisition by plants through symbiotic relationships such as mycorrhizal or rhizobial associations with plant roots. The microbial community also represents a dynamic pool of organic matter that serves as a nutrient reservoir. Many studies (Verchot et al. 1999, 2000, 2006; Cleveland et al. 2003; Ishizuka et al. 2002; Erickson et al. 2001; Crill et al. 2000; Veldkamp et al. 1997; Neill et al. 1995) have looked at how land-use change affects biogeochemical processes. The general trend is that nutrient availability decreases as forests are converted to agriculture and pasture, the nitrogen economy changes from one dominated by NO_3^- to one dominated by NH_4^+, and extracellular enzyme activities decrease (Fig. 3.5).

Ecologists have been thinking about how the changes in microbial community structure relate to biogeochemical function (Marschner 2007; Chapin et al. 1997). Schimel and Gulledge (1998) suggested that land-use change alters microbial community activity in two principal ways (Fig. 3.6). First, change can alter the function of the existing assemblage of organisms. For example, the rates of many

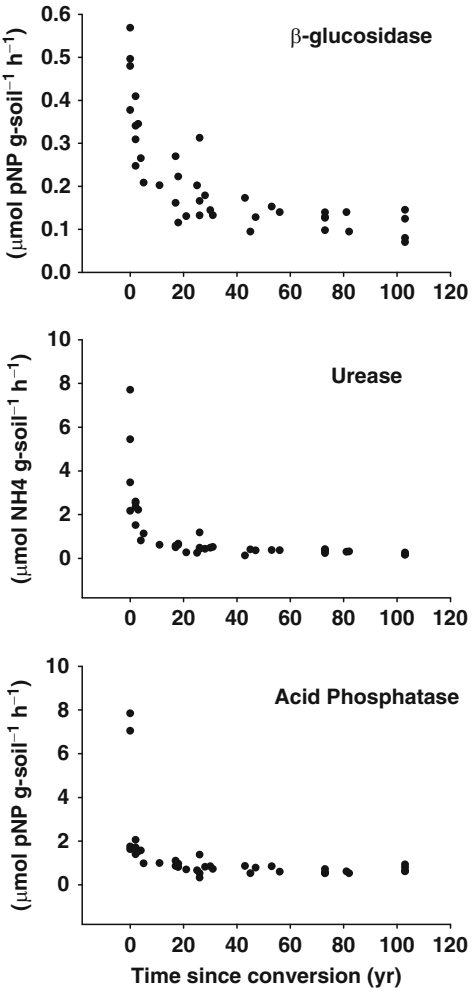

Fig. 3.5 Effects of conversion of forest to agriculture on extracellular enzyme activity in soils in Western Kenya (Verchot et al. unpublished). For the enzymes associated with narrow metabolic processes (acid phosphatase and urease), new equilibrium levels were established around 20 years after conversion, before SOC stabilized and when forest-derived SOC made up most of the total SOC. For the enzyme associated with the broader metabolic process (β-glucosidase), new stable levels of activity were established around 50 years following conversion, when forest-derived SOC made up only around 40% of the total SOC

biochemical processes increase with temperature up to an optimum and then decrease as enzymes denature. By provoking an increase in soil temperature, vegetation removal would alter the rates of decomposition, but not the nature of the physiological processes in the microbial community. Second, land-use change can alter the structure of the microbial community, which in turn would modify the physiological processes that drive biogeochemical cycling. For example, the temperature sensitivity of the decomposer community might shift, or the population of lignin decomposers may become dominated by N-insensitive fungi (Schimel and Gulledge 1998; Kaal et al. 1993). In an extreme case, key functions (e.g., denitrification, sulfate reduction, lignin decomposition) could be lost from the community. Thus, two categories of effects result from land-use change. In the first case, the rates of processes vary and this variation is reversible; in the second case the nature

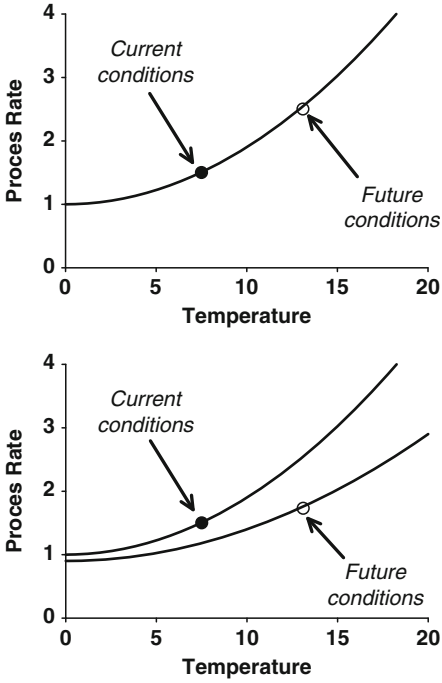

Fig. 3.6 Example adapted from Schimel and Gulledge (1998) of how land-use change could alter the relationship between a process rate and an environmental variable. *Top panel*: the community remains unchanged, and the process rate is altered by the changed environment. *Bottom panel*: the microbial community changes, altering the underlying drivers of the relationship between the environmental factor and the process

of the microbial community is modified in such a way that alterations in biogeochemical processes are not readily reversible, as in the case of the old farmed sites that we discussed at the end of Sect. 3.4.

The information presented in the preceding sections leads us to suggest that both reversible and irreversible phenomena are likely to result from land-use change. Very few studies examine quantitatively or qualitatively how land-use change alters the microbial community and how any modification in community structure, in turn, affects function. Limits imposed by the current biogeochemical and microbiological measurement methods make it difficult to collect appropriate datasets. For example, any relevant ecosystem process is the result of the activities of a subset of organisms in the microbial population. Differences captured in whole community profiles as defined by PLFA, or in profiles of major segments of a community, as revealed by 16S rDNA approaches, may not capture structural changes that are significant for the process in question. The difference in scale that exists between experimental designs of biogeochemists and environmental microbiologists is also an impediment to improving our understanding. Microbes accomplish their work at the scale of 10^{-6} m and many microbiologists are working at scales of the order of 10^{-4} m. By contrast, ecosystem processes are important at the scale of around 10^{3}–10^{4} m^2 (Groffman et al. 2006). Thus, it has been difficult for ecologists to demonstrate that the composition and structure of the microbial community matter to ecosystem function.

There are good reasons to believe that microbial community structure is unimportant for understanding biogeochemical processes within the scale of a whole ecosystem. Indeed, various ecosystem models are successful over a wide range of temporal and spatial scales without taking variation in microbial community structure into account. This is the case of models of soil respiration, which often rely on temperature functions and organic carbon inputs (Davidson et al. 2006). Given the widely held assumption in microbiology that everything is everywhere and the environment selects (Hooper et al. 2008; Finlay 2002; Finlay and Clarke 1999; Baas-Becking 1934; see Chap. 12), it is unlikely that land-use change would eliminate whole groups of organisms responsible for the efflux of CO_2 from the soil. Thus, modifications of substrate availability, rather than alterations to microbial community structure, are likely to be the long-term driver of ecological alterations accompanying land-use change.

On the other hand, the importance of microbial community structure is suggested by site-specific differences in the functional relationship between microbially-mediated processes and environmental conditions. For example, the wide range of temperature response values for soil respiration obtained by Neff et al. (1996), in a standard incubation of soils from different sites, suggests that different microbial communities have different temperature responses. The incubations were short enough that consumption of the labile C during the incubations was unlikely. Organic matter quality may have been a factor, requiring different enzymes for decomposition.

Approaches using analyses of extracellular enzymes are shedding light on the importance for key processes of certain functional groups within microbial communities. To get a handle on the relationship between the structure of the microbial community and function, we will digress briefly from the theme of land-use change and look at several studies that have examined this relationship by manipulating the microbial community composition or by looking at different ecosystems within a landscape. This work generally focuses on metabolically "narrow" processes.

In one experiment, Lucas et al. (2007) showed that different parts of the microbial community responded differently to inputs of a high quality organic N source; in particular, ectomycorrhizal fungi and Gram-positive bacteria responded positively to N addition. No response was obtained with more complex substrates, despite similar levels of N addition to the system. Fungi play an important role in the breakdown of lignin and produce extracellular lignases. The authors manipulated several components of the microbial community and showed that changes in the fungal component had little effect on extracellular lignase activities. They looked at two lignases: phenol oxidase and peroxidase. Neither of the enzyme activities increased as a result of the increased importance of fungi in the microbial community structure.

Denitrification is not specific to one phylogenetic group; rather it can be found in about 50 genera, most of which belong to Proteobacteria (Zumft 1999). Rich and Myrold (2004) looked at the denitrifier component of the microbial community using the functional *nosZ* gene, which is responsible for producing N_2O reductase. They worked on four adjacent sites in a landscape in Willamette Valley in Oregon

and compared different parameters of the denitrification process, namely denitrifying enzyme activity (DEA) and maximum potential N_2O reductase activity. The strongest correlations were between the nonmetric multidimensional scaling ordination results of *nosZ* and the DEA, but the ordination results between *nosZ* and the proportion of gas emitted as N_2O differed across habitats. The authors concluded that denitrifying community composition and activities were uncoupled across the ecosystems. However, in this study DEA was generally low at all sites, and hence the variation was low as well. In a study on sites with DEA activities an order of magnitude greater, Rich et al. (2003) found tighter coupling between denitrifying community composition and functioning in adjacent meadow and forest soils in Oregon. While Rich and Myrold (2004) concluded that relationships between denitrifying community structure and activities appeared to be ecosystem-specific, it is altogether possible that low variations may sometimes make this relationship undetectable.

It appears that there are only two studies in the literature that explore the effect of land-use change on microbial communities and how this translates into altered function. Waldrop et al. (2000) looked at the effects of conversion of tropical forest to pineapple plantations on microbial community structure and function in Tahiti. Bossio et al (2005) looked at different land uses in several landscapes and used a replicated experiment to explore these relationships in Kenya.

Using a chronosequence of newly established pineapple plantations, Waldrop et al. (2000) showed that SOC and nutrients decreased in the soil over time. This was associated with an increase in saturated fatty acids, which are generally indicative of bacteria, and a decline in branched fatty acids, which are indicative of Gram-positive bacteria. The markers for fungi and actinomycetes also increased in the pineapple plantations. These authors used extracellular enzyme activities to assess community function and showed that activity was largely driven by the size of the microbial community, which as we know is correlated with SOC. Specific activities (enzyme activity per unit of microbial biomass) of phenol oxidase, peroxidase, phosphatase, and sulphatase, all enzymes involved in relatively narrow metabolic processes, correlated significantly with site scores on the first principal component axis of the PLFA assessment of community composition. Specific activities of β-glucosidase and β-xylosidase, enzymes involved in broad metabolic processes, were not correlated with community composition.

In the second study, Bossio et al. (2005) used several methods to investigate microbial community structure and function in distinctly different soil types at five sites of western Kenya. In this study, 16S rDNA analysis by DGGE using universal bacterial primers showed that ecosystem and site were the primary determinants of total bacterial community composition. The 16S rDNA and PLFA profiles showed differences between forested and agricultural soils. Higher levels of Gram-negative bacteria in the forested soils accounted for the difference in PLFA profiles. Agricultural soils separated into two groups, one with higher relative abundances of branched fatty acids, and a second group with higher relative abundances of monounsaturated fatty acids. Extracellular enzyme activities and BIOLOG Gram-negative microtiter plates were used as functional indicators. These showed less

specificity with respect to soil type, and greater variability than DNA- and PLFA-based measures. Thus, there appeared to be a high degree of functional redundancy in the microbial community. In replicated field experiments comparing traditional continuous maize cropping with an improved N-fixing tree fallow system in which both maize yields and microbial biomass C increased, 16S rDNA and PLFA analyses revealed differences in microbial communities between treatments, although these differences were not necessarily associated with increases in microbial diversity. Microbial biomass and enzyme activities were generally found to increase in soils with the N-fixing tree fallows; the relationship with soil type was not significant. The differences between the fallows and conventional agricultural practices were largely explained by increases in activities of enzymes associated with carbon cycling, and decreases in activities of those associated with P cycling. Thus, management practice such as the reintroduction of trees affected both microbial community composition and function.

In the studies on land-use change, the relative abundances of different microbial groups appear to affect function. To the degree that land-use change induces repeated stress on the soil microbial community (e.g., stress due to increased severity of drying/wetting cycles), substrate availability may be less important for rates of biogeochemical processes than the size and structure of the population, which would be controlled by the stress-induced death and regrowth cycles (Schimel and Gulledge 1998).

3.6 Conclusions

There is a rich body of knowledge about the effects of land-use change on carbon stocks and on biogeochemical processes. However, these studies often give conflicting results and we cannot always draw generalizations. Certainly, microbial activity depends on carbon availability, but the processes that are the result of microbial activity — soil respiration, N mineralization, trace gas production and consumption — defy generalizations. Our biogeochemical models are poor at predicting the magnitudes and sometimes even the direction of fluxes at new sites. Davidson and Janssens (2006) called for a more reductionist approach to assess the importance of kinetic properties of individual components of organic matter and the effect of in situ constraints on organic matter decomposition. Few studies have tried to develop an understanding of how alteration of environmental conditions produces physiological responses in the microbial community and alters community composition so as to modify processes at higher spatial scales. Thus, any reductionist approach to improving our biogeochemical models might also factor these elements into the research.

Difficulties in measurement remain a constraint to advance in this area. Even though we are now capable of measuring unculturable organisms, we cannot easily measure microbial diversity at meaningful scales. Assays that measure microbial function usually determine the overall rate of an entire metabolic process and do not

break the process down into steps that can be associated with particular organisms. It also appears that diversity in itself will be a meaningless measure for understanding microbial function as there is significant redundancy within the community. Community composition may be more meaningful.

As Schimel et al. (2007) noted, plant ecology offers useful conceptual frameworks for advancing efforts to integrate microbial ecology into ecosystem ecology. In plant ecology, understanding how individual organisms respond to environmental stress has been the key to integrating population and ecosystem ecology. However, there are significant differences between plants and microbes that we need to consider as we design research to achieve the integration of microbial ecology into ecosystem ecology. In ecosystem ecology, we often differentiate between stress and disturbance. Recurrent stress factors such as drought, pollution or seasonal fire pose chronic challenges to organisms and engender physiological costs. Occasional disturbance (provoked or accidental fire, flooding, windstorms, land-use change) results from pulse events that involve physical disruption to the ecosystem; these induce direct mortality of organisms and alter, at least temporarily, the composition and structure of the ecosystem. For microbes, the distinction may be less clear. Microbes are likely to experience both stress and disturbance events through altered microclimate and resource availability that impose physiological costs. With the exception of tillage, which disrupts fungal hyphae, microbes will not experience physical disturbance as plants do.

Schimel et al. (2007) went on to propose that concepts related to life strategies, similar to those used to characterize plants (e.g., Grime 1977), may be useful for characterizing microbes. Looking at how microbes deal with stress — they may be inherently resistant or else physiological costs may be associated with acclimating to the stress — will provide a basis for understanding life history strategies of microbes. Thus, in addition to the processes that different suites of organisms undertake, integrating the nature of their response to stress will provide for more robust models of function.

Extrapolating future conditions based on observations of current responses to environmental change will be inadequate as environmental change accelerates. We are not yet capable of integrating the physiological ecology of microbes with population biology to explain ecosystem processes. However, the state of knowledge reviewed in this chapter suggests that we are at the point of being able to open the black box of microbial ecology and integrate this new knowledge into ecosystem ecology. This is likely to be essential for building more robust ecosystem models that can help us address the challenges posed by global environmental change.

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