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Darkness visible: reflections on underground ecology

A. H. FITTER
Department of Biology, University of York, York YO10 5YW, UK

Summary

1 Soil science and ecology have developed independently, making it difficult for ecologists to contribute to urgent current debates on the destruction of the global soil resource and its key role in the global carbon cycle. Soils are believed to be exceptionally biodiverse parts of ecosystems, a view confirmed by recent data from the UK Soil Biodiversity Programme at Sourhope, Scotland, where high diversity was a characteristic of small organisms, but not of larger ones. Explaining this difference requires knowledge that we currently lack about the basic biology and biogeography of micro-organisms.

2 It seems inherently plausible that the high levels of biological diversity in soil play some part in determining the ability of soils to undertake ecosystem-level processes, such as carbon and mineral cycling. However, we lack conceptual models to address this issue, and debate about the role of biodiversity in ecosystem processes has centred around the concept of functional redundancy, and has consequently been largely semantic. More precise construction of our experimental questions is needed to advance understanding.

3 These issues are well illustrated by the fungi that form arbuscular mycorrhizas, the Glomeromycota. This ancient symbiosis of plants and fungi is responsible for phosphate uptake in most land plants, and the phylum is generally held to be species-poor and non-specific, with most members readily colonizing any plant species. Molecular techniques have shown both those assumptions to be unsafe, raising questions about what factors have promoted diversification in these fungi. One source of this genetic diversity may be functional diversity.

4 Specificity of the mycorrhizal interaction between plants and fungi would have important ecosystem consequences. One example would be in the control of invasiveness in introduced plant species: surprisingly, naturalized plant species in Britain are disproportionately from mycorrhizal families, suggesting that these fungi may play a role in assisting invasion.

5 What emerges from an attempt to relate biodiversity and ecosystem processes in soil is our extraordinary ignorance about the organisms involved. There are fundamental questions that are now answerable with new techniques and sufficient will, such as how biodiverse are natural soils? Do microbes have biogeography? Are there rare or even endangered microbes?

Key-words: biodiversity, soil, mycorrhizas, global change, invasive species

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Soil, science and civilization

All sciences are influenced by their own history. The founders of ecology were either botanists such as Arthur Tansley, Frederick Clements and Henry Gleason, principally interested in community ecology and patterns of vegetation, or zoologists such as Charles Elton, whose focus was on the behaviour of animal populations. All of them worked on terrestrial or freshwater systems. Marine biology had already developed its own body of concept and practice by the time ecology became an identifiable science; hence, marine ecology is typically the province of oceanographers rather than ecologists. A similar narrative applies to soil science.

Correspondence: Alastair Fitter (e-mail ahf1@york.ac.uk)

Vasiliy Dokuchaev in Russia and Hans Jenny in America, two of the founders of the discipline, would not have regarded themselves as ecologists, but as geomorphologists or agronomists. The subsequent development of soil science and ecology as separate disciplines has not been to either's advantage.

Virtually all terrestrial ecosystems are founded on soil. Plants rely on it for water and nutrients, as consequently does everything else in the ecosystem, including us. Yet our species' blithe disregard for soil is evidence of our reluctance to understand its fundamental role in our welfare. Edward Hyams was one of the first to highlight this blind spot in his classic book *Soil and Civilization* (Hyams 1952), a work that should be required reading for all ecologists. He charted the links between the longevity of civilizations and their good fortune in being founded either on soils that were annually renewed by winter flooding and silting (Nile, Ganges, Yellow River), or on soils that were young (because of recent glaciation) and in climatic zones that enabled them to generate new soil at a rate to match our destructive power (much of western Europe). These soils are resilient to damage. Others are much less so. Many of the great ecological disasters in history occurred when inappropriate farming techniques were applied to fragile soils, a well known example being the dust-bowl of the American mid-west that inspired John Steinbeck's classic novel *The Grapes of Wrath* (Steinbeck 1939).

Soil as a resource

Our appetite for destroying soil continues. About 10% of the earth's land area is currently under cultivation (as opposed to grazing management), and this figure could only be increased at great environmental cost. Assuming a bulk density of 1.6 t m^{-3} and a soil depth of 1 m, the estimated stock of soil on these 14 million km^2 is perhaps 22 000 Gt, and that is declining due to soil erosion (by wind and water), urbanization and salinization, at a rate much greater than the slow processes of soil formation can possibly counter. Estimating the rate of decline due to erosion is very difficult, because of wide variations in erosion rates across the globe and unresolved discrepancies amongst the available models (Nearing *et al*. 2000; Parsons *et al*. 2004). A mean figure of 0.38 mm $year^{-1}$ has been suggested as the present global soil erosion potential (Yang *et al*. 2003). On the same assumptions for cultivated land, 1 mm of soil is equivalent to 22 Gt of soil; the current loss rate would therefore yield a mass loss rate of *c.* 8 Gt $year^{-1}$. Both higher and lower figures have been proposed; what is certain is that rates are far greater in some regions, notably Southeast Asia, than in others.

The historic loss of soil carbon due to agriculture globally is put at 78 ± 12 Gt of soil carbon (Lal *et al*. 2004); if that were all due to soil loss rather than decomposition of organic carbon, it would represent as much as 20–30 times that mass of soil, but the true figure will be much lower (Barrett 2001). An upper limit of soil loss estimates therefore might be that we have already have lost the equivalent of 10 cm of cultivated soil globally, to which we must add the 5% of cultivated land degraded by salinization (Metternicht & Zinck 2003) and the 2% of total land area (mostly cultivatable) lost to urbanization (Svirejeva-Hopkins *et al.* 2004).

Soil plays a major role in the global carbon cycle. The well-known diagrams of the cycle (Fig. 1) demonstrate that soils contain the largest pool of fixed C within the active cycle: there is estimated to be three times as much organic C in soils as in vegetation, twice as much as in the atmosphere and 50% more than in the surface ocean, and those figures omit soil inorganic carbon, which accounts for 40% of soil C world-wide. Around half of the organic C is stored in deep peats in northern latitudes (Post *et al*. 1982), but all but the most degraded or arid soils contain significant amounts of C as organic matter (Zinke *et al*. 1998); indeed, the presence of an organic component is a defining feature of soil. Although the figures for total C stores are now probably quite accurate, we have only poor information on the rates of transfer among the stores and, especially, on the sensitivity of those rates to environmental factors. The well-known 'missing sink' problem is simply that we do not know where in the global set of soils the carbon that is not accumulating in the atmosphere as CO_2 or dissolving in the oceans is going (Grace 2004). Those latter pools are relatively well-mixed and so it is quite feasible to estimate the global fluxes from sufficient point measurements; soils, in contrast, are highly heterogeneous and such extrapolation is almost impossible.

One of the more alarming aspects of the current environmental crisis is the likelihood that soils will cease to be a sink for CO_2 at some time in the near future and become a source; indeed this appears already to be true of some soils (Oechel *et al*. 1997). For some years we have been partially protected from the consequences of our collective idiocy – in pouring CO_2 into the atmosphere faster than global systems can remove it – by the fact that soils have been absorbing somewhere between 2 and 4 Gt C $year^{-1}$ (Schimel *et al*. 2001; Grace 2004). That will not continue, both because there are physical limits to C storage in soils and, more importantly, because as climate warms, decomposition of the soil C stores will increase (Turetsky *et al.* 2002). Remarkably, we cannot predict the temperature sensitivity of this heterotrophic respiration, which is currently the single largest uncertainty in the global C cycle (Lloyd & Taylor 1994; Giardina & Ryan 2000; Fang *et al.* 2005). The problem is not easily amenable to experimental investigation: studies at small scales are confounded by the complexity of the pathways for C transformation in soil and by the fact that the soil C pool can be viewed as comprising a series of subpools with very different potential turnover rates, from days (microbes and fungi, and some roots) to years, decades or even millennia (corresponding to the different elements of the organic matter pool; see Pendall *et al*. 2004).

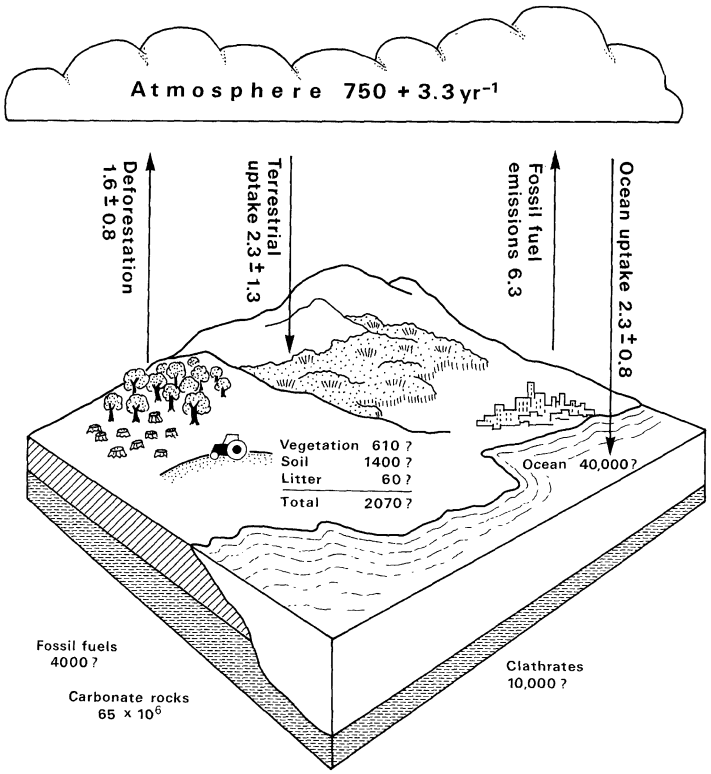

Fig. 1 Schematic illustrating major pools and fluxes in the global carbon cycle. From Grace (2004), with permission.

Biodiversity in soil

Why is any of this important to an ecologist? Soils contain more uncharacterized biodiversity than any of the rest of the terrestrial biosphere and it is partly that diversity that renders their behaviour so difficult to predict. Prokaryotes, in particular, have exceptional diversity in soils, although quantifying it is currently problematic thanks to a failure to devise a satisfactory conceptual framework for defining taxonomic units in such organisms. Our data on bacterial diversity in soils are based on assumptions about the degree of nucleic acid sequence similarity that can differentiate taxa, on the sequencing of particular regions of the genome (most commonly 16S rDNA) and on statistical estimators that can be used to extrapolate from the inevitably small samples that have been examined in depth by molecular ecologists. Estimates of the total number of bacterial 'species' range upwards from 0.5×10^6; in the soils at the Sourhope experimental farm, Scotland, that hosted both the UK Soil Biodiversity Programme (Fitter *et al*. 2005) and the Scottish Micronet project, the estimated diversity at the site, based on 16S rDNA, was 500–5000 species (McCaig *et al.* 2001). More generally, Torsvik *et al*. (1990, 2002) have suggested that typical soils may contain 10^4 species g^{-1}, at least half (and perhaps as many as 95%) of which are likely to be unculturable by current techniques (Sait *et al*. 2002; Joseph *et al*. 2003).

As yet, we have no systematic studies available that will allow us to make clear statements about either local (α) or global (γ) diversity of soil organisms. Probably the most detailed study was the UK Soil Biodiversity Programme. For example, Finlay & Fenchel (2001) found 365 species of protozoa in the Sourhope soils, representing one-third of the global total. For this group then, α diversity appears to be high and γ diversity low, a result found repeatedly in samples from lakes and other systems (Finlay *et al*. 2001). In contrast, nematode diversity at Sourhope apparently exceeded the total number of species known from the UK: using molecular techniques, Floyd *et al*. (2002) identified 140 species of nematode from the Sourhope soils, but estimated that the total would have exceeded 400 had more intensive sampling been done. The most species-rich (for nematodes) site previously studied in the UK had 154 species of nematode (Hodda & Wanless 1994); this site was on chalk grassland at Porton Down, a vegetation type that is rich in plant species and contrasts markedly with the species-poor vegetation at Sourhope. Since the total UK list has only 369 terrestrial and freshwater species (http://nbn.nhm.ac.uk/nhm/bin/nbntaxa.dll/), it is clear that previous assessments based on morphology have greatly under-estimated nematode diversity. For this group, then, we can expect both α and γ diversity to be high.

Is Sourhope then an exceptionally rich soil ecosystem? That seems unlikely: it was deliberately chosen to be biologically dull, a few hectares of semi-improved, acid, temperate, upland grassland on the slopes of the Cheviot Hills on the border between Scotland and England, with around 50 species of plant (including mosses) and no unusual species. The diversity in its soil therefore raises the question: do all soils have high α

diversity? And, if the protozoa result were general, is the global richness (γ diversity) of soil taxa low, relative to α diversity? These questions have a long pedigree, back to Beijerinck (1913), who famously declared 'everything is everywhere, the environment selects'. If that is right, and the protozoa model applies to other taxa, then microbes have no biogeography. For that to be true, it follows that dispersal is a much more rapid process than speciation. Since we have no data on the number of species, let alone rates of speciation, in most microbial groups, it is of course impossible to determine whether that is so, but it seems likely that dispersal is a much more rapid process for aquatic organisms than for those in soil, where movement within the solid medium is very restricted. The most likely large-scale dispersal agent for soil organisms is wind; certainly some soil organisms, such as fungal spores (Moyersoen *et al.* 2003) and collembola (Dunger *et al.* 2002), can be blown great distances. However, wind dispersal will inevitably be most important for organisms that are active in the surface few mm of soil, and the spatial patchiness that characterizes the distribution of many soil organisms suggests that dispersal may often be very limited (Ettema *et al.* 2000; Tixier *et al.* 2000). In other words, although we might expect some taxa to have global distributions, others will be much more localized.

On the other hand, the larger taxa at Sourhope – collembola, mites, earthworms, basidiomycete fungi – were not especially rich: the exceptional diversity in soils may be confined to the smallest organisms. This pattern may also reflect the physical nature of soil: as a solid medium, it displays extreme heterogeneity at a range of temporal and spatial scales, with closely adjacent patches having quite distinct characteristics (Jackson & Caldwell 1993; Fitter 1994; Ettema & Wardle 2002). One consequence is that there is the potential for many taxa to coexist in soil, exploiting different spatial locations with varying effectiveness, or reacting to temporal heterogeneity on distinct time-scales; another is that the structure of soil is fractal, and in fractal systems there is fundamentally more space available to smaller organisms (Morse *et al*. 1985). That heterogeneity is likely to be the key to understanding soil biodiversity is emphasized by the very different picture that emerges from studies of marine nematodes, where early expectations that the taxon would prove to be hyperdiverse are now being scaled back (Lambshead & Boucher 2003). There is a good theoretical basis for expecting diversity to be high in systems where populations are aggregated, irrespective of whether they partition resources (Kouki & Hanski 1995; Harley & Shorrocks 2002), although the models have not previously been applied to soil ecosystems.

If we could resolve some of these fundamental questions in microbial ecology – such as what is a microbial species, and do microbes have biogeography? – we could begin to tackle others which as yet have little meaning except in a few extreme environments, such as Yellowstone National Park (USA), where the uniqueness of the microbial communities is demonstrable and their economic importance well known (Varley & Scott 1998). For any other group of organisms, these questions would be of active concern to conservation biologists: for example, we do not know whether there are such things as rare microbial species. It has been suggested that population sizes of all microbes will be large (at least locally), because of their ability to generate new cells rapidly (Horner-Devine *et al.* 2004); if that is true, then microbes are different from other types of organisms for which a log-normal or similar distribution of abundance against frequency typically applies, as indeed suggested by the analyses of Mulder *et al*. (2005). If it is not true, and we do know that not all microbes have very short generation times, then it follows from our knowledge of the rates of soil degradation that there must be some endangered species of microbe, maybe even extinct species. At present, lists of known extinctions include no microbes (the smallpox virus being a possible exception), but it seems unlikely that their absence reflects anything beyond our ignorance.

An urgent need therefore is to begin to understand some of this basic ecology for microbes, things that we take for granted when studying other types of organisms. The population dynamics of microbes are well known in cultured systems, but simply unknown beyond those. We do know that turnover times of microbial populations in soils can be exceptionally slow: in the Broadbalk experimental soils at Rothamsted, UK, they were estimated at 2.5 years (Brookes *et al*. 1985), but this almost certainly shows that the bulk of the population at any one time is in resting stages or dormant. What we need to understand is how microbial populations react to briefly and locally available pulses of nutrients, which is how resources manifest themselves in soil (Fitter 1994). Remarkably, the best known model used in soil biology (Hunt *et al*. 1987) assumes constant population sizes. The Hunt *et al*. model has been used successfully to reflect trophic relationships among functional groups in soil and to follow a pulse of applied $^{13}CO_2$ through the soil ecosystem (J.W. Pitchford, unpublished data). A recent parameterization of the model to allow Lotka–Volterra dynamics of the populations resulted in importantly different patterns of appearance of a ^{13}C signal in consumers than was predicted by the standard model (J.W. Pitchford, unpublished data). However, any realistic models of the population dynamics and structure of soil communities will have to move beyond the linear presentations of such models. The heterogeneity of soil means that metapopulation ideas are necessary, or even metacommunity or metaecosystem approaches (Wilson 1992; Ozinga *et al*. 2004).

Does biodiversity matter?

The arguments in favour of biodiversity conservation are well known; here I wish to ask whether there is

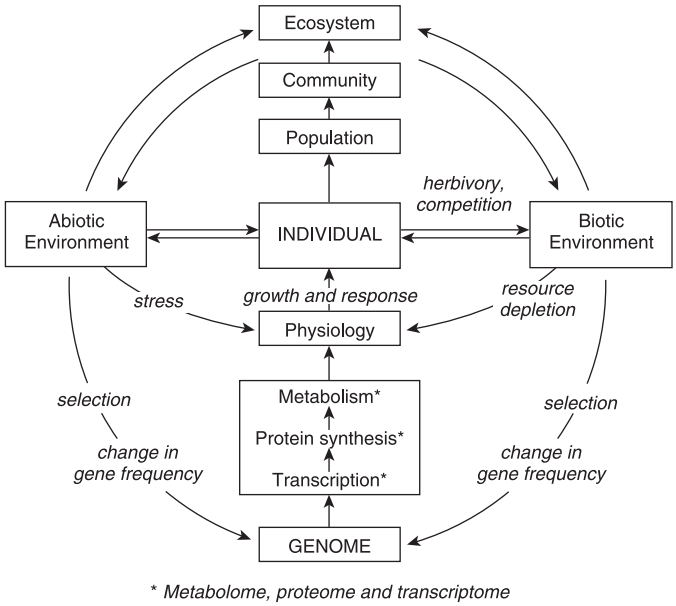

Fig. 2 The ecological hierarchy. From Fitter & Hay (2002).

evidence that species-rich systems, especially in soil, have distinct properties that determine their ability to process materials, such as organic carbon compounds. Ecologists frequently refer to the hierarchy of levels of organization that characterizes their subject (Fig. 2). It is a tenet of ecology that populations can be viewed as groups of interacting individuals, communities as sets of interacting populations, and ecosystems as those communities in their interaction with the abiotic environment. Higher levels of organization (landscape, biome, biosphere) can be added to this hierarchy, but the basic plan of individual-population-community-ecosystem describes much of the subject of ecology. However, although population biologists recognize the importance of individual-level behaviour in understanding population phenomena, and similarly community ecologists often use population dynamic models in explaining community structure, ecosystem ecologists do not routinely use community-based models. Indeed ecosystem ecology has developed almost as a separate discipline from the rest of ecology. Where ecosystem ecology does call on other strands of the discipline, it usually employs physiological ecology, because explaining environmental impacts on ecosystem processes (for example, the effect of temperature on heterotrophic respiration) requires the mechanistic approach of the physiological ecologist.

This dichotomy has left us poorly equipped to understand what linkages exist between biodiversity – which is a function of population and community ecology – and ecosystem processes. We have few conceptual models that will allow us to understand how signals are propagated through the ecological hierarchy: if the conditions at the population level are changed (e.g. by changes in the relative abundance of species, or in their presence), will that result in a change in a process at the ecosystem level (e.g. carbon mineralization, denitrification)? The debate has largely been framed in terms of functional redundancy, a concept derived from genetics that proposes that, in species-rich ecosystems, more than one species can perform a given function. Wohl *et al.* (2004), for example, define functional redundancy as 'multiple species, while biologically unique, contributing with similar intensity to the same process within an ecosystem'. However, a debate framed in these terms is largely semantic. The only way to test the concept is by measuring the contribution of different species (or functional groups of species) to a process, which in turn defines a function as something that can be performed by a defined species or group of species. Assuming that we can recognize and identify species, let us suppose that we find two types of bacterium in a soil to be capable of degrading a pesticide, and that we have some way of manipulating the soil to alter the relative abundance of these types. If the consequence of reducing one type is to reduce the rate of pesticide degradation, we deduce that there is no functional redundancy and that both types are needed for the maximum rate of the process. In contrast, if the process is unaffected by loss of one type, then we will claim to have discovered functional redundancy. We must then ask why both types persist in the normal soil: the answer is likely to be that they have different controlling factors on their populations. Perhaps one is better able to cope with drought. It follows therefore that there is no functional redundancy, since under dry soil conditions (and we probably made the original test in moist soil), loss of this type would reduce the process rate. Ultimately, the question of functional redundancy reduces to one with which all ecologists are familiar: what determines the ability of numerous species with similar ecological 'functions' (be they finches, dragonflies, grasses, bracket fungi or whatever) to coexist in a single community. The concept of functional redundancy is therefore itself redundant.

Whether there is a relationship between the number of species or functional groups in a community and processes at the ecosystem level remains a key question in ecology. If we are to come up with useful answers, we must ensure that we convert the question into hypotheses that can be tested experimentally. A prerequisite is to define our terms carefully; what, for example, do we mean by an ecosystem process? It is tempting to identify the high-level phenomena such as primary productivity (which incidentally are also often the easiest to measure) and seek to link those to measures of diversity. However, we must be cautious about the length of the chain of inference that we generate. If it is productivity we are interested in, we can legitimately ask questions about green plant diversity, but whether we are wise to do the same with the associates of those plants (herbivores, symbionts) or with secondarily linked taxa (such as many soil organisms) is more doubtful.

A case study: the Glomeromycota

I want to illustrate these ideas by considering a single group of organisms, the Glomeromycota, a phylum within the Fungi whose members all form mycorrhizal symbioses with plant roots. These fungi are obligate symbionts: we cannot yet grow them other than in culture with roots and in the wild that is how they always occur. Typically, they form characteristic structures ('arbuscules') inside roots (Fig. 3), hence the name for the symbiosis as a whole – arbuscular mycorrhiza. The arbuscule is a finely branched hyphal structure that develops within the cell wall of a root cortical cell and invaginates the plasmalemma of the cell, creating a massive surface area of membrane–membrane contact between plant and fungus. Almost certainly, phosphate ions move from fungus to plant across this membrane interface, while the fungus receives fixed carbon from the plant, either at this same interface or in the apoplasts where the fungal hyphae grow between the cortical cells (Smith *et al.* 2001). This exchange of C for P is fundamental to the symbiosis and has probably been so for 400 million years.

When plants first colonized the land, the most serious problem they faced was likely to have been acquiring phosphate rather than water, since they probably started in wet microhabitats. Phosphate ions are very poorly mobile in soils because they form insoluble compounds with most of the dominant cations in soils – Al^{3+}, Fe^{3+} and Ca^{2+}. Hence absorbing structures in soil rapidly become surrounded by a depletion zone and uptake is then strongly limited by the rate of diffusion. The earliest land plants, such as *Aglaophyton*, had no roots and relied for nutrient uptake on little-branched rhizomes, which would have been quite inadequate for P uptake. Remarkably, the Devonian fossils of these plants have clear arbuscules in their rhizomes (Fig. 3). That evidence, taken with the molecular clock evidence that places the origin of the Glomeromycota at between 400 and 500 million years ago (Simon *et al*.

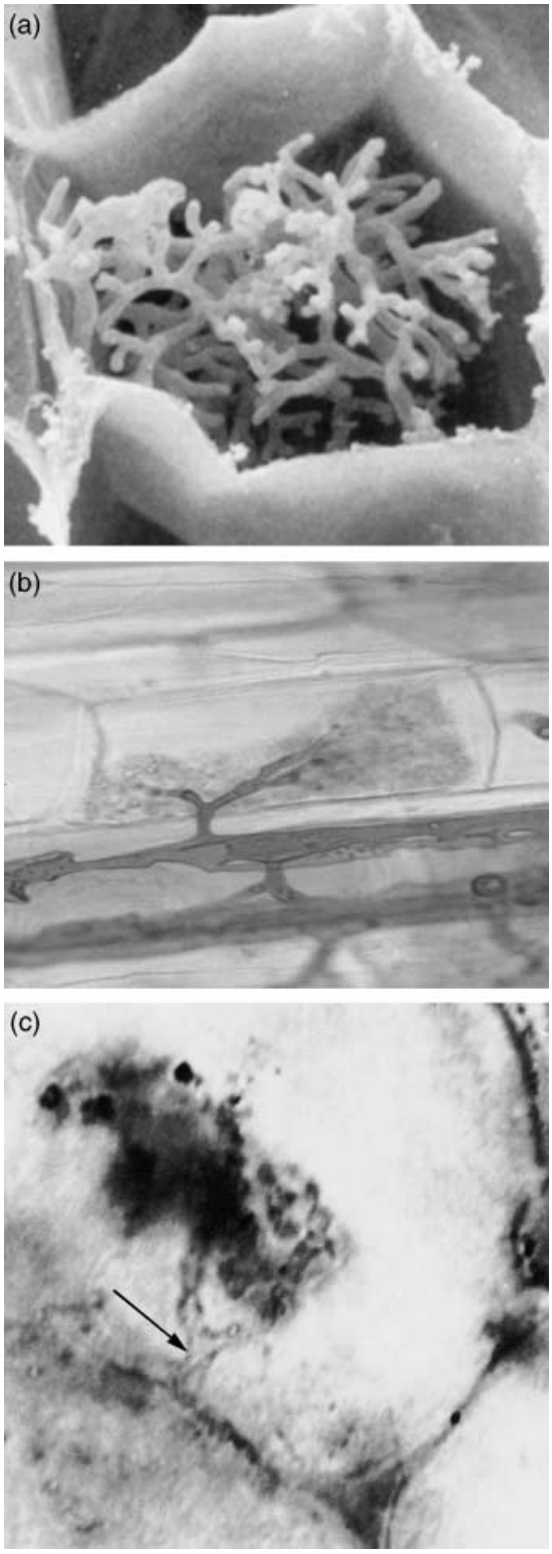

Fig. 3 Arbuscules of arbuscular mycorrhizal fungi (Glomeromycota). (a) SEM of an arbuscule in root cell of *Ginkgo biloba* (courtesy P. Bonfante), (b) arbuscules in modern root of *Hyacinthoides non-scripta* (courtesy J. Merryweather), and (c) arbuscule in fossil rhizome of *Aglaophyton major*. The arrow points to the dichotomously branching hypha that gives rise to the arbuscule, as also seen in the modern root. From Taylor *et al.* (1995), with permission. Copyright (1995). The Mycological Society of America.

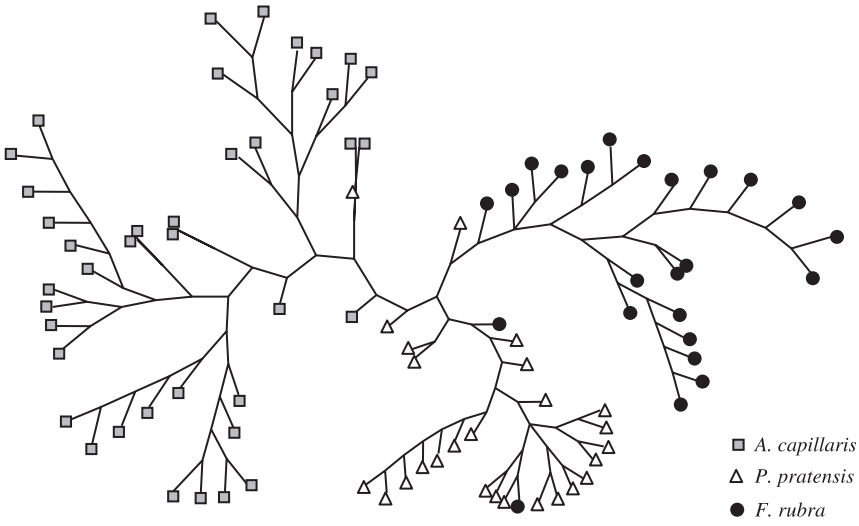

Fig. 4 Maximum parsimony tree revealing that quite distinct communities of arbuscular mycorrhizal fungi colonize the roots of three coexisting plant species, *Festuca rubra, Poa pratensis* and *Agrostis capillaris*, at the Sourhope experimental site, Scotland. Each branch ending represents the arbuscular mycorrhizal fungal community in a single root. From Vandenkoornhuyse *et al.* (2003), with permission).

1993; Redecker *et al.* 2002) and the fact that plants forming the arbuscular mycorrhizal symbiosis are found in every major clade in the plant tree, shows that the symbiosis was a key factor in the colonization of land by plants (Nicolson 1967; Pirozynski & Malloch 1975).

About two-thirds of modern plants form arbuscular mycorrhizas (Fitter & Moyersoen 1996), making this the most ubiquitous and abundant terrestrial symbiosis. In addition, several mycorrhizal types have evolved more recently (ectomycorrhizas, ericoid and orchid mycorrhizas, for example); all involve different fungi, different plant species and distinct ecological functions, compared to the ancestral arbuscular mycorrhiza. The Glomeromycota are traditionally viewed as a species-poor group, with around 150 species recognized by conventional, spore-based taxonomy (Morton & Benny 1990). Since these 150 species can colonize perhaps 250 000 plant species, it follows that they must be non-specific, and indeed the few types that have been cultured are promiscuous, leading to the view that any fungus can colonize any susceptible plant. Such a view has theoretical respectability: Law & Lewis (1983) pointed out that mutualists, in contrast to species in antagonistic relationships, should have broad host ranges, because there would be benefit in being able to acquire carbon from as many hosts as possible.

However, evidence is now accumulating that challenges that view. The advent of molecular techniques makes it possible to collect pieces of root from natural communities and identify sequences of fungal DNA within them, and whenever this is done, the results are the same (Helgason *et al*. 2002; Husband *et al*. 2002; Vandenkoornhuyse *et al*. 2002, 2003; Öpik *et al*. 2003; Johnson *et al*. 2004; Rosendahl & Stukenbrock, 2004): first, there are many types of mycorrhizal fungus in any one community and even on the roots of one species, with sometimes as many as 20 associated with a single plant; second, many of those types are not ones known from the culture collections and so represent new taxa, while others are clearly widespread taxa that are found almost ubiquitously in very diverse habitats; and third, the sets of species found in the roots of coexisting plants are typically distinct from each other (Fig. 4). One issue that remains unresolved is the extent of variation in gene sequence within a single genetic individual fungus: some of the sequence diversity encountered in these studies maybe within rather than among individuals (Pawlowska & Taylor 2004; Rosendahl & Stukenbrock, 2004). There is no doubt that fungal populations that can be described as single morphospecies can contain extensive genetic variation (Lloyd-MacGilp *et al*. 1996; Munkvold *et al*. 2004) and the evolutionary and ecological significance of this variation remains an urgent research question.

Nevertheless, these findings contradict the traditional view of the Glomeromycota: it appears that the phylum is genetically diverse and that many of its members are specialists, associated with one or a few host plant species. It should not surprise us that the view we obtain by studying the fungi in the field is different from that we get by studying the small subset of easily cultured species, nor that the latter turn out to be generalists.

That the phylum may have many species, however, raises a new problem. If the basis of the symbiosis is exchange of C and P between plant and fungus, why is there not in all circumstances one fungus which is best at doing this and so the preferred partner for all plant species? There are two ways to resolve this paradox. First, we can recognize that the symbiosis is multifunctional (Newsham *et al.* 1995): mycorrhizal fungi can provide many other benefits to plants beyond increasing P uptake, including increasing uptake of other nutrients (Hodge *et al.* 2001), altering palatability, improving water relations by binding roots to soil, and protecting plants from pathogens. Importantly, these

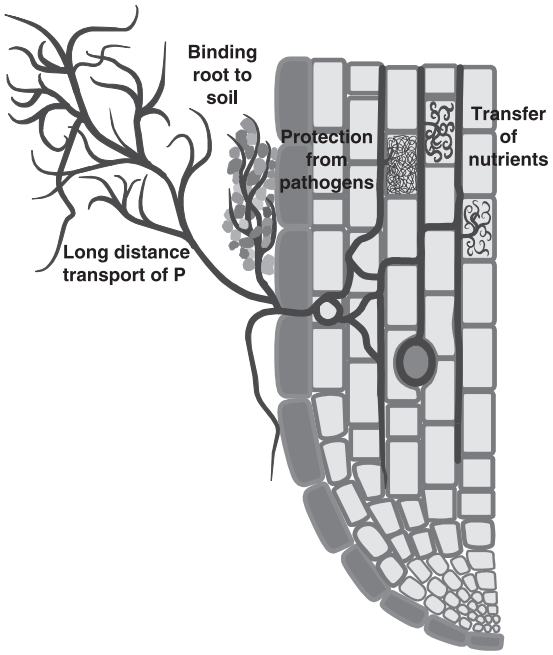

Fig. 5 Diagram to illustrate the incompatible morphological requirements of different mycorrhizal functions: P transport necessitates extensive development of the extra-radical mycelium remote from the root (beyond the phosphate depletion zone); improved water relations is based on maintaining the root–soil bond and hence water pathway as soil dries, and involves extra-radical mycelial development in the rhizosphere; protection from pathogens and P transfer both depend on the intra-radical mycelium, but the former involves the hyphae, the latter the arbuscules (Diagram courtesy of S. Sparrow).

functions are mutually incompatible: acquiring phosphate ions requires an extensive extra-radical mycelium, deployed far from the root beyond the depletion zone, whereas binding roots to soil implies that the extra-radical mycelium develops close to the root, and protection from pathogens involves the internal mycelium (Fig. 5). A fungus good at one of these is unlikely to be the best at another, and therefore even within this biotic niche there is scope for diversification based on function. The second resolution to this paradox lies in recognizing that the fungus has to respond to its environment in the same way as does its host, and that environment includes both abiotic and biotic factors. It is reasonable to assume that these fungal taxa respond distinctively to soil pH, temperature, soil moisture and other factors, and also that the internal environment of the roots of one host plant is not identical to that of another. Both biotic and abiotic niche differentiation is therefore likely.

The picture that emerges of the symbiosis from these findings is therefore very different from the traditional one. In any community there are many species of fungi; perhaps 30–50 is quite typical, a number often similar to that of the plant species. These fungi are not randomly distributed among the host plants; rather they exhibit a strong selectivity. Almost certainly, too, they differ in their functional attributes. It follows therefore that the diversity of fungi in a community should have ecological consequences, as shown in an experiment by John Klironomos and colleagues at Guelph, Canada, in which plant communities from an old-field site were reconstructed with increasing numbers of mycorrhizal species (van der Heijden *et al*. 1998). As the number of fungi increased from 0 to 14 species, so most of the obvious community and system attributes also changed: plant biomass and diversity and fungal biomass all increased, and soil phosphate availability declined, presumably because the more diverse fungal communities were more effective at mining the soil.

Does variation in mycorrhizal diversity have ecosystem consequences?

If the diversity of the mycorrhizal fungal community can determine the characteristics of a plant community in this way, several important predictions can be deduced. For example, the ability of plant species to invade new communities may depend either on their ability to gain sufficient benefit from generalist fungi in the community or the presence of specialist fungi with which they can form a mycorrhiza. Mycorrhizal fungi have been largely overlooked as controllers of plant invasions, despite the enormous economic cost of invasions (Perrings *et al*. 2002) and the remarkable failure of intensive research effort to produce any general rules that can be used to predict invasion potential (Williamson & Fitter 1996; Hierro *et al.* 2005). One experimental study has suggested an indirect role of particular mycorrhizal fungal species in controlling the ability of dominant species to resist invaders (Stampe & Daehle 2003), but there may well be undiscovered direct effects (Klironomos 2002).

Naturalised species are those that have successfully invaded: they have self-sustaining populations that do not require repeated reintroduction. There are around 200 of these in the British flora, of which around 20 (10%) could be described as invasive, a reflection of the empirical Tens rule (Williamson 1993). Naturalised species are not a random selection of introduced species; they are disproportionately either woody or plants of disturbed ground (Peat & Fitter 1993). It is unsurprising that naturalised species tend to favour disturbed ground, since competition will be least there; however, that is the habitat in which non-mycorrhizal species (which probably represent < 10% of flowering plants) are also most frequent, probably both because disturbed soils are rarely deficient in phosphate and because disturbance will tend to disrupt the extra-radical mycelium of mycorrhizal fungi from which new colonisation principally occurs. What is surprising, therefore, is to find that naturalised species are over-represented in plant families that are predominantly mycorrhizal (Table 1). There are no comprehensive records of the mycorrhizal status of naturalised plants in any flora, and so the analysis can only be undertaken at the family level, even in the well-studied British flora, and there are obvious pitfalls in attempting to draw inferences about the mycorrhizal status of a plant species from the

Table 1 The proportion of naturalized and native species in Great Britain that occur in families of distinct mycorrhizal status. Families have been assigned to mycorrhizal categories on the basis of their predominant symbioses. A strict definition of naturalization has been used, omitting species that are widely planted or only established in very restricted geographical ranges. Data are given as percentages; statistical analysis was performed using raw data

Family status	Naturalized spp. (n = 121)	Native spp. (n = 1479)
Non-mycorrhizal	17	26
Arbuscular mycorrhizas	80	67
Other mycorrhizas	2	8
	$\chi^2 = 10.7$, $P = 0.005$	

occurrence of colonisation in other species in the same family. Nevertheless, Table 1 implies that being mycorrhizal may increase the chance of a plant becoming naturalised. The high proportion of naturalised species that are found on disturbed soil probably reflects the much higher proportion of casual introductions (of which naturalised species are a subset) that is found in such places. Analysis at the family level also highlights some remarkable patterns. The two largest families that are predominantly non-mycorrhizal are the Brassicaceae (mustards) and the Cyperaceae (sedges). The Cyperaceae are predominantly plants of undisturbed communities: there are 104 native Cyperaceae and no naturalised species. In contrast, the Brassicaceae are almost all found in disturbed habitats: there are 49 native Brassicaceae and 9 naturalised species. These differences may suggest that non-mycorrhizal plants have difficulty in invading undisturbed communities. Such preliminary analyses must be interpreted with care, but it seems safe to suggest that mycorrhizal biologists have a role to play in the understanding of invasions.

Naturalized species can have immense impacts at the ecosystem scale: a notable example is the N-fixing *Myrica faya* in Hawai'i (Vitousek & Walker 1989) which invades young, N-limited forests of the native *Metrosideros polymorpha*, which harbour no N-fixing plants. The consequent large increases in soil N availability are more beneficial to invasive, non-native tree species than to the *Metrosideros* itself, which is adapted to low N soils. Virtually all N-fixing plants are mycorrhizal, including all legumes, which may reflect both the similarity of the molecular cross-talk and the genetic control that underlies the two symbioses (Ana *et al*. 2004), and the fact that N-fixers tend to have a high P demand. It is likely therefore that the composition of the mycorrhizal fungal community may exert control on the process of N fixation. At a larger scale the impact of mycorrhizal fungi is even more apparent. Read (1991) was the first to highlight the coincidence of the major biomes with the type of mycorrhizal symbiosis characteristic of the dominant plant species. In ecosystems where decomposition is rapid, notably tropical and most temperate systems, N supply is good relative to that of P, and the arbuscular mycorrhizal symbiosis predominates (Fig. 6), with the major exception that Southeast Asian forests are dominated by ectomycorrhizal dipterocarps. However, in cool temperate and boreal systems, decomposition is slower and N is typically the limiting nutrient; these systems are dominated by deciduous trees in the Fagaceae (oaks and beeches) and some

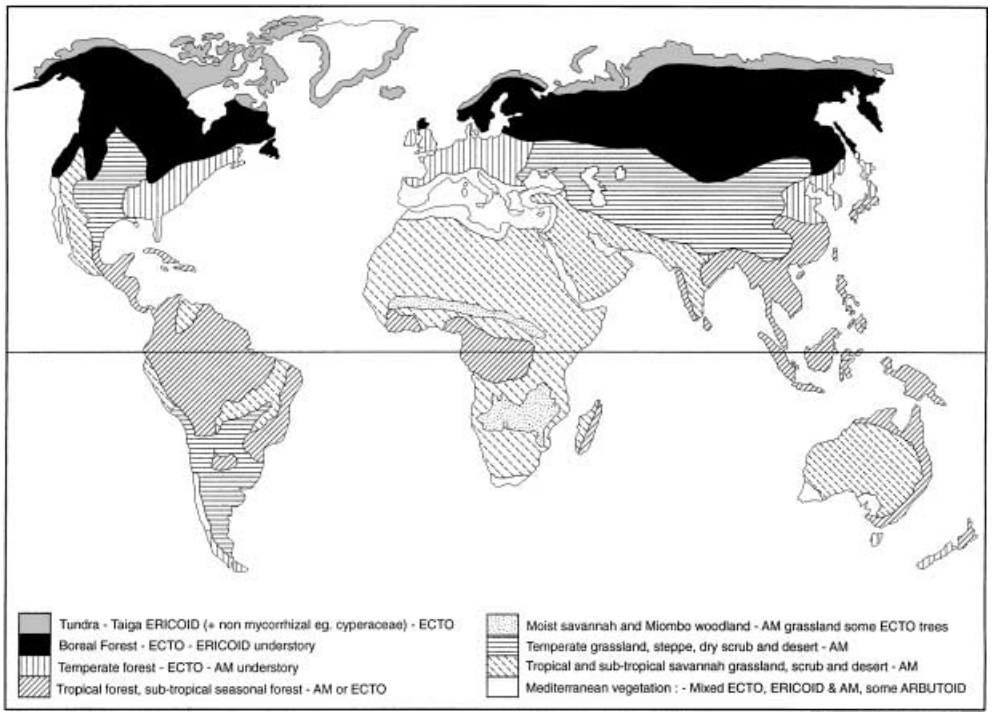

Fig. 6 The dominant mycorrhizal types in plant communities map closely onto the major biomes (Read 1991; Read *et al*. 2004). Reproduced with permission from Read *et al*. (2004).

other angiosperm families, or by evergreen conifers (mainly Pinaceae), all of which form ectomycorrhizas, a symbiosis with diverse members of the fungal phyla Ascomycota and Basidiomycota, which can typically degrade organic material and so acquire N from them directly for transport back to the host plant. In the extreme case of peat formation, in tundra and heathlands, the N cycle has effectively ceased and the dominant higher plant species are in the Ericales (heathers); the fungal partner is an ascomycete that actively degrades organic material and acquires N for the host. Across these systems (tropical–temperate–boreal–tundra) there is a gradient of declining N : P availability that is matched by the mycorrhizal symbiosis of the dominant plants, and the symbiosis can be said to control the vegetation.

Lessons and challenges

Mycorrhizal fungi exemplify many of the problems inherent in understanding soil biodiversity and its potential role in ecosystem processes. Morphologically, there are few recognizable types, but beneath this uniformity there is extensive cryptic variation. Almost certainly, the majority of types within the phylum Glomeromycota are unculturable with current techniques, and those that can be cultured are an ecologically distinct (and unrepresentative) subsample, being promiscuous in their choice of hosts. These fungi play large roles in a range of ecosystem processes, including the cycling of N, P and C, and may well control the composition and invasibility of plant communities. If we are to understand how the structure and dynamics of the fungal communities (i.e. their biodiversity) affects, regulates or even controls processes at the ecosystem level, we need to gain a deeper knowledge of the basic biology and ecology of the fungi (Fitter *et al*. 2004). For example, we do not know what is the life cycle of the Glomeromycota: are they permanently asexual and hence clonal and what therefore is the nature of species in the group? We do not know how they persist and disperse (in time and space): is it by spores, which some (but certainly not all) taxa produce in abundance, or is the mycelium in soil the major mechanism? We do not even know how their principal functional attribute – the exchange of C and P with the plant – operates, nor (astonishingly) exactly where in the root this occurs. Finally, we do not understand the most basic aspect of their biology: why are they obligate symbionts, and why can we not grow them in culture by supplying them with suitable fixed carbon sources, mimicking those they receive from the plant?

Such ignorance is not uncommon in soil biology. It matches our inability to make any quantitative statements about the numbers of species (or other taxa) to be found in soils. At this time, probably the world's best-known soil is at Sourhope in Scotland (Fitter *et al*. 2005). Even there, we do not have accurate counts of numbers of species in most of the major groups, although where data do exist they show that we can expect soils generally to be exceptionally rich. There is an urgent need for a co-ordinated programme of soil biodiversity research, building on the UK Soil Biodiversity Programme and others, in which common techniques would be used to target selected groups on a range of contrasting (but replicated) sites world-wide. The cost would be large, perhaps £50–100 million over 5 years, but the goal is now attainable. The fundamental question that we need to answer in such a programme is whether α, β and γ diversity have the same relationship in soil microbial taxa as in larger organisms; in other words, we need finally to test Beijerinck's hypothesis.

The next set of key questions in soil biology concern population dynamics: are there rare microbial species in soil and is extinction a serious risk for these? This will follow from answering Beijerinck's question, since if local diversity merely represents an environmentally determined sample of the universally distributed global diversity, then rarity and other essentially biogeographical concepts are meaningless. Assuming that we find that microbial population dynamics in soil are not wholly different from those of larger organisms, we shall need to seek answers to questions about the determinants of population size and structure. Those answers will certainly involve consideration of heterogeneity, and the research programme that will provide them will involve a new type of collaboration between ecological modellers, microbiologists and ecologists.

Only once these problems have been resolved are we likely to get clear answers to questions about diversity and ecosystem processes, because at present we find it difficult to frame experimentally tractable questions about that relationship. New technologies will be the key to progress: one novel approach that has enormous potential is stable isotope probing (SIP; Radajewski *et al*. 2000; Manefield *et al*. 2002), in which a resource labelled with the stable isotope ^{13}C is introduced to a system, and nucleic acids are subsequently extracted and separated on a density gradient. The heavy DNA (or better still, since it better reflects metabolic activity, RNA) is then amplified and identified by sequence, allowing the organisms utilizing that resource to be identified. As yet, the technique works best in simple systems where a highly enriched resource can be added, but it is already being extended to the field with the label being added as $^{13}CO_2$ and transmitted via photosynthesis to the rhizosphere community (Ostle *et al*. 2003).

Ultimately all these questions hark back to one fundamental problem: to what extent can or should we use a reductionist approach to explaining high-level phenomena in the ecological hierarchy (Fig. 2)? There must be some level of aggregation of the individual organisms (even, perhaps, the genes) within an ecosystem that allows a sufficient explanation of the behaviour of the ecosystem. In other words, ecosystems have emergent properties and we need to discover the level of aggregation of complexity within the system that allows these to be identified. It is improbable that the

correct level is the species (whatever that may mean for most microbes), and in some sense it must be the functional group of species. Our problem is in knowing how to define those groups. At present, we do that largely by intuition, guided by an imperfect understanding of both taxonomy and biology of the organisms. With improved understanding, and a proper collaboration among modellers, ecologists, microbiologists and others, we may be able to formulate a framework that allows us to reach the grail.

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