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REVIEW AND SYNTHESIS

The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems

Marcel G. A. van der Heijden[1,2]* Richard D. Bardgett[3] and Nico M. van Straalen[1]

[1]*Department of Animal Ecology, Faculty of Earth and Life Sciences, Institute of Ecological Science, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands*

[2]*Agroscope Reckenholz-Tänikon, Research Station ART, Reckenholzstrasse 191, 8046 Zurich, Switzerland*

[3]*Soil and Ecosystem Ecology, Lancaster University, Lancaster LA1 4YQ, UK*

**Correspondence: E-mail: marcel.vanderheijden@art.admin.ch*

Abstract

Microbes are the unseen majority in soil and comprise a large portion of life's genetic diversity. Despite their abundance, the impact of soil microbes on ecosystem processes is still poorly understood. Here we explore the various roles that soil microbes play in terrestrial ecosystems with special emphasis on their contribution to plant productivity and diversity. Soil microbes are important regulators of plant productivity, especially in nutrient poor ecosystems where plant symbionts are responsible for the acquisition of limiting nutrients. Mycorrhizal fungi and nitrogen-fixing bacteria are responsible for *c.* 5–20% (grassland and savannah) to 80% (temperate and boreal forests) of all nitrogen, and up to 75% of phosphorus, that is acquired by plants annually. Free-living microbes also strongly regulate plant productivity, through the mineralization of, and competition for, nutrients that sustain plant productivity. Soil microbes, including microbial pathogens, are also important regulators of plant community dynamics and plant diversity, determining plant abundance and, in some cases, facilitating invasion by exotic plants. Conservative estimates suggest that *c.* 20 000 plant species are completely dependent on microbial symbionts for growth and survival pointing to the importance of soil microbes as regulators of plant species richness on Earth. Overall, this review shows that soil microbes must be considered as important drivers of plant diversity and productivity in terrestrial ecosystems.

Keywords

Biological diversity and ecosystem functioning, microbial consortia, microbial diversity, mycorrhizal fungi, nitrogen, nitrogen fixation, phosphorus, soil.

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INTRODUCTION

Soil microbes play key roles in ecosystems and influence a large number of important ecosystem processes, including nutrient acquisition (Smith & Read 1997; Sprent 2001), nitrogen cycling (Tiedje 1988; Kowalchuk & Stephen 2001), carbon cycling (Hogberg *et al.* 2001) and soil formation (Rillig & Mummey 2006). Moreover, soil microbes represent the unseen majority in soil and comprise a large portion of the genetic diversity on Earth (Whitman *et al.* 1998). For instance, it has been estimated that one gram of soil contains as many as 10^{10}–10^{11} bacteria (Horner-Devine *et al.* 2003), 6000–50 000 bacterial species (Curtis *et al.* 2002), and up to 200 m fungal hyphae (Leake *et al.* 2004). However, while it is widely recognized that microbes perform crucial roles in biogeochemical cycling, the impact of microbes on plant productivity and diversity is still poorly understood.

In this review, we explore how microbes that live belowground indirectly and directly influence the productivity, diversity and composition of plant communities. We identify research gaps and propose new avenues of research. First, we discuss the impact of microbes on plant productivity and plant diversity. Second, we investigate the significance of microbial diversity. Third, we discuss the characteristics of bacterial and fungal dominated soil ecosystems and how the relative abundance of bacteria and fungi affect ecosystem

functioning. We end with conclusions and identify future research priorities. Our ultimate aim is to highlight the significance of soil microbes for the productivity and diversity of plant communities, and the strong interdependence of plant and soil microbial communities.

Impact of soil microbes on plant productivity

Soil microbes have a big impact on plant productivity (Fig. 1; Table 1). Two main mechanisms can be distinguished: direct effects on plants via root-associated organisms that form mutualistic or pathogenic relationships with plants, and indirect effects via the action of free-living microbes that alter rates of nutrient supply and the partitioning of resources.

Positive direct effects

A wide range of soil microbes form intimate symbiotic associations with plants and can stimulate plant productivity by supplying limiting nutrients to the plants. Symbiotic associations between plants and nitrogen (N)-fixing bacteria that convert atmospheric N into ammonium-N are perhaps best studied (Sprent 2001). Nitrogen-fixing bacteria are important regulators of plant productivity because plants cannot fix atmospheric N and because N is, together with phosphorus (P) and potassium, the main element that limits plant productivity (Chapin 1980). The contribution of N-fixing bacteria to plant productivity is thought to be biggest in tropical savannah, and some grasslands and tropical forests that are dominated by legumes; in these situations, N-fixing bacterial symbionts of the legumes can

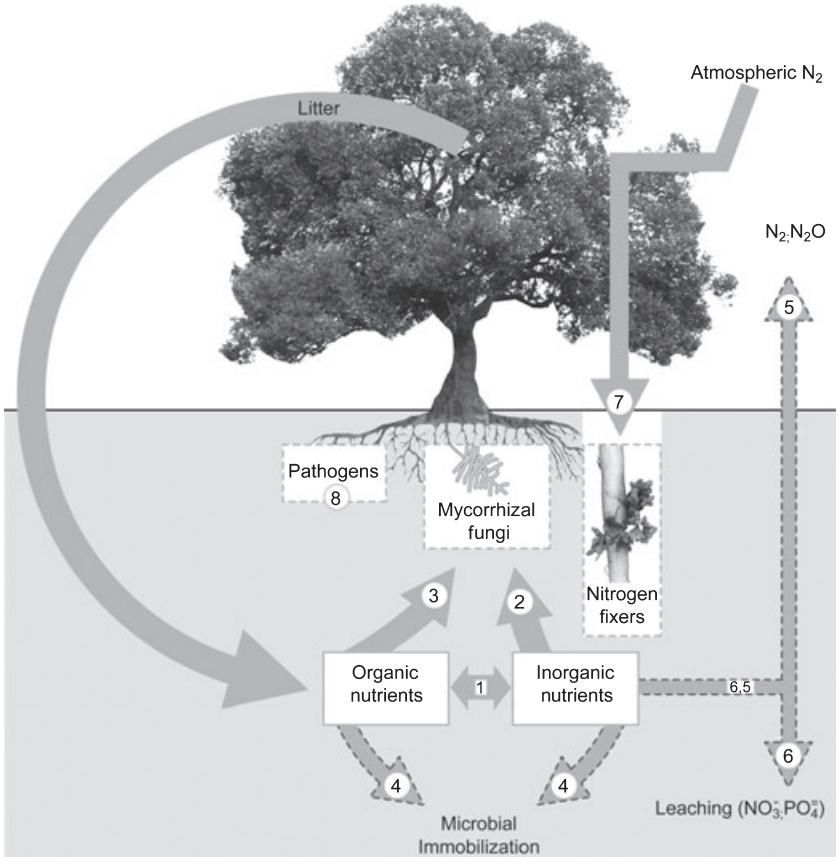

Figure 1 Schematic representation showing the impact of soil microbes on nutrient acquisition and plant productivity in natural ecosystems. Plant litter is decomposed by a wide range of bacteria and fungi (1) making nutrients available for uptake by mycorrhizal fungi (2) and plant roots or immobilizing nutrients into microbial biomass and recalcitrant organic matter (4). Ecto-mycorrhizal fungi and ericoid mycorrhizal fungi have also access to organic nutrients and deliver these nutrients to their host plants (3). Some plants can also acquire organic nutrients directly. Nutrients can also be lost from soil caused by denitrification of ammonium into di-nitrogen gas or nitrogen oxides by denitrifying bacteria (5) or when nitrifying bacteria and Archaea facilitate nitrogen leaching by transforming ammonium into nitrate (6), which is much more mobile in soil. The contribution of microbes to leaching losses of other nutrients (e.g. phosphorus) is still poorly understood. Nitrogen-fixing bacteria (both free-living and symbiotic) transform nitrogen gas into ammonium (7), thereby making it available to plants, enhancing plant productivity. Finally, microbial pathogens attack plants and can reduce plant productivity (8) (modified after Leake *et al.* 2002).

Table 1 Influence of soil microbes on various ecosystem processes

Ecosystem process	Microbes involved	Estimated microbial contribution to ecosystem process
Carbon cycle		
Plant productivity	Nitrogen-fixing bacteria, mycorrhizal fungi	0–50%*
	microbial pathogens	−50–0%†
Decomposition	Bacteria, fungi	Up to 100%‡
Nitrogen cycle		
Plant nitrogen acquisition		
Nitrogen fixation	Rhizobia, actinomycetes, free-living bacteria	0–20%§ (sometimes higher)
Soil uptake	Mycorrhizal fungi	0–80%¶
Nitrogen loss		
Denitrification	Denitrifiying bacteria and some fungi	Up to 60%**
Enhanced leaching because of nitrification	Nitrifying bacteria, Archaea	??
Phosphorus cycle		
Plant phosphorus acquisition	Mycorrhizal fungi; P-solubilizing bacteria	0–90%††
Phosphorus loss because of leaching after mineralization		??
Regulation of plant diversity		
Stimulation of plant diversity	Arbuscular mycorrhizal fungi, rhizobia	0–50%‡‡
Reduction of plant diversity	Arbuscular mycorrhizal fungi	−20–0%§§

*Spehn *et al.* 2002; Van der Heijden *et al.* 2006a, 2006b; Klironomos *et al.* 2000; Vogelsang *et al.* 2006.
†Note it is difficult to estimate the impact of pathogens on plant productivity in natural plant communities because other plant species increase in abundance when others decline.
‡Bardgett 2005; Hattenschwiler *et al.* 2005.
§Vitousek & Walker 1989; Cleveland *et al.* 1999; DeLuca *et al.* 2002.
¶Simard *et al.* 2002; Hobbie & Hobbie 2006.
**Houlton *et al.* 2006.
††Leake *et al.* 2002; Van der Heijden *et al.* 1998, 2006b; the impact of P-soluble bacteria is unresolved.
‡‡Grime *et al.* 1987; Klironomos *et al.* 2000 Van der Heijden *et al.* 1998, 2006a.
§§Hartnett & Wilson 1999; O'Connor *et al.* 2002.
??The impact of soil microbes on nitrate and phosphorus leaching is still unresolved.

contribute up to 20% of all plant N that is annually acquired by the vegetation (Cleveland *et al.* 1999; Van der Heijden *et al.* 2006a).

Several other plants form associations with N-fixing bacteria, including *c.* 400 shrubs that associate with actinomycetes (Bond 1983), approximately 150 cycad and 65 *Gunnera* species that associate with cyanobacteria (Rai *et al.* 2000), and an unknown number of plant species that harbour endophytes and can fix N. Numerically most abundant are actino-rhizal plants, such as *Casuarina, Myrica*, *Hippophae* and *Alnus* (Bond 1983). Their invasion into new areas has been attributed to their ability to associate with N-fixing actinomycetes, with far reaching consequences for ecosystem properties. For example, the invasion of N-fixing actino-rhizal shrubs into N limited forests in Hawaii dramatically enhanced soil N availability and plant productivity in these ecosystems (Vitousek & Walker 1989).

Another important group of plant symbionts that enhance plant productivity by supplying limiting nutrients are mycorrhizal fungi. Mycorrhizal fungi are widespread and form symbiotic associations with the roots of *c.* 80% of all terrestrial plant species (Smith & Read 1997). Mycorrhizal fungi can provide resistance to disease and drought, and supply a range of limiting nutrients including N, P, Copper, iron and zinc to the plant in exchange for carbon. Mycorrhizal fungi often enhance resource complementarity by providing nutrients that are otherwise inaccessible to plant roots. The most abundant and important groups of mycorrhizal fungi are the arbuscular mycorrhizal (AM) fungi, the ecto-mycorrhizal (EM) fungi and the ericoid mycorrhizal (ERM) fungi. AM fungi are abundant in grassland, savannah and tropical forests and associate with many grasses, herbs, tropical trees and shrubs (Read & Perez-Moreno 2003). EM fungi associate with *c.* 6000 tree species and are abundant in temperate and boreal forests and in some tropical forests (Alexander & Lee 2005). Ericoid mycorrhizal fungi are most abundant in heath land where they associate with members of the Ericaceae (Smith & Read 1997).

Several experimental studies reported that AM fungi enhance plant productivity in grassland, and up to two-fold increases have been found (Van der Heijden *et al.* 1998;

Vogelsang *et al.* 2006). In contrast, others have found that AM fungi alter the distribution of nutrients amongst co-existing grassland species without altering total plant productivity (Grime *et al.* 1987; Van der Heijden *et al.* 2006b). Enhanced P uptake is one of the mechanism by which AM fungi can enhance plant productivity and experiments with single plants or experimental plant communities have shown that AM fungi contribute to up to 90% of plant P uptake (Jakobsen *et al.* 1992; Van der Heijden *et al.* 1998, 2006b). Enhanced P uptake is especially important for plant species with high P-requirement such as legumes, or under conditions when plant productivity is strongly determined by P availability such as in the tropics. Some recent studies have also shown that AM fungi can contribute to enhanced N-acquisition under some conditions (Hodge *et al.* 2001). However, the significance of AM fungi for N uptake is unresolved, in that several studies report no effects of AM fungi on plant N-acquisition (e.g. Reynolds *et al.* 2005; Van der Heijden *et al.* 2006b).

The presence of ecto-mycorrhizal fungi is of pivotal importance for plant productivity in most boreal and temperate forests. Nutrient availability in these ecosystems is usually low and most nutrients are present in organic form in litter and humus (Read & Perez-Moreno 2003). Ecto-mycorrhizal fungi can acquire N from litter through extensive hyphal networks that forage for nutrients and by excreting a wide range of extracellular enzymes that can degrade organic matter (Leake & Read 1997). Pot experiments (reviewed by Simard *et al.* 2002) and field studies (Hobbie & Hobbie 2006) have shown that up to 80% of all plant N in boreal forests is derived from EM fungi. However, the actual contribution of mycorrhizal fungi to plant nutrition and productivity in natural ecosystems is difficult to determine because no suitable bio-markers are present (but see Hobbie & Hobbie 2006). Also, most communities already contain mycorrhizal fungi, making it difficult to perform experiments in the field to test their importance.

Negative direct effects

Microbes can also reduce plant productivity and this can have dramatic consequences for ecosystem processes, especially when dominant or keystone species, such as forest trees are affected. For instance, soil pathogens including *Phytophthora* spp., *Fusarium* spp. and *Pythium* spp. have been shown to attack a range of dominant forest trees including oak, acacia and *Eucalyptus* (see Burdon *et al.* 2006). It is difficult to estimate the impact of microbial pathogens on plant productivity in natural communities because a reduction of biomass of one species is often compensated by additional growth of other species, especially in species rich plant communities. The significance of soil pathogens will be further discussed in the section: 'Impact of soil microbes on plant diversity and community composition'.

Positive indirect effects

Microbes can also indirectly influence plant productivity via the action of free-living microbes that alter rates of nutrient supply and resource partitioning. These effects can either stimulate plant productivity, through the actions of microbes that enhance the availability of nutrients for plant uptake, or reduce plant productivity through competition for nutrients with plant root and/or by promoting nutrient loss via leaching of mobile nutrient forms (see below). Perhaps the most important route by which free-living microbes influence plant nutrient availability, and hence plant productivity, is via processes of nutrient mineralization, whereby soil microbes break down soluble and insoluble organic matter and convert it into inorganic, plant available forms. Most soil N (some 96–98%) is contained in dead organic matter as complex insoluble polymers such as proteins, nucleic acids and chitin, and these polymers are broken down into dissolved organic N (DON) by extracellular enzymes that are produced by soil microbes (Schimel & Bennett 2004). This DON, which can constitute a significant portion of the total soluble N pool, is either absorbed by free-living soil microbes, or it is mineralized by the microbial biomass (under conditions when microbial growth is C limited), thereby liberating inorganic-N into the soil environment. Alternatively, plants might take up DON directly from soil, in the form of amino acids, thereby by-passing the microbial mineralization step. This was shown to be the case in many ecosystems, but especially in those that are strongly N limited, such as in arctic (e.g. Nordin *et al.* 2004) and alpine tundra (e.g. Raab *et al.* 1999), boreal (e.g. Nasholm *et al.* 1998) and temperate forest (Finzi & Berthrong 2005), and low productivity grassland (e.g. Bardgett *et al.* 2003). This growing awareness of the ability of plants to use organic N and compete with soil microbes for N has led to a radical rethink of terrestrial N cycling and especially the processes that control N availability to plants (Schimel & Bennett 2004).

Free-living N-fixing bacteria, which are ubiquitous in terrestrial ecosystems, can also contribute significantly to the N budget of some systems; they fix relatively small, but significant amounts of N (< 3 kg N ha^{-1} $year^{-1}$) (Cleveland *et al.* 1999). Nitrogen-fixing cyanobacteria also contribute to the N economy of terrestrial ecosystems, such as deserts (Belnap 2003), and boreal forest, where N fixation has traditionally been thought to be extremely limited. For example, DeLuca *et al.* (2002) showed that a N-fixing symbiosis between a cyanobacterium (*Nostoc* sp.), which inhabits the incurves of leaves of the feather moss *Pleurozium schreberi* fixes significant quantities of N (1.5–2.0 kg N ha^{-1} $year^{-1}$) and acts as a major contributor to N accumulation and cycling in boreal forests, especially in late successional systems where rates of N fixation via this route are greatest (Zackrisson *et al.* 2004). This finding is especially

important because *P. schreberi* is the most common moss on Earth, and accounts for as much as 80% of the ground cover in boreal forests (DeLuca *et al.* 2002).

Microbial uptake of nutrients also has important implications for ecosystem nutrient storage and temporal partitioning of nutrients between plants and soil microbial pools. Immobilization of N by microbes, for example, has been shown to act as a short-term sink for N in several terrestrial ecosystems (Zogg *et al.* 2000; Bardgett *et al.* 2003), thereby potentially limiting the export of N to adjacent ecosystems and groundwater (Brooks *et al.* 1998). Seasonal patterns of N immobilization by microbes are also important for plant N-acquisition, especially in strongly N limited ecosystems where microbial communities immobilize N maximally in autumn, after plant senescence, and retain it throughout the winter until spring, when it is released for plant uptake (Bardgett *et al.* 2005). Microbial uptake of N is also important for longer-term ecosystem N retention, via the transfer of the nutrients from within microbial tissues to more stable organic matter pools after cell death (Zogg *et al.* 2000).

Other routes by which microbes can alter plant nutrient availability include weathering of soils via the exudation of organic acids (Landeweert *et al.* 2001) and the solubilization of various forms of precipitated P; on the basis of laboratory assays, it was shown that P-solubilizing bacteria may constitute up to 40% of the cultivable population of soil bacteria (Kucey 1983). The significance of these bacteria in natural ecosystems is still unclear and is an area that warrants further attention. Another route by which microbes affect plant productivity is disease suppression, for example through the production of antifungal metabolites by *Pseudomonas* sp. (Weller *et al.* 2002). These bacteria protect several major agricultural crops against diseases, a phenomenon that is likely to be also important in natural ecosystems.

Negative indirect effects

As discussed above, microbes compete with plants for nutrients in soil solution, with possible negative effects on plant nutrient acquisition and growth. This is most likely the case in strongly nutrient limited ecosystems, such as arctic and alpine tundra, where soil microbes have been shown to compete effectively with plants for N (Nordin *et al.* 2004) leading, in some cases, to similar quantities of N being found in the microbial and plant pool (Jonasson *et al.* 1999). Moreover, it is demonstrated that if microbial activity is stimulated through the addition of labile carbon (C) to the soil, plant N uptake and plant productivity decline (e.g. Schmidt *et al.* 1997). Likewise, Dunn *et al.* (2006) stimulated the soil microbial community of a grassland soil by adding glucose and followed the transfer of added ^{15}N-labelled N into the microbial and plant biomass of two grass species. They found that the stimulation of microbial biomass by glucose addition increased microbial ^{15}N capture, but reduced plant ^{15}N capture and growth. Collectively, these studies illustrate the importance of changes in microbial biomass, and probably community structure, for regulating N-acquisition by plant roots.

Another route by which microbes reduce ecosystem N availability, is by transforming N to more mobile forms, such as nitrate which is produced by the bacterial process of nitrification (e.g. Kowalchuk & Stephen 2001). Nitrate is much more mobile in soil than ammonium and can be lost easily via leaching into ground water and surface run-off (Scherer-Lorenzen *et al.* 2003). Hence, nitrifying bacteria can indirectly reduce plant productivity because they reduce the availability of a nutrient that is often limiting plant productivity. Substantial amounts of nitrate can be found in groundwater or subsurface water and this can represent a substantial loss of N, especially in humid ecosystems in the Western world (Canter 1997). It is often difficult to assess how much N is lost from ecosystems because leaching is temporally variable and weather dependent (mainly occurring in wet seasons and depending on temperature, soil water concentrations and soil properties). Nitrifiers, other bacteria and some fungi can transform nitrate into N gases (denitrification) under anaerobic conditions. The impact of denitrifiers on plant productivity and plant community composition has rarely been tested. It should be large because up to 50% of available soil N can be lost by denitrification from tropical forest (Houlton *et al.* 2006). Some recent studies have shown that differences in denitrifier populations explain variations in denitrification rates (e.g. Holtan-Hartwig *et al.* 2000). Hence, changes in the composition of denitrifying communities could influence N availability and, related to that, plant productivity. However, other studies could not relate denitrification rates to the composition of denitrifying communities (e.g. Enwall *et al.* 2005) and additional work is required to test whether denitrification rates are responsive to changes in the composition of denitrifying communities. Such studies should not only focus on prokaryotes, as is usually the case, but should include soil fungi which have been reported to denitrify (Laughlin & Stevens 2002). It is important to understand the impact of denitrifying communities on denitrification rates because world-wide, an estimated 105–185 tons of N are lost yearly through denitrification by bacteria (Tiedje 1988). This equals *c.* 7% of the world-wide terrestrial productivity, assuming that N is limiting plant productivity (Schlesinger 1997).

Estimates of microbial effects on plant productivity are often difficult because populations and communities of soil microbes are affected by a wide range of other soil biota, especially their consumers, such as protozoa, *Collembola* and

nematodes. For instance, bacterial grazing by protozoa and nematodes has been shown to enhance plant productivity via stimulation of nitrogen mineralization through the microbial loop (e.g. Bonkowski 2004). Moreover, *Collembola* feed on a wide range of fungi (including mycorrhizal fungi) and this can alter soil nutrient availability, plant nutrient uptake and growth, and carbon exudation into the rhizosphere, thereby altering plant-microbial competition for N (Johnson *et al.* 2005).

Impact of soil microbes on plant diversity and community composition

A major goal in ecology is to understand the factors that determine the composition and diversity of plant communities. Factors such as soil fertility, geographic position, climate, herbivory and disturbance are known to influence plant species richness. There is now increasing evidence that soil microbes, especially those that live in symbiosis with plants, also contribute to plant diversity (Table 1).

Direct effects

Several studies reported that AM fungi increase plant diversity in European grassland by as much as 30% (e.g. Grime *et al.* 1987; Van der Heijden *et al.* 1998). The fungi do this by promoting seedling establishment and enhancing competitive ability of subordinate plant species relative to dominants (Grime *et al.* 1987; Van der Heijden *et al.* 2006b). In some cases, however, AM fungi can reduce plant diversity; especially in ecosystems where the dominant plants have a high mycorrhizal dependency and obtain most benefit from AM fungi, such as in tall grass prairie (Hartnett & Wilson 1999) or some annual plant communities in Australia (O'Connor *et al.* 2002). Similarly, it is proposed that in tropical rainforests ectomycorrhizal associations encourage dominance of certain tree species, at the expense of arbuscular mycorrhizal trees that are less able to acquire nutrients and tolerate pathogen attack, thereby reducing species co-existence (Connell & Lowman 1989).

It has also been shown that symbiotic bacteria influence plant community composition and diversity. An estimated 15 000 legume species form symbiotic associations with N-fixing rhizobia bacteria (Sprent 2001), *c.* 400 shrub species form root nodules that are hosted by N-fixing actinomycetes, and an unknown number of plant species harbour endophytic N-fixing bacteria such as *Azoarcus* spp. and *Acetobacter* spp. (Boddey *et al.* 1995). The presence of N-fixing symbionts, or their arrival in un-colonized habitats, enhances growth and competitive ability of their host plants. This in turn can influence vegetation succession (Vitousek & Walker 1989), plant productivity (Spehn *et al.* 2002), plant invasibility (Parker *et al.* 2006), plant community composition (Van der Heijden *et al.* 2006a) and plant diversity (Van der Heijden *et al.* 2006a). Many hectares of the unique and fragile Fynbos vegetation in South Africa, which is one of the biodiversity hotspots on Earth, has been ruined by *Acacia* spp. (Sprent & Parsons 2000). The success of *Acacia* in colonizing these habitats is probably interlinked with their ability to associate with N-fixing bacteria (Sprent & Parsons 2000).

Recent work has emphasized that soil pathogens contribute significantly to spatial and temporal patterns in natural plant communities through mechanisms of negative plant–soil feedback (Van Der Putten 2003). This is when plant species change soil communities in such a way, for example, because of the accumulation of specific plant pathogens, that their own growth is more suppressed than the growth of other co-existing plant species (Bever *et al.* 1997; Van Der Putten 2003). For instance, establishment of *Prunus serotina* seedlings below adult plants was hampered by the accumulation of the soil fungus *Pythium* below adult plants (Packer & Clay 2000), and seedling survival away from the adult plants was higher (Packer & Clay 2000) suggesting that soil pathogens can enhance the spatial variation in plant communities (see Van Der Putten 2003 for a discussion and examples). Models predict that soil pathogens may even contribute to the maintenance of plant diversity by specifically suppressing dominant plants (Bever *et al.* 1997). These models assume that the negative effects of soil pathogens on plant species increase with increasing plant abundance, an observation that was recently confirmed by Bell *et al.* (2006) who observed that effects of pathogenic soil fungi on seedling mortality of a neotropical tree (*Sebastiana longicuspis*) were greatest at highest plant density. However, in contrast to this, an elegant study by Klironomos (2002) showed that rare plant species were much more affected by negative plant–soil feedback compared with abundant plants, thus indirectly suggesting that soil pathogens determine plant rarity and reduce plant diversity.

Soil pathogens can also drive succession when the accumulation of pathogens beneath a dominant plant leads to its demise and replacement by plant species that are not, or are less sensitive to pathogens, as observed for Dutch foredune succession (Van der Putten *et al.* 1993). In a recent paper, Kardol *et al.* (2006) proposed that early successional species from ruderal plant communities are more sensitive to soil pathogens than species from more stable communities, indicating that soil pathogens contribute to ecosystem development. Interestingly, AM fungi can also reduce growth of several ruderal plant species (Francis & Read 1995), perhaps suggesting that ruderal species are more sensitive to microbial colonization. The studies mentioned above are based on a limited number of plant species and future work is needed to make systematic comparisons for a wide range of plants of different successional status to

derive at general conclusions of how plant–soil feedback drives community dynamics.

Soil pathogens are also thought to play an important role in plant invasions (reviewed in: Reinhart & Callaway 2006; Wolfe & Klironomos 2005). Several studies indicate that soil biota from the home range of invasive exotic species have a stronger inhibiting effect than soil biota from areas that are invaded. Thus, the escape from natural enemies in the soil is a key mechanism explaining the success of invasive species. A similar mechanism was reported by Van Grunsven *et al.* (2007) for plant species that expand their range because of climate change. By comparing six species (three native species and three immigrating species), they observed that immigrating plant species were less affected by soil pathogens compared with native species. Moreover, invasive plants can also indirectly benefit from soil pathogens, as suggested by a recent paper by Mangla *et al.* (2007). These authors investigated the invasive tropical weed, *Chromolaena odorata*, and observed that root exudates from this species stimulated the abundance of the soil pathogen *Fusarium spp*, a soil pathogen that reduced seedling growth of one naturalized and one native species with which the invader co-existed.

Indirect effects

Free-living microbes also contribute to the maintenance of plant diversity through their influence on the availability of different N forms, both organic and inorganic, in soil. The idea here is that co-existing plant species partition a limited N pool, and thereby avoid competition for resources, through the uptake of different chemical forms of soil N, both organic and inorganic, which have been produced by microbial enzymes and mineralization processes. Three lines of evidence support this idea. First, microbial activities produce a wide variety of chemical forms of N in soil solution, including inorganic N forms and different types of amino acids of varying complexity (Kielland 1994), providing a variety of possible resources for plant uptake. Second, laboratory studies show that plant species differ in their ability to uptake different chemical forms of N, indicating that species have fundamental niches based on N form (Weigelt *et al.* 2005). Third, co-existing species of strongly N limited arctic tundra have been shown to be differentiated in uptake of chemical forms of N – with the dominant plant species using the most abundant N form that is present in soil – suggesting the existence of species' realised niches based on N form (McKane *et al.* 2002; but see Harrison *et al.* 2007).

Plant species richness in a world without microbes

A large number of plant species are completely dependent on microbial symbionts for growth and survival. Orchids are perhaps the best example. Orchids have extremely tiny seeds (0.3–14 μg). It is thought that most, if not all, of the estimated 20.000–35.000 orchid species require colonization by soil fungi before they can germinate and establish in their natural environment (Smith & Read 1997). Mycorrhizal fungi provide the germinating orchid seeds with carbon and nutrients (Cameron *et al.* 2006). Moreover, *c.* 400 species of Orchids and members of the *Ericaceae* lack chlorophyll and are completely dependent on soil fungi from which they obtain carbon and nutrients (Taylor *et al.* 2002). These plants act as epiparasites on fungi. Furthermore, several other green plants have a mixed strategy and are thought to acquire carbon through photosynthesis and via fungal links (Tedershoo *et al.* 2007; but see Zimmer *et al.* 2007). It has been postulated that at least some *Pyrola* species obtain up to 50% of carbon from fungal hyphae (Tedershoo *et al.* 2007). This strategy might be especially important in dark forests or other habitats where light availability limits plant productivity. However, it is still unclear how many plant species use this strategy, and whether ecologically significant amounts of carbon are transferred from the fungus to the plant (Selosse *et al.* 2006).

Microcosm studies with experimental plant communities have shown that several legumes and herbs that grow in nutrient poor environments require N-fixing bacteria and mycorrhizal fungi to grow and co-exist with other plants. Studies by Van der Heijden *et al.* (1998, 2006a) showed that 72% and 25% of the plant species in nutrient poor grassland could not grow and survive in the absence of mycorrhizal fungi or N-fixing bacteria, respectively. Plant species such as *Centarium erythrea* (Grime *et al.* 1987), *Clusia multiflora* (Cuenca *et al.* 2001), *Anthyllis cytisoides* (Diaz *et al.* 1996) and *Hyacinthoides nonscripta* (Merryweather & Fitter 1996) have been shown to be completely dependent on the presence of AM fungi. Moreover, seedlings of the tropical tree species *Dicorynia guianensis* were unable to absorb P in the absence of mycorrhizal associations, also making this species dependent on AM fungi (De Grandcourt *et al.* 2004). Plants with thick roots appear to be especially reliant on mycorrhizal fungi for nutrient acquisition (Hetrick *et al.* 1992). It is difficult to estimate the number of plants that rely on microbes for survival because only a few studies have been executed. However, cumulative evidence from the above examples suggests that at least 20 000 plant species require microbial symbionts to persist in natural, and especially nutrient poor, environments. The number of plants that are dependent on symbionts is probably much higher given the high frequency of mycorrhiza-/rhizobia-dependent plant species in microcosm studies and the restricted occurrence of many plant species in nutrient poor ecosystems.

The relationship between microbial diversity, plant diversity and plant productivity

There is currently much interest in the relationship between soil microbial diversity and ecosystem functioning. Key

questions are whether diverse microbial communities are better adapted to perform specific functions in ecosystems compared with species poor microbial communities. This question is also important in view of reduced microbial diversity in many anthropogenically disturbed soil ecosystems (Torsvik *et al.* 1996; Gans *et al.* 2005). So far, only a few studies have examined effects of microbial diversity on plant diversity and productivity. Several studies have manipulated the diversity of mycorrhizal fungal symbionts and determined how this affected plant productivity and diversity. Some of these studies observed that plant productivity, plant diversity and nutrient acquisition increased with increasing fungal diversity (Van der Heijden *et al.* 1998; Jonsson *et al.* 2001; Maherali & Klironomos 2007), while other studies found no effects (e.g. Van der Heijden *et al.* 2006b). For instance, Van der Heijden *et al.* (1998) observed that grassland microcosms with the greatest mycorrhizal fungal diversity had 105% higher plant diversity, and 42% higher plant productivity, respectively, compared with microcosms where only one fungus was inoculated. In recent work, Maherali & Klironomos (2007) provided a mechanistic explanation for the observation that AM fungal diversity can promote plant productivity. They observed that there is functional complementarity between different AM fungal families: one mycorrhizal fungal family (the *Glomeraceae*) provided protection against fungal pathogens, while another family (the *Gigasporaceae*) enhanced plant P uptake. Subsequently plant productivity was enhanced when members of both fungal families were simultaneously present. However, in contrast to the this, Vogelsang *et al.* (2006) showed that biomass in microcosms inoculated with a mixture of six AM fungi was comparable with the biomass in the treatment with the best single mycorrhizal fungus, pointing to the importance of species identity rather than diversity per se. Thus, there are alternative explanations and supportive studies to explain effects of mycorrhizal diversity, and additional experiments are required to solve this issue.

It is still unclear whether bacterial diversity promotes plant diversity or ecosystem functioning. Several legumes form host specific associations with N-fixing rhizobia bacteria (Sprent 2001; Van der Heijden *et al.* 2006a). This suggests that the presence of a diverse rhizobial community is required to enhance legume diversity. Moreover, endophytic and root-associated bacteria might stimulate plant diversity if different bacteria promote growth of different host plants.

A number of studies have examined how microbial communities that vary in composition and diversity influence the decomposition of plant material, and hence the liberation of nutrients for plant growth. Some of these studies found that microbial diversity enhanced decomposition while others found no effect, negative effects, or observed that specific microbial species, and not diversity *per se*, determined decomposition (reviewed by Hattenschwiler *et al.* 2005). For instance, a study by Bonkowski & Roy (2005) showed that microbial diversity (measured as functional diversity) enhanced decomposition and nitrogen leaching from grassland microcosms. Moreover, diversity effects appear to be strongest at the species poor end of diversity gradients when only few microbes are present (e.g. Setala & McLean 2004; Wertz *et al.* 2006). It also appears that there is considerable functional redundancy among decomposing microbes (Hattenschwiler *et al.* 2005) and many microbes have similar effects on decomposition. However, some studies only mention initial differences in microbial composition and it is likely that microbial treatments have changed during the experiment, making it difficult to make firm conclusions.

There are a number of mechanisms by which microbial diversity might enhance decomposition, and hence the provision of nutrients for plant productivity. Some biochemical reactions require specific conditions, are incompatible, or are performed by specialised microbes with unique physiological properties (e.g. lignin degradation by specialised fungi – De Boer *et al.* 2005). Hence, division of metabolic labour, or compartmentalization, might be necessary to perform specific reactions during decomposition. For instance, a recent study by Lindahl *et al.* (2007) showed that litter decomposition by fungi is spatially separated and performed by two distinct groups of fungi that inhabit different parts of the soil horizon. Saprotrophic fungi are confined to the surface layer decomposing freshly fallen litter and they are mainly responsible for the mineralization of carbon. Mycorrhizal fungi, in contrast, dominate the underlying soil horizons and are specialized on more decomposed litter and humus, most likely mobilizing nitrogen and delivering it to their host plants. Moreover, the chemical composition of litter from different plant species is variable and different microbes might be needed to decompose the various litter types. Furthermore, fungal hyphae can act as vectors for bacterial transport, enabling bacteria to colonize new substrate faster (Kohlmeier *et al.* 2005). This so-called 'fungal highway' could facilitate decomposition by bacteria, especially under dry conditions when bacteria could use hyphal biofilms for dispersal and colonization of new substrate (Perotto & Bonfante 1997). Hence, these observations point to the importance of microbial diversity for decomposition, but more studies are needed to better understand the mechanisms involved.

Microbial diversity can also promote plant diversity and productivity when microbes associate with different plant species or when different microbes provide different resources. For instance, AM fungi and rhizobia can act synergistically and stimulate plant productivity by supplying different limiting nutrients to the plant (e.g. N by rhizobia and P by AM fungi). Many legumes benefit from this

principle as they form tri-partite symbiotic associations with AM fungi and rhizobia thus, profiting from the distinct characteristics of both symbionts (Pacovsky *et al.* 1986). AM fungi have even been found to colonize root nodules (plant organs designed for N-fixation by rhizobia) of several legumes pointing to direct plant–AM fungi–rhizobia interactions (Scheublin *et al.* 2004).

Recent work has shown that microbial diversity in soil ecosystems is reduced because of land-use intensification and increased nutrient availability (e.g. Helgason *et al.* 1998; Fig. 2), nitrogen deposition (e.g. Lilleskov *et al.* 2002), and chemical contamination (Gans *et al.* 2005). The impact of this reduced diversity on plant diversity and productivity is unclear. We hypothesize that significance of microbes is highest at low nutrient availability (Fig. 2) and we expect that nutrient poor ecosystems are more vulnerable to reductions in microbial diversity and losses of specific microbial species or functional groups. These expectations are based on several observations. First, plant productivity in nutrient poor ecosystems is often enhanced by a range of microbial symbionts that acquire various limiting nutrients (see Impact of soil microbes on plant productivity for references). Several of these symbionts have a restricted host range (e.g. several rhizobia and some mycorrhizal fungi) and a reduction in microbial diversity could reduce growth of plant species that depend on specific microbial symbionts. For instance, Jonsson *et al.* (2001) observed that effects of fungal diversity were strongest at low nutrient availability, perhaps because different mycorrhizal fungi obtained limiting nutrients from different sources in the soil. In contrast, plants are often less dependent on mycorrhizal fungi and N-fixing bacteria when nutrient availability is high (e.g. Smith & Read 1997; Sprent 2001). Second, nutrient poor ecosystems are especially vulnerable to nutrient loss (e.g. because of microbial denitrification or leaching) because plant productivity is limited by nutrients in these ecosystems (Chapin 1980). Thus, small nutrient losses will immediately lead to a reduction of plant productivity in nutrient poor ecosystems. Third, chemical diversity in nutrient poor ecosystems is often high because such ecosystems are usually species rich, containing many different plant species that produce a wide range of secondary metabolites and recalcitrant defence compounds, including lignin and tannins (Lambers & Poorter 1992). It is likely that a wide range of physiological diverse microbes contributes to the break down of plant litter in nutrient poor ecosystems. Hence, these observations indicate that microbes and microbial diversity are likely to have the biggest impact on ecosystem performance in nutrient poor ecosystems. Following this, we hypothesize that the relationship between microbial diversity and ecosystem functioning is different for nutrient poor and nutrient rich ecosystems. We expect that microbial communities from nutrient rich ecosystems are functionally more redundant compared with microbial communities from nutrient poor ecosystems where microbes need specific adaptations to obtain resources [e.g. during decomposition or when forming (host specific) symbiotic associations with plants].

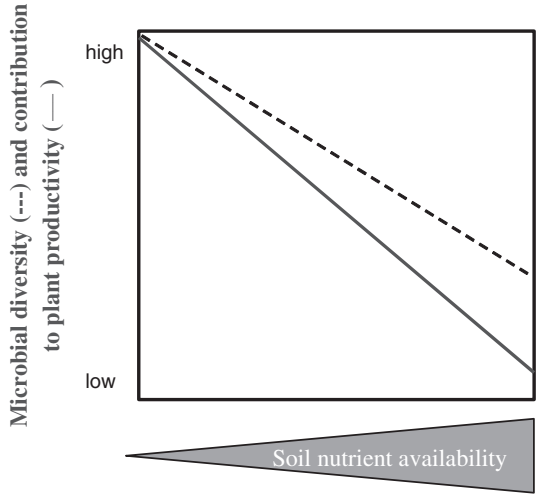

Figure 2 Hypothetical relationship between nutrient availability and the microbial contribution to plant productivity. Microbes are hypothesized to be most important for the productivity of nutrient poor ecosystems. It is also hypothesized that microbial diversity (– – –) is negatively correlated with nutrient availability.

Effects of increasing microbial diversity on plant productivity probably also depend on the number of functional groups that are present. Adding increasing numbers of species from a particular functional group (within functional group diversity) will probably add some degree of functional diversity and have slight effects on ecosystem functioning. However, adding different functional groups (between functional group diversity) or specific keystone species will probably have a bigger impact on plant productivity and particular ecosystem processes (Hooper *et al.* 2002). For instance, AM fungi, N-fixing bacteria and fungal decomposers all have different functions in ecosystems, and the absence of one group may have a big impact on plant productivity. The level of functional diversity may also be related to the phylogenetic relatedness among soil microbes. Microbial communities with diverse lineages may have a bigger impact on ecosystem processes because they are functionally more diverse, as was recently shown for AM fungi by Maherali & Klironomos (2007). Interestingly, despite the high level of bacterial species diversity found in soil, they have a lower phylogenetic diversity than other environments (Lozupone & Knight 2007), perhaps suggesting that soils contain a large number of microbial species with similar functions. Future work should address this issue, also focusing on the diversity of functional genes that

affect particular ecosystem processes (see Conclusions and perspectives).

The question of whether microbial diversity is important to ecosystem functioning is interlinked with questions about the distribution of microbes and whether microbial diversity varies between ecosystems. Earlier work suggested that most microbes have a cosmopolitan distribution (Finlay & Clarke 1999). However, recent studies have shown that many microbes have restricted biogeographic distributions (e.g. Peay *et al.* 2007) suggesting that variations in the composition of microbial communities can impact ecosystem functioning. Also, little is known about factors that regulate microbial diversity at different temporal and spatial scales (Green & Bohannan 2006) and its interdependency with plant diversity (Zak *et al.* 2003); this is an area that needs much more attention, especially if microbial ecologists want to predict how microbial communities influence ecosystem functioning.

Bacterial and fungal dominated soil ecosystems

So far, we have focussed on the significance of microbial diversity and the importance of specific groups of soil microbes for ecosystem functioning. However, one biological property of soil that receives a large amount of attention is the relative abundance of bacteria and fungi in ecosystems, and associated changes in the faunal component of the soil food web. Bacteria and fungi often have very distinct functions, and ecosystems are often characterized by having fungal-dominated or bacteria dominated microbial communities and food webs, or combinations of both (Wardle *et al.* 2004b). Ecosystems with bacterial dominated microbial communities are characterized by high levels of disturbance, have a high nutrient availability, a neutral or mildly acidic pH, and often have reduced soil organic matter content, because of elevated biological activity (Table 2). In contrast, fungal dominated microbial communities occur in less disturbed, late successional sites, often with acid soils that are of high organic matter content and low resource quality (Table 2). Moreover, these types of soil communities are interchangeable: bacteria-dominated communities can change to fungal dominated communities, for example during primary succession (Bardgett *et al.* 2005) and following land abandonment (Zeller *et al.* 2001), whereas fungal dominated communities can shift to bacteria-dominated communities as a result of nutrient enrichment and intensive farming (e.g. De Vries *et al.* 2006).

Table 2 Suggested characteristics of fungal and bacterial dominated soil food webs

Fungal dominated food web	Bacterial dominated food web
Closed nutrient cycles (internal cycling)	Open nutrient cycling (nutrient addition and loss)
Slow cycling of nutrients	Fast cycling of nutrients
Low nutrient availability	High nutrient availability
Slow growing plant species	Fast growing plant species
Low net primary productivity	High net primary productivity
Low leaf litter quality	High leaf litter quality
Low resource quality	High resource quality
Developed soils	Undeveloped soils
Rich in organic matter	Poor in organic matter
Late succession	Early succession

Little is know about the functional significance for plant community dynamics of shifts between fungal and bacteria-dominated microbial communities and food webs. One general idea is that bacteria-dominated food webs enhance rates of nutrient mineralization and the availability of nutrients to plants, whereas fungal-dominated food webs promote 'slow' and highly conservative cycling of nutrients (Wardle *et al.* 2004b). This idea is supported by a number of studies that show shifts from fungal towards bacteria-dominated microbial communities to be associated with enhanced rates of nutrient cycling, and *vice versa*. For example, Bardgett *et al.* (2006) showed that the presence of the hemiparasite *Rhinanthus minor* in grassland lead to increased plant diversity and a shift in the composition of the microbial community towards increasing dominance of bacteria, which was associated with a significant increase in rates of nitrogen cycling in soil. Conversely, Wardle *et al.* (2004a) studied a series of long-term chronosequences (i.e. for 6000 to over 4 million years) where a decline in standing plant biomass over time occurred. This decline was associated with increasing substrate P limitation for microbes, which was paralleled with a shift in the composition of microbial communities towards fungal dominance. Together, these changes resulted in reduced rates of litter decomposition and mineralization of nutrients, setting a negative feedback in motion, which further intensified nutrient limitation leading to ecosystem decline.

Such feedback mechanisms between plants and soil communities also operate at the individual plant level. One suggestion is that specific plant species might select for bacteria or fungal dominated food webs which creates a feedback on the dominance and persistence of the same species within the plant community (Wardle 2002). For instance, fast-growing species produce large amounts of high-quality (i.e. N-rich) litter and root exudates, which promote 'fast cycling' bacteria-dominated food webs, leading to enhanced decomposition and nutrient cycling which further enforce the dominance of fast growing species within the community. In contrast, slow-growers produce low-quality, phenolic-rich litter which favours fungal-dominated food webs that are typically associated with low rates of nutrient cycling, hence further favouring the dominance of slow-growing species that are adapted to low nutrient availability.

This framework suggests a form of mutualism between plants and their associated microbial community that is related to soil fertility. While these ideas have been discussed extensively in the literature they have not yet been tested experimentally and the mechanisms involved are unknown; this represents a major challenge for the future.

CONCLUSIONS AND PERSPECTIVES

In this review, we have shown that soil microbes play key roles in ecosystems: they drive major biogeochemical processes and contribute to the maintenance of plant productivity and species richness on Earth. Soil microbes regulate plant productivity via a variety of mechanisms. Positive effects of microbes on plant productivity are most common in nutrient poor ecosystems where they enhance the supply of growth limiting nutrients such as N and P to plants. In such situations, up to 90% of P and N is provided by mycorrhizal fungi and N-fixing bacteria, pointing to their importance in regulating plant productivity. Negative effects of soil microbes on plant productivity can also occur when they act as pathogens, compete with plants for nutrients, or transform nutrients into forms that are inaccessible to plants. Several groups of soil microbes also regulate plant diversity by altering competitive interactions or promoting growth of specific plant functional groups. Of particular importance are plant pathogens, which cause negative feedback thereby promoting plant species co-existence, and microbial symbionts, which associate with over 20 000 plant species that are completely dependent upon them for growth and survival. Recent studies point to the importance of microbial diversity because different microbes perform different functions in ecosystems, contributing to decomposition, by associating with different plant species, and facilitating plant productivity by supplying different limiting nutrients.

To better understand how microbial communities influence plant diversity and productivity, several key questions still need to be answered. First, understanding how changes in microbial diversity and composition influence vegetation productivity and plant community dynamics is a major challenge for the future. Answering this question, however, is complicated and will require the development of experimental systems in which it is possible to manipulate microbial diversity without influencing other factors and contamination from the outside. Second, recent studies show that human induced global changes (e.g. altered land use, climate change and nitrogen deposition) sometimes have a large impact on microbial diversity and community structure. It is important to understand whether and how such changes in microbial communities might feedback to influence changes in plant diversity and plant productivity. Third, the impact of relatively unexplored but common functional groups of soil microbes, such as free-living N-fixers, root-associated bacteria and fungi, on plant productivity and community dynamics is poorly understood. For example, a recently discovered soil fungus that belongs to the *Sebacinales* (Verma *et al.* 1998) was shown to stimulate plant productivity (Waller *et al.* 2005), acting like a mycorrhizal fungus. This fungus could change plant community structure considerably if the growth of specific plant species is stimulated. Fourth, an important problem in microbial ecology is the fact that many microbes cannot be cultured. Estimates suggest that < 5% of all soil bacteria and Archaea (e.g. Curtis *et al.* 2002; Van Straalen & Roelofs 2006) and < 5% of all soil fungi (Hawksworth 2001) have been brought into culture. The function of these non-culturable microbes in ecosystems is poorly understood, because it is difficult to test how these microbes respond to, or modify, their environment. A few examples show that many discoveries still await us. For instance, the impact of microbes on the N cycle has drastically changed over the last few years. Only recently was been discovered that Archaea are likely to be largely responsible for nitrification in a wide range of terrestrial ecosystems (Leininger *et al.* 2006). Moreover, until recently it was thought that legumes form N-fixing associations with members of the Rhizobiaceae (belonging to the α-Proteobacteria). However, recent work has shown that members of *ß-Proteobacteria*, including *Ralstonia* and *Burkholderia*, can also nodulate legumes (Elliott *et al.* 2007), showing that the symbiosis between bacteria and legumes is more diverse than previously anticipated. Many members of well known microbial taxa also still await discovery. For instance, molecular techniques have shown that *c.* 60% of environmental sequences of arbuscular mycorrhizal (AM) fungi do not match with AM fungi that have been brought into culture (Fig. 3). Those AM fungi

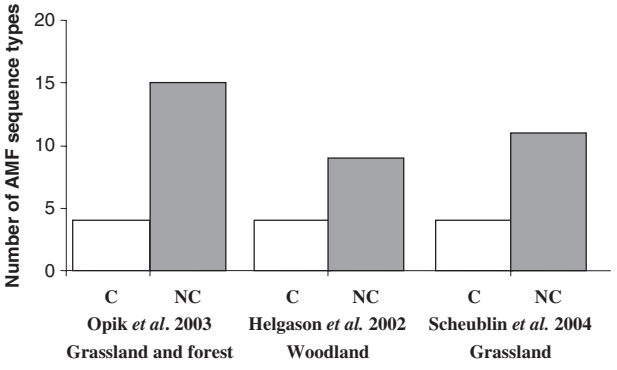

Figure 3 Estimated frequency of cultivated and uncultivated arbuscular mycorrhizal fungi in several ecosystems. White and grey columns represent sequences, respectively of cultivated and uncultivated AMF types in three different studies where the composition of mycorrhizal fungal communities in plant roots was investigated.

that are easily cultured often have a ruderal lifestyle (e.g. *Glomus intraradices* and *Glomus mosseae*) and a global distribution (Opik *et al.* 2006). A recent study indicated that these generalist and easily cultured AM fungi are also more resistant to soil perturbation, while specialist AM fungi (several of them still uncultured) declined (Helgason *et al.* 2007). An intriguing question, and challenge for the future, is to test in which way such uncultured and specialist AM fungi contribute to plant diversity and productivity in natural communities. Hence, it will be extremely important to cultivate the non-culturable and assess their ecological role. Fifth, in recent years ecologists have started to investigate patterns of microbial diversity and the forces that govern them (Horner-Devine *et al.* 2004; Green & Bohannan 2006). Until now most of these studies have focused on the diversity of ribosomal gene sequences. However, microbes with the same ribosomal gene sequences are often functionally diverse. Thus, to link microbial diversity to ecosystem function it is necessary to focus on functional traits and functional genes that are important for biogeochemical processes. Ecological genomics (Van Straalen & Roelofs 2006) and the use of micro-arrays to detect key genes responsible for important ecosystem processes (e.g. nitrogen fixation; denitrification; decomposition; phosphorus acquisition) are essential in this respect (e.g. see He *et al.* 2007 for the description of such a micro-array). These tools will allow us to identify factors that regulate microbial functional gene diversity in soil and provide insights into its importance for plant community dynamics in terrestrial ecosystems.

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