MARSCHNER REVIEW

Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development

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Abstract

Background and scope Plant communities and underlying soils undergo substantial, coordinated shifts throughout ecosystem development. However, shifts in the composition and function of mycorrhizal fungi remain poorly understood, despite their role as a major interface between plants and soil. We synthesise evidence for shifts among mycorrhizal types (i.e., ectomycorrhizas, arbuscular and ericoid mycorrhizas) and in fungal communities within mycorrhizal types along long-term chronosequences that include retrogressive stages. These systems represent strong, predictable patterns of increasing, then declining soil fertility during ecosystem development, and are associated with coordinated changes in plant and fungal functional traits and ecological processes.

Conclusions Mycorrhizal types do not demonstrate consistent shifts through ecosystem development. Rather, most mycorrhizal types can dominate at any stage of ecosystem development, driven by biogeography (i.e., availability of mycorrhizal host species), plant community assembly, climate and other factors. In contrast to coordinated shifts in soil fertility, plant traits and ecological processes throughout ecosystem development, shifts in fungal communities within and among mycorrhizal types are weak or idiosyncratic. The consequences of these changes in mycorrhizal communities and their function for plant–soil feedbacks or control over long-term nutrient depletion remain poorly understood, but could be resolved through empirical analyses of long-term soil chronosequences.

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Introduction

Long-term development of ecosystems comprises both progressive and retrogressive stages and involves interactions between soil pedogenesis and plant communities (Walker and Chapin 1987; Wardle 2002; Richardson et al. 2004; Peltzer et al. 2010). Despite a wealth of literature on vegetation change during ecosystem development (see Peltzer et al. 2010 and references therein) there has been relatively little attention paid to the role of mycorrhizal fungi. This is somewhat surprising given that mycorrhizal fungi are a major interface between soils and most plant species, and thus act directly in both pedogenesis and the development of plant communities, as well as modulating interactions between soil processes and plants. Recognising this critical role, Professor T. Walker, a pioneer of pedogenic research along chronosequences (Stevens and Walker 1970; Walker and Syers 1976), frequently noted that he would choose to work on mycorrhizas if he were to start his research career afresh.

The processes of ecosystem development have most commonly been assessed using long-term soil chronosequences, i.e., space-for-time sites differing in age but having similar parent material, climate, and regional species-pools (Jenny 1980). The early phases of ecosystem development (i.e., typically lasting a few hundred years) have been well documented, revealing strong and somewhat predictable shifts in plant community composition, biodiversity, and ecosystem processes such as primary productivity, biomass accumulation, nutrient cycling and decomposition (Walker and Chapin 1987; Wardle 2002). In contrast, far less is known about longer term changes in ecosystems, including the later decline or retrogressive phase (Wardle et al. 2004; Peltzer et al. 2010). Several studies have examined interactions between plants and soils throughout ecosystem development and retrogression (Jenny 1980). Soil nitrogen (N) is nearly absent at the start of primary succession, but increases through biological N-fixation of atmospheric di-nitrogen and plant decomposition, and subsequently declines during ecosystem retrogression, due to diminishing abundance of N-fixers and changes to less bioavailable forms of N. In contrast, phosphorus (P) is primarily rock-derived, and is initially relatively plentiful in primary succession in forms that are readily available to plants (e.g., calcium phosphate). However, P declines during ecosystem development through leaching, transformation to more

recalcitrant pools, accumulation in microbial biomass and other mechanisms (Walker and Syers 1976). For example, at the well-studied Franz Josef soil chronosequence in New Zealand (NZ), total mineral soil N (in the top 100 mm) peaks at c. 9 gkg^{-1} within 500 years of ecosystem development and then declines to c. 3 gkg^{-1} thereafter, whereas inorganic P declines from c. 800 to <100 $mgkg^{-1}$ by the oldest stages studied (Richardson et al. 2004). As a consequence of these different trajectories for N and P, nutrient limitation of primary production is expected to shift from N-limitation during early succession, to co-limitation by N and P during the mature phase, and finally to P limitation during retrogression; these predictions are confirmed in nutrient concentrations in leaves, the nutrient resorption proficiencies of litter, the physiology of roots, and nutrient limitation of leaf physiological processes including photosynthesis and respiration (Richardson et al. 2005; Turnbull et al. 2005; Whitehead et al. 2005; Peltzer et al. 2010; Holdaway et al. 2011).

At the latest stages of ecosystem development, and in the absence of rejuvenating disturbance (sensu Peltzer et al. 2010), ecosystems can become retrogressive. Retrogression is driven by diminishing nutrient availability leading to declines in ecosystem processes or properties such as primary productivity, plant height and vegetation biomass. In general, there are predictable, coordinated shifts in soils and plant communities during ecosystem development, converging on nutrient-poor soils, stress-tolerant soil biota (Doblas-Miranda et al. 2008), and highly conservative plant strategies (Vitousek 1998; Richardson et al. 2004). Because soil chronosequences represent strong environmental gradients of soil properties, nutrient availability, and plant species composition and strategy, they are ideal systems for testing ideas about the long-term effects of interactions between above- and below-ground processes. A critical component of these interactions is nutrient acquisition and uptake by plants and their associated biota.

The vast majority (c. 94 %) of plant species are mycorrhizal (Brundrett 2009), and most plants depend on mycorrhizal fungal symbionts for their nutrient uptake (Lambers et al. 2008). The mycorrhizal symbiosis includes different types of mycorrhizas, the most common of which are arbuscular mycorrhizas associated with c. 74 % of plant species (Brundrett 2009). Ectomycorrhizas and ericoid mycorrhizas are associated with relatively few plant species (2 % and 1 %,

respectively), but include widespread and dominant plant species of temperate, boreal and some tropical forests. Orchids form their own type of mycorrhiza and include another 9 % of plant species (Brundrett 2009). Little is known of how orchid mycorrhizas respond to ecosystem development (but see Diez 2007; McCormick et al. 2012) and they never dominate ecosystems, so we do not include them in detail here. Three other types, ectendo-, arbutoid and monotropoid mycorrhizas significantly overlap with ectomycorrhizas in fungal identity and we consider them in that section (Brundrett 2004).

Plants allocate substantial, but variable, quantities of carbon to mycorrhizal fungi, averaging *c.* 10–20 % of net primary productivity (Leake et al. 2004; Hobbie 2006; Hogberg and Read 2006). In turn, the vast majority of plant uptake of several major nutrients is obtained via mycorrhizal fungi (Leake et al. 2004). As a consequence, mycorrhizal fungi can mediate ecosystem processes at the root–soil interface, including nutrient acquisition and uptake. Despite the importance of mycorrhizal fungi to plant nutrient uptake, few studies have directly studied mycorrhizal interactions along the major, well-characterised retrogressive chronosequences (Peltzer et al. 2010; Turner et al. 2012a, b), and those few have included only limited measurement of mycorrhizal fungal communities (e.g., Jehne and Thompson 1981; Holdaway et al. 2011).

For this review, we focus on understanding the links between fungal communities and long-term soil development throughout ecosystem development spanning primary succession through to retrogression. There have been a large number of studies of secondary successions of mycorrhizal fungal communities on planted trees (e.g., Fleming et al. 1984, 1986) or following disturbance (e.g., Gassibe et al. 2011; Kipfer et al. 2011). From these studies, broad concepts of 'early-stage' and 'late-stage' fungi have developed. These 'stages' in their original meaning refer to shifts in fungal communities over decadal time frames (typically over the lifespan of individual trees) and may have limited relevance to the much longer timescales involved with pedogenesis and ecosystem development. In secondary successions, previous vegetation has strong ecological legacy effects via soil properties and persistent fungal spores. We have therefore generally excluded studies of secondary-succession because of their limited relevance to ecosystem development and pedogenesis, and to avoid confusion

over what comprises 'early-stage' versus 'late-stage'. Further, for clarity, we use the word 'colonisation' to refer to the establishment of plants or fungi within a new habitat or landscape, and 'infection' to refer to fungal growth within or on plant roots.

Shifts among types of mycorrhizas

We begin by considering shifts among types of mycorrhizas (ectomycorrhizas, arbuscular mycorrhizas, ericoid mycorrhizas), and consider shifts in fungal community composition within these types in subsequent sections. Each of these types contains considerable variation in both plant and fungal physiology. Nonetheless, each type is also characterised by a particular phylogenetic grouping of fungi or plant components (e.g., fungi in the Glomeromycota form arbuscular mycorrhizas, most plants in the Ericaceae form ericoid mycorrhizas) and have some ecological traits in common (Read 1993; Read and Perez-Moreno 2003; but see Koele et al. 2012). Further, plants within a mycorrhizal type can frequently share mycorrhizal fungal symbionts, potentially influencing plant interactions and succession (e.g., Bever et al. 1997, 2010; Dickie et al. 2004; Nara 2006b; Mangan et al. 2010; Spence et al. 2011).

Read (1993) proposed a predictable sequence of mycorrhizal types during primary succession and subsequent ecosystem development in temperate and boreal forests. He suggested that non-mycorrhizal plant species colonise bare, high-P substrates in early succession, that these are replaced by arbuscular mycorrhizal plant species, followed by ectomycorrhizal trees with an arbuscular mycorrhizal understory, followed by ectomycorrhizal trees with an ericoid mycorrhizal understory, and finally to dominance by ericoid mycorrhizal vegetation. Lambers et al. (2008) augmented this model, noting that non-mycorrhizal cluster-rooted species (predominantly in the Proteaceae plant family) dominate on the oldest, most highly P-limited ecosystems. Despite these predicted trends in the mycorrhizal status of dominant vegetation, it has been recognised that all mycorrhizal types can occur across stages of ecosystem development and retrogression (Read 1993; Cázares et al. 2005; Lambers et al. 2008). For example, ectomycorrhizal and ericoid mycorrhizal vegetation may achieve peak dominance in mature and retrogressive ecosystems, but both types can also be

present very early in primary succession (Cázares et al. 2005; Hobbie et al. 2005). Equally, arbuscular mycorrhizal vegetation is not eliminated during ecosystem development, and can either persist or even dominate on very old soils (Lambers et al. 2008).

Peltzer et al. (2010) identified nine well-studied long-term soil chronosequences that capture all stages of ecosystem development from primary succession through to retrogression. Using vegetation descriptions along these nine chronosequences, and overlaying data on plant mycorrhizal status predicted from plant phylogeny (Brundrett 2009; Koele et al. 2012), we find that few sequences follow a clear progression or shift in the dominance of mycorrhizal types (Table 1). For example, ectomycorrhizal plants dominate throughout the Glacier Bay sequence (Alaska, USA) including during the earliest stages of succession (Helm et al. 1999). Conversely, the Hawaiian (USA) and Franz Josef (NZ) chronosequences lack ectomycorrhizal plant species and are dominated by arbuscular mycorrhizal plants across most stages of ecosystem development. The absence of ectomycorrhizal plants in Hawaii may reflect biogeographic dispersal barriers, but *Leptospermum* in the oldest sites at Franz Josef is consistently arbuscular mycorrhizal (Holdaway et al. 2011) despite being ectomycorrhizal elsewhere in New Zealand (Moyersoen and Fitter 1999). Given the known ability of fungi to disperse both from Australia (Moyersoen et al. 2003) and elsewhere to New Zealand it seems unlikely this reflects biogeographic barriers to fungal dispersal. Instead, it has been suggested that climate, soils, or other factors may determine mycorrhizal status (Weijtmans et al. 2007). Ectomycorrhizal trees are also present in the San Joaquin Valley chronosequence, but never dominate (Brenner et al. 2001). Plant species that occur on retrogressive stages can be associated with arbuscular mycorrhizas (e.g., *Metrosideros* in Hawaii (USA), *Lepidothamnus* and *Quintinia* in Franz Josef (NZ), *Juniperus* in Northern Arizona (USA)), ectomycorrhizas (e.g., *Picea* in Arjeplog (Sweden) and *Nothofagus* in Waitutu (NZ)) or ericoid mycorrhizas (e.g., *Vaccinium* and *Empetrum* in both Glacier Bay (USA) and Arjeplog (Sweden); Table 1). Even where shifts in mycorrhizal type occur, a single type may dominate for much of the sequence despite strong turnover in plant community composition (i.e., host plant species) and major shifts in soil properties including nutrient status and physical characteristics.

The failure of most well-studied retrogressive chronosequences to follow the hypothesised trajectories of Read (1993) and others raises the question of whether the hypothesis should be rejected. Most literature on mycorrhizal fungi concerns relatively young soils and short-term chronosequences in the Northern Hemisphere, which may provide a biased view of mycorrhizal ecology (Dickie and Moyersoen 2008). In addition, the most commonly-studied secondary successions (i.e., abandoned agricultural systems dominated by arbuscular mycorrhizal species succeeding to forests dominated by ectomycorrhizas) conflate agricultural abandonment and old-field succession with ecosystem development. On the other hand, long-term soil chronosequences are not a representative sample of landscapes (Porder et al. 2007), but are space-for-time model systems for understanding long-term processes such as pedogenesis whilst holding other state factors (sensu Jenny 1980) steady. In some cases, a mycorrhizal type may not be available in the regional species pool (e.g., the absence of ectomycorrhizal plants in Hawaii) or other ecological factors may overwhelm pedogenesis as a determinant of mycorrhizal dominance. For example, the cold climate of Arjeplog (Sweden) and Glacier Bay (Alaska) may explain the absence of a stage dominated by arbuscular mycorrhizal plants. Despite these biases, two points are clear. First, a predictable shift from arbuscular to ectomycorrhizal dominance is not common across long-term chronosequences (Table 1). Second, a single mycorrhizal type can dominate ecosystems on geological timescales despite major shifts in plant species composition, changes in soil physical properties such as pH and organic matter content, and strong shifts in soil nutrient status.

An additional complication is that some plants form more than one type of mycorrhiza. For example, dual arbuscular mycorrhizal and ectomycorrhizal infection is reported in many tree genera including *Eucalyptus* (Bellei et al. 1992), *Salix* (Dhillion 1994), *Uapaca* and *Leptospermum* (Moyersoen and Fitter 1999) and more limited arbuscular mycorrhizal infection in predominately ectomycorrhizal genera such as *Quercus* (Dickie et al. 2001) and *Pinus* (Horton et al. 1998). Because some dual-mycorrhizal-status plants appear common in early succession, Read (1993) suggested that dual-mycorrhizal-status plants might establish early in succession with arbuscular mycorrhizas and then facilitate a transition to ectomycorrhizal dominance. This mechanism can be important in secondary succession, where arbuscular mycorrhizal inoculum is

Table 1 Summary of mycorrhizal types along nine long-term chronosequences that include distinct retrogressive stages and for which detailed vegetation data are available based on predicted mycorrhizal type by plant species. Mycorrhizal plant groups in **bold** are significant in that they account for the majority of plant biomass; those in plain text are present but minor

Sequence	Vegetation	Ages	Early	Mature	Retrogressive	Absent	References
Cooloola, Australia	Subtropical forest	Early: 0–100 yrs Retrogressive: 450 000 yrs +	**ECM** (Allocasuarina; Callitris) AMF (e.g., Phebalium) **Ericoid** (Monotoca) **Non Myc** (Banksia)	**ECM** (e.g., Lophostemon; Eucalyptus) **AMF** (e.g., Jacksonia; Conospermum) **Ericoid** (Monotoca) Orchid (Acianthus) **Non Myc** (Banksia)	**ECM** (e.g., Angophora; Eucalyptus) AMF (e.g., Conospermum) **Ericoid** (Monotoca) **Non Myc** (Banksia)	None	Walker et al. (1981) Wardle et al. (2004) Unpublished permanent plot data
Franz Josef, NZ	Temperate rainforest	Early: 0–130 yrs Retrogressive: 60,000 yrs +	**AMF** (e.g., Olearia; Melicytus) Ericoid (Gaultheria; Dracophyllum) Orchid (Corybas) Non Myc (Cardamine; Uncinia)	**AMF** (e.g., Metrosideros; Weinmannia; Dacrydium) Ericoid (Gaultheria) Orchid (Earina, Corybas) Non Myc (Uncinia)	**AMF** (e.g., Quintinia; Lepidothamnus; Leptospermum[a]) **Ericoid** (e.g., Leptecophylla) Orchid (Corybas) **Non Myc** (Gahnia)	ECM	Richardson et al. (2004) Holdaway et al. (2011)
Waitutu, NZ	Temperate rainforest	Early: 3000 yrs Retrogressive: 291,000 yrs +	**AMF** (e.g., Blechnum; Olearia) Non Myc (Cardamine; Juncus)	**ECM** (Nothofagus) **AMF** (e.g., Metrosideros; Weinmannia; Dacrydium) Ericoid (e.g., Leptecophylla) Orchid (e.g., Corybas) Non Myc (Carpha) [very minor and prob. with wetlands]	**ECM** (Nothofagus; Leptospermum[a]) **AMF** (e.g., Lepidothamnus) **Ericoid** (e.g., Dracophyllum; Androstoma) Orchid (e.g., Aporostylis) **Non Myc** (Gahnia; Isolepis)	None	Mark et al. (1988)
Hawaiian Islands, USA	Subtropical rainforest	Early: 300–400 yrs Retrogressive: 1.4 – 4.1 m yrs	**AMF** (e.g., Metrosideros; Cibotium) **Ericoid** (Vaccinium) Non Myc (e.g., Uncinia)	**AMF** (e.g., Metrosideros; Cibotium) **Ericoid** (Vaccinium) Orchid (Liparis) Non Myc (e.g., Polypodium, Uncinia)	**AMF** (e.g., Metrosideros; Cibotium) **Ericoid** (Vaccinium) Non Myc (e.g., Carex)	ECM	Kitayama and Mueller-Dombois (1995)
Northern Arizona, USA	Woodland	Early: 1000 yrs Retrogressive: 3000 yrs	**ECM** (Pinus) **AMF** (Juniperus; Fallugia; Rhus)	**ECM** (Pinus) **AMF** (Juniperus; Fallugia; Rhus)	**ECM** (Pinus) **AMF** (Juniperus; Bouteloua; Oxytropis) Non Myc (Lupinus)	Orchid; Ericoid	Selmants and Hart (2008)
Glacier Bay, USA	Boreal forest	Early: up to 25 yrs	**ECM** (Dryas, Salix; Populus) **AMF** (Epilobium latifolium)	**ECM** (Tsuga, Pinus, Alnus) AMF (e.g., Oplopanax) Non Myc (Lupinus)	**ECM** (Tsuga, Pinus) AMF (e.g., Rubus; Gentiana)	None	Crocker and Major (1955) Reiners et al. (1971)

Table 1 (continued)

Sequence	Vegetation	Ages	Early	Mature	Retrogressive	Absent	References
		Retrogressive: 14,000 yrs (muskeg bog)	Non Myc (*Equisetum variegatum*; *Carex*)	Ericoid (*Vaccinium*; *Menziesia*) Orchid (*Platanthera*; *Listera* (= *Neottia*); *Goodyera*) Non Myc (*Equisetum variegatum*)	Ericoid (*Empetrum*; *Oxycoccus*; *Ledum* [= *Rhododendron*]) Non Myc (*Carex*; *Trichophorum*; *Menyanthes*)		Chapin et al. (1994) Wardle et al. (2008)
Arjeplog, Sweden	Boreal forest	Early: 40+ yrs Retrogressive: up to 5330 yrs	ECM (*Pinus*; *Picea*; *Betula*) Ericoid (*Vaccinium*; *Empetrum*) AMF (*Deschampsia*; *Rubus*; *Sorbus*)	ECM (*Pinus*; *Picea*; *Betula*) Ericoid (*Vaccinium*; *Empetrum*) AMF (*Deschampsia*; *Rubus*; *Sorbus*) Non Myc (*Melampyrum*)	ECM (*Pinus*; *Picea*; *Betula*) Ericoid (*Vaccinium*; *Empetrum*) AMF (*Deschampsia*; *Rubus*; *Sorbus*) Non Myc (*Melampyrum*)	Orchid	Wardle et al. (2004, 2012)
Mendocino, USA	Forest	Early: 65,000 yrs (White et al. 2008) Retrogressive: >240,000 yrs	AMF (*Sidalcea*; perennial bunchgrasses; composites) Non Myc (*Lupinus*; *Castilleja*)	ECM (*Pinus*) AMF (*Cupressus*; *Trilium*) Arbutoid (*Arctostaphylos*) Non Myc (*Polystichum munitum*)	ECM (*Pinus*) AMF (*Cupressus*) Ericoid (*Vaccinium* [= *Ledum* [= *Rhododendron*]; *Rhododendron*) Arbutoid (*Arctostaphylos*) Non Myc (*Carex californica*)	Orchid not documented as present	Jenny (1980) Westman (1975) Johnston (1994) Northup et al. (1998)
San Joaquin Valley, California, USA	Grassland	Early: 3,000 yrs Retrogressive: 3,000 000 yrs	AMF (*Bromus*; *Hordeum*; *Erodium*) ECM (*Quercus*) Non Myc (*Trifolium*; *Lotus*)	AMF (*Bromus*; *Vulpia*; *Avena*) ECM (*Quercus*) Non Myc (*Trifolium*; *Lotus*)	AMF (*Deschampsia*; *Sporobolus*) ECM (*Quercus*) Non Myc (*Trifolium*; *Lotus*)	Orchid not documented as present	Harden (1982) Brenner et al. (2001)

[a] *Leptospermum* is confirmed to be solely arbuscular mycorrhizal at Franz Josef (Holdaway et al. 2011), but is variously arbuscular mycorrhizal, ectomycorrhizal or dual-mycorrhizal (having both arbuscular and ectomycorrhizal associations) elsewhere in NZ (Moyersoen and Fitter 1999; Weijtmans et al. 2007). *Leptospermum* is likely to be ectomycorrhizal at Waitutu based on fungal sporocarp observations elsewhere in the same region but this remains unconfirmed

likely to be present (e.g., Arveby and Granhall 1998). However, evidence that dual-mycorrhizal-status plants switch from being arbuscular mycorrhizal to ectomycorrhizal in primary succession is weak. Rather, it appears that arbuscular mycorrhizal fungi are often slower to arrive than ectomycorrhizas (e.g., Cázares et al. 2005), and a number of studies now suggest that Salix and other dual-mycorrhizal plants establish relying primarily on ectomycorrhizal symbionts and potentially dark-septate endophytes (discussed below), with very limited arbuscular mycorrhizal infection (Trowbridge and Jumpponen 2004; Hobbie et al. 2005; Nara 2006a; Obase et al. 2007). As an alternative explanation for the prevalence of dual-mycorrhizal plants in early succession, van der Heijden and Vosatka (1999) suggested that relatively low levels of arbuscular mycorrhizal infection (<10 % of root length) can increase uptake of soil mineral P by plants in early succession. Thus dual-mycorrhizal plants may establish as ectomycorrhizal in early succession and subsequently acquire arbuscular-mycorrhizas to maximise mineral P uptake in young soils. A third, myco-centric explanation for dual infection in early succession is also possible. Ectomycorrhizal development can supress arbuscular mycorrhizas in individual root segments. If ectomycorrhizal inoculum is limiting, or if soil nutrients are sufficient to suppress ectomycorrhizal development, this may reduce competitive exclusion of arbuscular mycorrhizal infection by ectomycorrhizal fungi.

Shifts in composition within mycorrhizal types

Given that a single mycorrhizal type can dominate over long periods of ecosystem development, it becomes important to consider shifts in fungal community composition within mycorrhizal type. Each mycorrhizal type contains considerable variation in function among fungal species (Table 2). Arbuscular mycorrhizas evolved once in fungi, but are an ancient lineage with substantial diversification in species and functional traits. Further, a separate group, the Mucoromycotina, can form arbuscular-mycorrhiza-like endomycorrhizal associations with some basal plant clades (Bidartondo et al. 2011). Ectomycorrhizas and ericoid mycorrhizas evolved multiple times in fungi and also display

high functional diversity among species within each type (Agerer 2001). Differences among fungal species in their dispersal traits, degree of host specificity and nutrient requirements will strongly determine the order in which species arrive during primary succession and the duration of species through ecosystem development into retrogression. In the following sections we review published studies of fungal community responses to ecosystem development and, where possible, identify how fungal traits underpin those responses.

Ectomycorrhizal fungi along chronosequences

Ectomycorrhizal plants dominate many boreal and temperate forest ecosystems, some tropical forests, and a range of other ecosystems including some alpine and boreal grasslands (Gao and Yang 2010). Although many ectomycorrhizal plants are woody, herbaceous ectomycorrhizal plants are commonly found in early succession (e.g., Kobresia mysuroides, Polygonum viviparum, Salix herbacea). On the fungal side, there is considerable variability in enzymatic capability for decomposition of organic matter (Bruns 1995; Courty et al. 2010), hyphal foraging strategies (Agerer 2001), lifespan and dispersal mechanisms (Fiore–Donno and Martin 2001), all of which may be important for understanding the ectomycorrhizal fungal community during ecosystem development.

Ectomycorrhizal fungi in early succession Mycorrhizas are horizontally transmitted symbioses: each generation of plants must obtain its symbionts independently of the parent plant. This can be an important limitation on plant establishment in early succession if fungal propagules are absent (Allen 1987; Allen et al. 1992). Despite this, ectomycorrhizal plants are early colonists of primary successional surfaces, and include woody shrubs and trees (e.g., Salix, Pinus, Alnus), and herbaceous plants (e.g., Kobresia and Polygonum viviparum; Muhlmann et al. 2008; Muhlmann and Peintner 2008). Relatively few fungal genera are reported as frequent early in succession (Fig. 1), notably Cenococcum, Cortinarius, Inocybe, Laccaria, Scleroderma, Sebacina, Thelephora and Tomentella, as well as fungi in the Pezizales. Some of these fungi are frequent across studies, but not necessarily abundant, either as sporocarps or belowground.

Others produce abundant sporocarps with few ectomycorrhizal root tips or, conversely, are abundant as mycorrhizal root tips but produce few, inconspicuous, or no sporocarps (e.g., *Tomentella*, *Cenococcum*).

Table 2 Examples of variability within the three main mycorrhizal types in terms of taxonomic origin, dispersal and soil interactions

Trait axis	Range of variability of three main mycorrhizal types		
	Ectomycorrhizas	Arbuscular mycorrhizas	Ericoid mycorrhizas
Fungal taxa/ evolution	Formed by Ascomycetes and Basidiomycetes, evolved multiple times (Bruns and Shefferson 2004).	Single evolutionary event, but diversification over time. The Mucoromycotina also form a similar endomycorrhizal association in some basal plant clades (Bidartondo et al. 2011).	Multiple evolutionary events in Ascomycetes and Basidiomycetes. No unequivocal evidence that ericoid mycorrhizal fungi are obligate symbionts, hence potential for greater evolutionary diversity (Brundrett 2002).
Host specificity		Highly specific to super generalists (Molina et al. 1992; Tedersoo et al. 2010)	Traditionally considered broad host-specificity, increasing evidence of specificity to plant functional groups (Öpik et al. 2009). Strong, species-specific variability in plant growth response to different fungal taxa (Bever et al. 2001)
No evidence of specificity within the Ericaceae family (Selosse et al. 2007; Kjøller et al. 2010; Walker et al. 2011).			
Dispersal strategies	Variable. Hyphal extension, wind, animal, soil borne	Spores highly variable in size (Bever et al. 2001), dispersed via animals, soil movement and wind (Warner et al. 1987; Allen and MacMahon 1988).	Some evidence for variable dispersal strategies: chlamydospores, hyphal extension via direct contact or contained in plant sloughed cells (Ashford et al. 1996), or very small ascospores from microscopic fruiting bodies (Read 1974). Reproduction strategies still unknown for many ascomycete and sebacinales species.Ability to function as saprotroph suggest persistence outside symbiosis.may not require specialised survival structures (Piercey et al 2002).
Hyphal foraging	Highly variable from contact-exploration with few hyphae to 200 m hyphae g^{-1} soil (Agerer 2001).	Variable from Gigasporaceae (extensively soil colonisation/limited colonisation of roots) to Glomeraceae (limited soil/extensive root colonisation) (Hart and Reader 2002)	Current view is that of limited extramatrical hyphal extension for ascomycetes (few centimetres beyond root surface), but limited evidence available.
Ability to utilise organic soil nutrients	Highly variable enzymatic production (Bruns 1995; Courty et al. 2010)	Traditionally viewed as limited, but increasing evidence that Glomeraceae enhance nitrogen capture from organic material (Hodge et al. 2001; Leigh et al. 2009) but Gigasporaceae may not (Reynolds et al. 2005). Direct experimental comparisons of multiple taxa needed.	Utilisation of a wide range of organic compounds of variable complexity with some interspecific variation in efficiency (e.g., Grelet et al. 2005).
Role in mineral soil	Some taxa notable for exudation of calcium oxalate, mineral tunnelling. Some taxa highly hydrophobic, others hydrophilic.	Variable in distance and degree of P transport to roots from mineral soil, e.g., *Acaulospora* longer than *Glomus*; *Scutellospora* found to play little role.	Functional variability largely unknown.

The ability to disperse may be a strong filter on the establishment of ectomycorrhizal fungal species early in primary succession. Many ectomycorrhizal fungi produce copious wind-dispersed spores. For example, *Suillus bovinus* may produce up to 1.2×10^9 spores per sporocarp (Dahlberg and Stenlid 1994). Although >95 % of spores fall within 0.5 m of sporocarps (Li 2005; Galante et al. 2011), the sheer number of spores produced appears sufficient for effective long-distance dispersal (Peay et al. 2012). For example, wind-dispersed spores arriving early in succession were observed at low density at Mt St Helens (Allen 1987), and Jumpponen (2003) detected DNA of many obligate, biotrophic fungal species at a glacial forefront in the absence of plant hosts, most likely representing aerially-deposited spores. Nonetheless, low ectomycorrhizal fungal inoculum potential can limit plant establishment during primary succession (Nara 2006b; Fujiyoshi et al. 2011), and many species detected in spore traps fail to infect seedlings (Peay et al. 2012). The paradox of producing copious wind-dispersed spores yet failing to establish remains largely unresolved (Peay et al. 2010a). In contrast, animal dispersal of fungal spores may be particularly important in primary succession, including dispersal by soil invertebrates (Lilleskov and Bruns 2005), small mammals (Terwilliger and Pastor 1999) and deer (Ashkannejhad and Horton 2006). These fungal species may also receive an initial boost via co-deposition of high-nutrient organic matter.

Dispersal ability is likely a major filter determining the composition of early-successional fungal communities. Dispersal traits of fungi (sporocarp height and palatability, spore volume and capacity to survive passage through animal guts) vary widely among species (Ashkannejhad and Horton 2006; Galante et al. 2011). Similarly, the ability to persist as dormant spores may be a strong filter on fungal communities, with some early-successional fungi such as *Wilcoxina*, *Rhizopogon* or *Suillus* having a spore longevity of at least several years and potentially much higher (Bruns et al. 2009). Equally important is an ability to germinate when a host root is available. Early-successional taxa (*Laccaria*, *Inocybe*) have much higher spore infectivity than late-successional taxa (Ishida et al. 2008). Finally, most fungal spores of ectomycorrhizal fungi are monokaryotic (having one haploid nucleus) and the fusion of two compatible monokaryotic mycelium – forming a dikaryon – is necessary for reproduction and the establishment of a population. Having

the ability to form a functional mycorrhiza as a monokaryon (e.g., *Laccaria*; Kropp and Fortin 1988) or to form even a limited number of binucleate heterokaryotic spores may therefore be a significant advantage in primary succession (Horton 2006). Once established on a single root, an ectomycorrhizal fungus can infect other roots on either the same or other plant hosts through hyphal growth. Low root densities in early succession may thus favour fungal species having relatively long hyphae and rapid growth (Peay et al. 2011).

An additional important factor in the composition of early-successional fungal communities may be plant host identity, with a number of early-successional fungi showing high host specificity (Molina et al. 1992). For example, *Rhizopogon* and *Suillus* are common in early successions where *Pinus* is present (Peay et al. 2012), but otherwise are generally absent (but see Krpata et al. 2007). Similarly, *Alnicola* (=*Naucoria*) and *Alpova* both show relatively high specificity to *Alnus* (Molina 1981; Moreau et al. 2006) and many *Leccinum* have a high specificity to various early-successional trees, including *Betula* (den Bakker et al. 2004). *Leccinum*, *Suillus* and *Rhizopogon* are notable in producing abundant and large sporocarps, while most other early-successional ectomycorrhizal fungi have small or inconspicuous sporocarps (Muhlmann and Peintner 2008). Bruns et al. (2002) suggested that high host-specificity may be related to increased symbiotic benefits received by a fungus. *Suillus*, for example, forms only a minor component of below-ground fungal communities but produces abundant sporocarps, implying that it is more efficient at converting host carbon into reproductive output (Bruns et al. 2002) or may be accessing other carbon sources (Chapela et al. 2001). The occurrence of high host specificity in early-successional communities may therefore be a mechanism for increasing host C-allocation under relatively high soil nutrient conditions, where host benefit is limited. However, whether high carbon cost implies a less mutualistic interaction depends on nutrient benefit and the cost : benefit ratio (Hobbie et al. 2005), which is poorly understood.

Wilcoxina, which often occurs in early succession, can form 'ectendomycorrhizas', in which a Hartig net and thin fungal mantle are formed (as in ectomycorrhizas) but fungal hyphae also penetrate plant root

cells, with the degree of root cell penetration related to soil nutrient status (Yu et al. 2001; Navarro-Ródenas et al. 2012). Somewhat similarly, arbutoid mycorrhizas are formed by the basal Ericaceae Arbutoideae (*Arbutus*, *Arctostaphylos*). Like ectendomycorrhizas, the fungi penetrate plant cells, but form a mantle and Hartig net. The fungi forming arbutoid mycorrhizas form ectomycorrhizas on other plant species (Horton

et al. 1999). The Monotropideae (also basal Ericaceae) form monotropoid mycorrhizas, in which the plant parasitises ectomycorrhizal fungi for carbon. While distinctive in some physiological traits, the strong overlap of fungal species suggests these categories can generally be considered as specialised variants of the ectomycorrhizal association (Brundrett 2004; Finlay 2008).
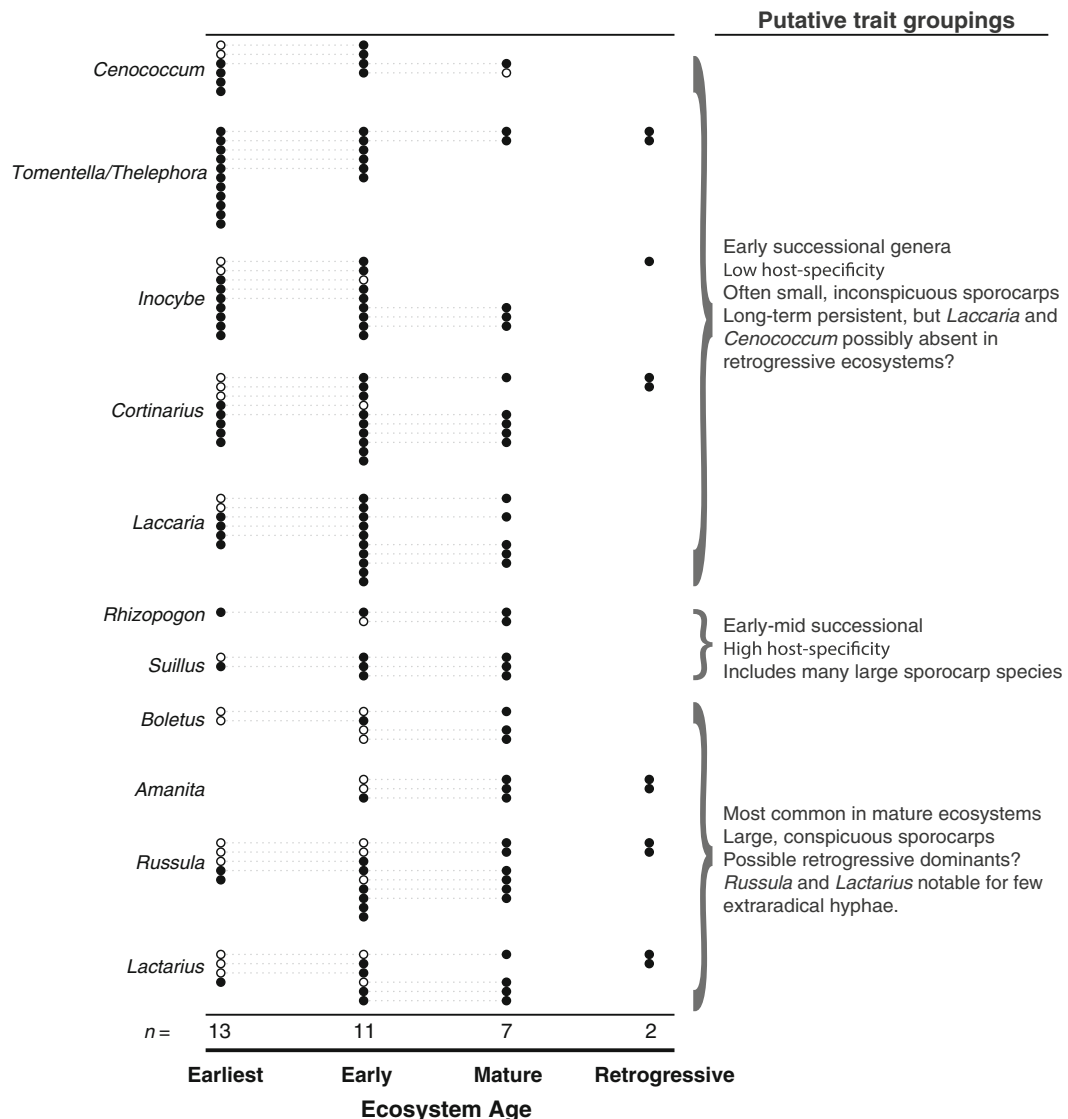
Fig. 1 Frequency of observation of common ectomycorrhizal fungal genera across soil chronosequences and putative trait groupings. *Filled circles* indicate presence of the genus at that site, *open circles* indicate that the species was absent at that site. *Dotted lines* connect observations from the same study. Number of studies (*n*) for each ecosystem age given at bottom. Based on

data from Helm et al. (1996); Jumpponen et al. (1999, 2002); Alfredsen and Hoiland (2001); Nara et al. (2003); Hobbie et al. (2005); Ashkannejhad and Horton (2006); Obase et al. (2007); Trocha et al. (2007); Muhlmann and Peintner (2008); Muhlmann et al. (2008); Reverchon et al. (2010); Fujiyoshi et al. (2011); Blaalid et al. (2012) and Peintner and Dammrich (2012)

Ectomycorrhizal fungi in mature ecosystems As ecosystems develop, communities of ectomycorrhizal fungi generally become more diverse, with early-successional species largely retained and additional species colonising later stages of ecosystem development (Nara et al. 2003; Peay et al. 2011). Genera commonly reported in mature ecosystems, but less frequently earlier in succession, include *Amanita*, *Boletus*, and *Russula* (Fig. 1; also see Peay et al. 2012). Some of these genera are frequently associated with soil organic layers and may depend on soil development to become established. For example, *Russula*, which increases in frequency in mature ecosystems, has also been shown to be positively correlated with total soil C and depth of the organic layer in mature forest (Dickie et al. 2009). Nonetheless, some genera such as *Cortinarius* are commonly dominant in soil organic layers in mature forest, but also occur earlier in succession (Muhlmann and Peintner 2008).

Fungi found in mature ecosystems, but absent earlier in succession, include many genera with large sporocarps (e.g., *Amanita*, *Boletus*), which may have high carbon demands relative to earlier-successional species (Gibson and Deacon 1990). Many of these genera appear to depend on mature trees in order to successfully infect seedlings, as trenching around seedlings in mature forests reduces the abundance of late-successional species and can increase seedling growth (Fleming 1984; Simard et al. 1997). Unlike large-sporocarp genera found earlier in succession, many of those found later in mature ecosystems can simultaneously infect multiple host species (e.g., Dickie et al. 2004), and the ability to switch plant host may be important in the long-term persistence of fungal taxa in mature ecosystems.

Ectomycorrhizal fungi in retrogression Because retrogression is a process, determining whether an ecosystem is in retrogression depends on having a comparable sequence of ecosystems on younger soils. Regrettably, few, if any, studies have examined ectomycorrhizal fungal communities along well-documented retrogressive sequences. As an imperfect interim solution, we can infer patterns from the lowland tropics, where much of the soil has characteristics similar to those of retrogressive ecosystems (i.e., strongly P-limited, with most nutrients in organic form). On one very-low-P sandy soil under Malaysian dipterocarp forest, Peay et al. (2010b)

found *Russula*-dominated communities, but also *Cortinarius*, *Tomentella*, *Amanita*, *Lactarius*, and *Gymnomyces*. Similarly, in tropical South America, Smith et al. (2011) found *Russula* to dominate ectomycorrhizal fungal communities along with *Clavulina*, *Tomentella*, *Tylopilus*, *Xerocomus*, *Cortinarius* and other genera. The dominance of *Russula* in these low-P soils may imply a unique role in P uptake. *Russula* is notable in having few emanating hyphae but abundant surface cystidia with associated calcium-oxalate crystals, which may be related to mining P from soils (Massicotte et al. 2005; Avis 2012). The occurrence of the early-successional genera *Tomentella* and *Cortinarius* on old, P-depauperate tropical soils in both studies suggests that at least some fungal genera can be present across most, or all, of pedogenic development and retrogression. Conversely, both *Cenococcum* and *Laccaria* are absent from both studies and most tropical ectomycorrhizal fungal communities, despite being common in both the Holarctic and Austral regions (Tedersoo et al. 2010). The absence of these two genera, which are common in early primary succession, could indicate a retrogression-driven loss of species. Further studies of ectomycorrhizal fungal communities in primary succession in the tropics are needed to resolve whether the absence of *Cenococcum* and *Laccaria* is driven by pedogenesis as opposed to biogeography.

Ectomycorrhizal summary The overarching pattern for ectomycorrhizal fungal communities during progressive and retrogressive phases of ecosystem development is an accumulation of diversity, with few host-generalist genera lost. Host-specialist genera, in contrast, appear to be more transient due to their dependence on the presence of compatible hosts. The persistence of early-successional fungal genera through the mature stages of ecosystem development is intriguing, and contrasts markedly with plant communities (e.g., Walker and del Moral 2003; Wardle et al. 2008). Some early-successional taxa may persist in the mineral soil layers later in ecosystem development, and perhaps considering these species to be 'mineral soil'-adapted is more useful than considering them to be 'early successional'. Three other factors may also contribute to the persistence of ectomycorrhizal fungal genera from early succession. First, fungi can occur as small genets, which may permit species to utilise small, localised disturbances and persist despite overall ecosystem development. *Laccaria*, for example,

persists in mature ecosystems but appears to be associated with localised disturbance (Dickie et al. 2009), and occurs as very small, short-lived genets (Gherbi et al. 1999). Alternatively, fungi can be extremely long lived and show strong priority effects, such that early-establishing species can persist for extended periods (Kennedy and Bruns 2005; Kennedy et al. 2009). It is possible that a single fungal genet might persist for thousands of years, even if conditions no longer favour its establishment. Finally, there is some evidence that peripheral roots (those far from the host plant stem) have a distinct fungal community of early-successional species (Last et al. 1984; Dickie and Reich 2005). It is possible that resource partitioning by host roots may allow low-carbon-demanding species to persist on peripheral roots of trees within contiguous forest.

Arbuscular mycorrhizal fungi along chronosequences

Arbuscular mycorrhizal fungi enhance plant-uptake of P and, to a lesser extent, N, but have a limited capacity to use insoluble soil nutrients relative to ectomycorrhizal fungi (George et al. 1995). Communities of arbuscular mycorrhizal fungi respond strongly to soil variables at local and regional scales, including soil pH and texture (Lekberg et al. 2007, 2011), and we thus anticipate there will be clear shifts in fungal community composition during ecosystem development.

Most studies of arbuscular mycorrhizal fungi during ecosystem development focus on abundance, particularly the extent of root infection, with few studies characterising community composition. Regrettably, we found no studies of arbuscular mycorrhizal fungal communities during retrogression. Our review is thus confined to compositional shifts during the early and mature phases of ecosystem development, but these cover a diverse range of situations including sand dunes (Jehne and Thompson 1981; Sikes et al. 2012), volcanic systems (Oba et al. 2004), and glacial moraines (Oehl et al. 2011a).

Early taxonomic efforts to characterise arbuscular mycorrhizal fungal communities were based largely on spore morphology, with many species grouped under the genus *Glomus*. Recent advances in molecular methods have resulted in new classifications of orders, families and genera, and an increase in the number of species from *c*. 170 to 220. Two recent classifications based on genetic characters have been proposed (Oehl et al. 2011b; Kruger et al. 2012), which presents a hurdle for reviewing studies that have used either the traditional taxonomy, one of the two more recent taxonomies, or various combinations thereof. Here, we have updated data from prior studies following the taxonomy of Oehl et al. (2011b) on the basis of its strength in using both genotypic and phenotypic characteristics.

Despite correcting taxonomy, we found no evidence of consistent shifts in arbuscular mycorrhizal fungal community composition during the early and mature phases of ecosystem development (Fig. 2; Jehne and Thompson 1981; Johnson et al. 1991; Oba et al. 2004; Pezzani et al. 2006; Wu et al. 2007; Oehl et al. 2011a; Sikes et al. 2012). Rather, fungal genera are present across a wide range of ecosystems from early to mature stages. For example, *Acaulospora* is frequent across studies in early succession, yet remains frequent as ecosystems mature (Fig. 2). There are also no consistent shifts in the diversity of arbuscular mycorrhizal fungi during ecosystem development, with diversity increasing (e.g., Pezzani et al. 2006), decreasing (Sikes et al. 2012; Zangaro et al. 2012), or remaining constant (Johnson et al. 1991). Increasing diversity was associated with the addition of new species and the persistence of pioneer species into the mature phase (Wu et al. 2007), similar to the pattern observed for ectomycorrhizal fungal communities.

Several factors may contribute to a lack of consistent compositional change in arbuscular mycorrhizal fungal communities during ecosystem development. First, communities of arbuscular mycorrhizal fungi may be more strongly structured by competition for plant roots than competition for soil resources (Maherali and Klironomos 2012), with host specificity playing a dominant role (Öpik et al. 2006) relative to soil development. Second, responses of arbuscular mycorrhizal fungi to fine-scale environmental variability and seasonal changes may overwhelm site-scale responses to ecosystem development, as has been observed in plant communities in early succession (del Moral et al. 2010). Third, the large spore size and short dispersal distances of arbuscular mycorrhizal fungi may result in fungal community composition being dominated by random dispersal from proximal landscapes, rather than globally dispersed propagules being filtered by environmental selection. There are also possible methodological explanations. For

example, most studies have been based on fungal spores, frequently measured at a single time point, and may not accurately reflect which species infect plant roots (Oba et al. 2004; Sanders 2004; Wu et al. 2007; Martínez-García et al. 2011). It is also possible that the phylogenetic concept of a genus in arbuscular mycorrhiza is sufficiently broad as to obscure ecological patterns.

Ericoid mycorrhizal fungi along chronosequences

Ericoid mycorrhizal fungi are characterised by their ability to form coils in the epidermal cells of the finest roots ('hair roots' as distinct from 'root hairs' of other plants) of most plants in the Ericaceae (excluding the basal clades, Arbutoideae, Monotropoideae and Enkianthoideae which form arbutoid, monotropoid and arbuscular mycorrhizas, respectively). Ericoid mycorrhizal fungi include taxa in the Ascomycota such as *Rhizoscyphus*, *Meliniomyces*, *Oidiodendron*, *Capronia* and *Cryptosporiopsis*, and in the Basidiomycota such as Sebacinales group B (Weiß et al. 2011). The Ericaceae and ericoid mycorrhizas occur worldwide but are absent from large parts of Africa, much of the lowland neotropics, and northern and central Australia. They are characteristic of low soil fertility and high soil acidity sites (Cairney and Meharg 2003). The few species of ericoid mycorrhizal fungi that have been studied in vitro show enhanced capability to degrade enzymes compared with all other mycorrhizal fungi (Smith and Read 2008). The ecological context of most laboratory studies has been that of mature and retrogressive phases of ecosystem development, focusing on how ericoid mycorrhizal fungi mobilise nutrients locked up in complex organic matter. Much less is known of the role of ericoid mycorrhizal fungi in nutrient uptake in high-P early-successional sites, despite the frequent occurrence of Ericaceae early in succession (Table 1).

We did not find any studies describing the community response of ericoid mycorrhizal fungi to long-term ecosystem development, perhaps reflecting difficulties identifying fungi having few distinctive morphological or spore types. Instead, the focus to date has been on the presence of the ericoid mycorrhizal type relative to other mycorrhizal types. Cázares et al. (2005) reported that ericoid mycorrhizal plants were absent from the earliest successional sites of the Lyman glacial chronosequence (USA) but present on moraines that were 35–60 year old, while the intensity
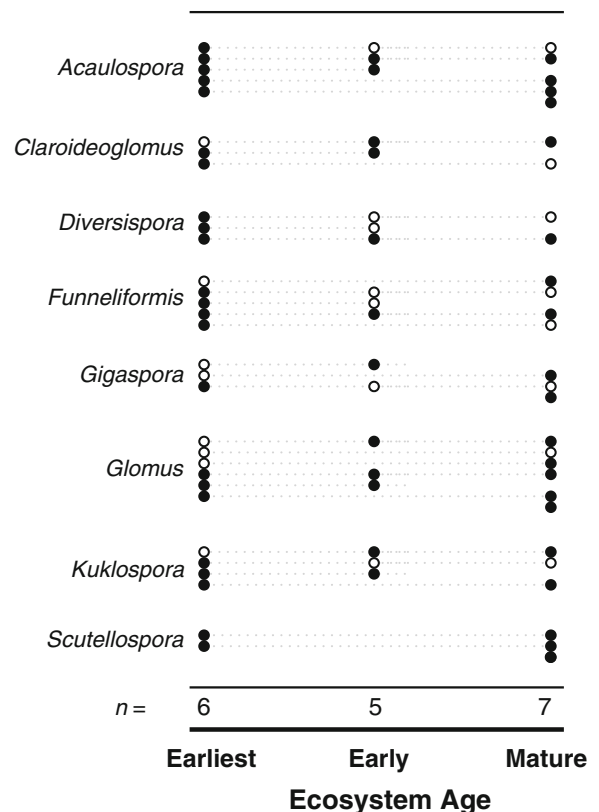
Fig. 2 Shifts in arbuscular mycorrhizal fungi across soil chronosequences from the earliest phase through to the mature phase (peak biomass). *Filled circles* indicate presence of the genus at that site, *open circles* indicate that the species was absent at that site. *Dotted lines* connect observations from the same study. Number of studies (*n*) for each ecosystem age given at bottom. Note that retrogressive phases remain entirely in the 'black-box' due to a lack of data, and are hence not shown. Based on data from Jehne and Thompson (1981); Oba et al. (2004); Pezzani et al. (2006); Wu et al. (2007); Oehl et al. (2011a); Sikes et al. (2012) and mature stage data from Johnson et al. (1991)

of root infection was unresponsive to ecosystem age. Typical coils of ericoid mycorrhizas have been observed at the youngest sites along the Franz Josef chronosequence (Table 1) in roots of *Gaultheria macrostigma* and *Dracophyllum longifolium* (G.-A. Grelet, unpublished data). The response by ericoid mycorrhizas to ecosystem development may be driven by the presence and depth of the organic horizon as there is evidence for vertical niche partitioning among soil horizons. For example, Wurzburger et al. (2012) found that communities of ericoid mycorrhizal fungi hosted in the roots of *Rhododendron maximum* varied strongly among soil horizons, with Basidiomycota taxa occurring more frequently in the organic horizon

and Leotiomycetes more frequently in the mineral horizon. Taxa closely related to the archetypal ericoid mycorrhizal *Rhizoscyphus ericae* and *Oidiodendron maius* were found at similar frequencies in both organic and mineral horizons. Their results suggest that ericoid mycorrhizal fungal communities might be more diverse later in ecosystem development once a mature organic horizon has developed.

An important factor in early-successional communities is dispersal, and observational evidence suggests that ericoid mycorrhizal fungi can be dispersal limited. For example, Hutton et al. (1997) observed that ericoid mycorrhizal infection in disturbed sites (in which top soil had been removed and subsequently replaced) took about 12 year to return to levels comparable to undisturbed sites. Furthermore these authors showed that infection levels dropped to virtually zero when bait plants were planted in soils > 40 cm away from established ericoid mycorrhizal plants. Dispersal strategies in ericoid mycorrhizal fungi remain poorly understood, hence the mechanisms by which they may colonise soil and infect host plants at the earliest stage of succession are largely unknown. In part, this is confounded by the difficulty of observing and characterising the cryptic sexual structures formed by microfungi, such as most of the ascomyceteous taxa forming ericoid mycorrhiza. We know that some ericoid mycorrhizal fungi produce microscopic ascocarps (e.g., *Rhizoscyphus ericae* produces apothecia up to 1 mm diameter; Read 1974) or asexual propagules (e.g., arthrospores in *Oidiodendron* species), but conditions under which those are produced, and how far they disperse, are unknown. Many ericoid mycorrhizal fungi have never been observed to sporulate, either sexually or asexually, and are still considered to be sterile (Hambleton and Sigler 2005). Ashford et al. (1996) documented the formation of thick-walled heavily colonised epidermal cells in hair roots of Western Australian Ericaceae. Based on the fact that these cells are often sloughed off the root, and that the fungus remains alive in sloughed cells, the authors suggested that these specialised cells could act as fungal propagules for year-to-year persistence. This points towards a dissemination strategy dominated by asexual propagules (hyphae from neighbouring plant or thick-walled detached epidermal cells), effective only over very short distances. On the other hand, Bergero et al. (2000) showed that viable ascomyceteous ericoid mycorrhizal fungal structures persisted in woodlands, for

possibly 10–20 year, in the absence of suitable ericoid mycorrhizal host. This may indicate the presence of viable persistence structures such as spores, but it may also reflect (1) the ability of some ericoid mycorrhizal fungi to colonise ectomycorrhizal roots, which then act as fungal refugia until the appearance of Ericaceae host plants (see below for further discussion on this point) or (2) the ability of some ericoid mycorrhizal taxa to also function as saprotrophs (Piercey et al. 2002). Hence for many ascomyceteous taxa, the available evidence suggests dispersal is local, short-scale and dominated by asexual propagules, but the physical constraints on propagule production and dissemination are largely unknown. Dispersal strategies of ericoid-forming Sebacinales group B are unknown due to a lack of morphological data (Weiß et al. 2011), no fruiting body descriptions, and an inability to culture these fungi. However, their dispersal strategies are expected to differ markedly from those of other ericoid mycorrhizal fungi given the contrasting fruiting body and morphological characteristics of members of Sebacinales group A. As with arbuscular mycorrhiza, further studies are needed of ericoid mycorrhizal fungal communities across chronosequences, particularly where ericoid mycorrhizal plants occur over long-term ecosystem development (e.g., Cooloola, Australia; Hawaii, USA; Franz Josef, NZ; Arjeplog, Sweden; Table 1).

There are several lines of evidence that fungal taxa traditionally regarded as ectomycorrhizal occur in field-grown ericoid roots and vice versa (e.g., Bergero et al. 2000; Vralstad et al. 2000; Bougoure et al. 2007; Tedersoo et al. 2007) with function demonstrated by structural data (Villarreal-Ruiz et al. 2004, 2012) and reciprocal transfer of resources between fungus and plant (Grelet et al. 2009). Genetic studies also demonstrate that neighbouring ericoid mycorrhizal and ectomycorrhizal roots share the same fungal genet (Grelet et al. 2010). However, the impact of infection by these potentially dual-mycorrhizal taxa on plant host is unclear. In a pot experiment, Kohout et al. (2011) found that the presence of ericoid-mycorrhizal plants suppressed the formation of ectomycorrhizas between neighbouring *Pinus* spp. and dual-mycorrhizal *Meliniomyces bicolor*. On the other hand, along a primary successional gradient on the dune shores of Bothnian Bay, Finland, Grau et al. (2010) reported a higher proportion of *Pinus sylvestris* seedlings established in early to mid-successional

patches already colonised by the ericoid mycorrhizal shrub *Empetrum nigrum*. The apparent facilitating role of *Empetrum* was also noticeable in its impact on the ectomycorrhizal fungal community, as it increased both morphotype diversity and the proportion of ecto-mycorrhizal root tips with abundant external mycelia. Nonetheless, in an older successional stage, *Empetrum* had a detrimental effect on both seedling recruitment and ectomycorrhizal symbiosis, possibly due to alle-lopathic or competitive interactions. Hence whether and how these potentially dual-mycorrhizal taxa play a significant role in shaping plant communities is unknown and requires further investigation.

Dark septate endophytes along chronosequences

In addition to mycorrhizal fungi, there is another com-mon group of root-associated fungi known as dark septate endophytes (DSE). The nature of the interac-tion between DSE and their host plant is still a matter of debate (Grünig et al. 2008; Newsham 2011). However, several papers have considered their role in early succession (e.g., Jumpponen and Trappe 1998; Cázares et al. 2005; Tejesvi et al. 2010; Day and Currah 2011). Additionally, there have been sev-eral reports of negative correlations between mycor-rhizal and DSE infection along defined environmental gradients (e.g., Vohník and Albrechtová 2011) and in both polar regions, DSE infection is more prominent than mycorrhizal infection (Newsham et al. 2009). Therefore we have included here a discussion of DSE in ecosystem development.

Dark septate endophytes are fungi with melanised septate hyphae which infect plant roots by growing within and between cells, and along the root surface, but which do not form intracellular coils. They have been found in the roots of over 600 plant species span-ning more than 100 plant families (Jumpponen and Trappe 1998) including the Ericaceae (although not restricted to hair roots in the Ericaceae unlike ericoid mycorrhizal fungi) and plants that are typically ectomy-corrhizal or arbuscular mycorrhizal. Dark septate endo-phytes include diverse unrelated genera of Ascomycete fungi (e.g., *Cadophora*, *Microdochium*, *Trichocladium*, *Phialophora*, *Leptodontidium* and *Phialocephala*). Functional differences aside; the structural and genetic distinction between DSE and mycorrhizal fungi is sometimes obscure. For example, some genera include both DSE and ectomycorrhizal taxa (e.g., *Cadophora*,

Acephala), and taxa initially considered as DSE have later been shown to form ericoid mycorrhizal associa-tions in vitro (Usuki and Narisawa 2005; Grelet et al. 2009) or in vivo (Vohník and Albrechtová 2011).

Unlike many other root-associated fungi, dark septate endophytes can precede plants in early succession be-cause they can persist and produce propagules in the absence of a host plant (Day and Currah 2011). Cázares et al. (2005) reported that DSE were present from the very earliest stages of succession of the Lyman glacial chronosequence (USA), albeit at low intensity (< 25 % of root length infected). Tejesvi et al. (2010) investigated the community composition of DSE along an early-successional vegetation gradient (~50–300 years) created by land uplift, using culture-based methods that favoured the growth of DSE taxa such as *Phialocephala fortinii* and precluded the growth of slow-growing ericoid mycorrhizal taxa (e.g., *Rhizoscyphus ericae*, *Capronia* spp.). Their results suggest that DSE fungal species richness increases through ecosystem de-velopment, at least during early succession through to peak biomass. The authors reported that taxa related to the *Phialocephala fortinii – Acephala applanata* species complex (PAC) were ubiquitous along the gradient, but *Phialophora* spp. were apparently restricted to the earli-est successional stage.

DNA of dark septate endophytes has been sampled from the forefront of the Lyman Glacier chronosequence (Jumpponen 2003) despite the absence of suitable host plants. Jumpponen (2003) suggested that this DNA was sourced from dormant spores, highlighting the impor-tance of airborne spore deposition early in succession for fungal communities. Dispersal limitation in DSE communities is poorly understood. DSE taxa typically produce asexual survival propagules (but see Zaffarano et al. 2011) such as microsclerotia and conidia, and some have been shown to do so even in the absence of host roots (Day and Currah 2011), which could also contribute to presence on glacial forefronts. As with ericoid and arbuscular mycorrhizas, further studies across chronosequences, particularly at later stages of ecosystem development, are needed.

Plants, fungi, and pedogenesis

The interaction of plant communities with pedogene-sis has long been recognised (Jenny 1958), with plant communities both responding to and influencing soil
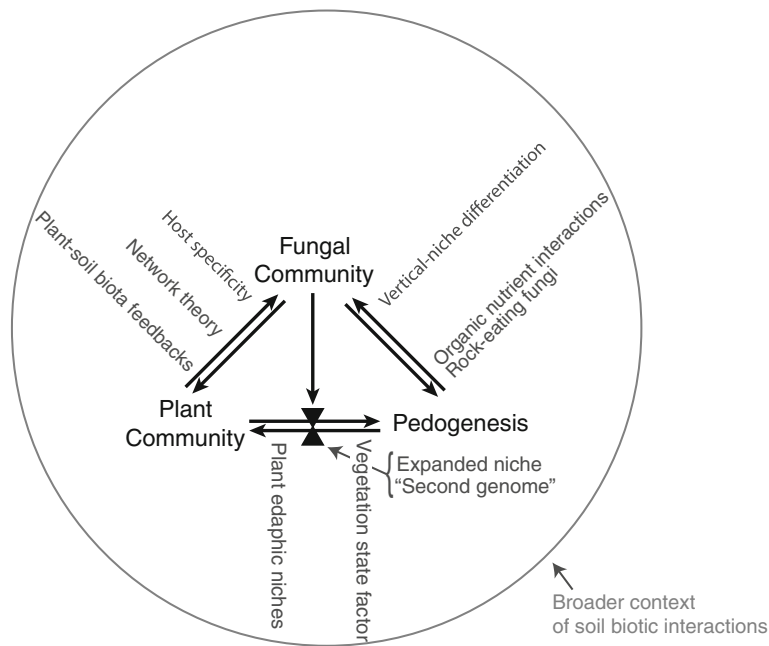
Fig. 3 Ecosystem development and retrogression includes the interaction between not just plant communities and pedogenesis but also the community of mycorrhizal fungi that form a major interface between plants and soils, and that can modulate plant–soil interactions (*thick arrows*). These latter interactions form the scope of this review. Some of the major theories and concepts for components of the interaction are shown in phrases in *grey text*. The position of each phrase along arrows reflects the degree to which it focuses on one end or the other of the interaction. For example, in plant–fungal interactions, plant–soil feedbacks have focused primarily on plant community outcomes, whereas host-specificity has tended to focus on fungal community effects, with network theory being more balanced between the two

properties (Northup et al. 1998; Reich et al. 2005). To the extent that mycorrhizal fungi have been considered, it has largely been in the context of their role in modulating the plant–soil interaction, particularly expanding the realised niche of plants (Bever et al. 2010; Rodriguez-Cabal et al. 2012). At the most extreme, mycorrhizal fungi have been considered as part of the plant's 'second genome'; effectively treating the fungal community as an extension of the plant's enzymatic and physiological capabilities (Berendsen et al. 2012). This approach has some merit, but fails to recognise that mycorrhizal fungi are, themselves, free-living macroorganisms, both responding to and driving pedogenesis and plant community composition. In this section we focus on the fungal parts of the interaction (see Fig. 3) considering interactions between mycorrhizal fungal communities and pedogenesis and interactions between mycorrhizal fungal communities and plant communities. In focusing on these two components, it is important to recognise that these interactions occur in a broader context of

rhizosphere and soil interactions. In particular, mycorrhiza helper bacteria (bacteria found in the mycorrhizosphere of arbuscular and ectomycorrhizal fungi; Frey-Klett et al. 2007) play important roles in the establishment and infection of the mycorrhizal fungi on the plant root (Garbaye 1994), the acquisition of nutrients from mineral or organic substrates for the plant–fungus symbiosis (Calvaruso et al. 2007; Koele et al. 2009; Uroz et al. 2009) and protection against pathogens (Frey-Klett et al. 2005). Mycorrhizal fungi also play a major role in soil trophic webs, and may be key components of the increasingly fungal dominance of soil food web dynamics as ecosystems age (Williamson et al. 2005).

Pedogenesis and mycorrhizal fungi

Soil chemical and physical properties strongly influence community composition of mycorrhizal fungi (Dickie et al. 2009), with fungal species responding to soil variables such as pH, nitrate, base cation status,

and P (Fitzsimons et al. 2008). Soil pH emerges from multiple studies as a relatively strong factor in fungal community composition compared to more apparent drivers (Fitzsimons et al. 2008). For example, in a study of geothermal grassland soils in Yellowstone National Park, USA, Lekberg et al. (2011) found that pH was a stronger determinant of arbuscular mycorrhizal fungal communities than either temperature or plant communities. Nitrogen also has strong effects on fungal communities, with numerous studies of atmospheric N deposition showing a shift in composition, change in function, and loss of diversity following N deposition (Lilleskov et al. 2002; Wright et al. 2009; Cox et al. 2010). The influence of P on fungal communities has received less attention, yet it may have stronger and more consistent effects than N on the degree of mycorrhizal infection of plants (Treseder 2004) and fungal community composition (Twieg et al. 2007; Dickie et al. 2009).

Young soils are characteristically highly inorganic, dominated by bare rock or mineral surfaces with little or no vegetation and limited soil microbial activity. As ecosystems develop, complex soils become dominated by organic materials, with nutrients increasingly sequestered within biomass or in recalcitrant soil-organic-matter complexes (Richardson et al. 2004; Wardle et al. 2004; Peltzer et al. 2010; Turner et al. 2012a, b). Through time, soils become vertically stratified with the development of an organic horizon and acidification of upper mineral horizons. This soil horizon development is an important axis of fungal niche differentiation (Taylor and Bruns 1999; Dickie et al. 2002b; Rosling et al. 2003; Genney et al. 2006; Lindahl et al. 2007; Wurzburger et al. 2012). The accumulation of organic materials creates a novel environment from the largely inorganic mineral soil, and mycorrhizal fungi can dominate the functioning of organic nutrient cycles. As discussed above, changes in mycorrhizal community structure with ecosystem development may be more closely related to the development of different organic and mineral soil horizons than with ecosystem stage. In support of this view, Dickie et al. (2002b) and Lindahl et al. (2007) have shown niche differentiation in different organic horizons and the top mineral soil, and Rosling et al. (2003) and Scattolin et al. (2008) found differences in ectomycorrhizal community structures between organic and mineral soil horizons. Arbuscular mycorrhizal fungal and ericoid mycorrhizal fungal communities are both also responsive to soil depth (Oehl et al. 2005;

Wurzburger et al. 2012). The degree to which vertical niche differentiation is driven by nutrient resources versus microsite conditions (e.g., absolute levels of, or variability in, pH, soil moisture, temperature, CO_2, and other factors) or other microsite differences remains largely unexplored.

Mycorrhizal fungal communities are not simply passengers in the process of pedogenesis, but can also be important drivers. Ectomycorrhizal and ericoid mycorrhizal fungi are commonly thought to decompose organic matter in soil (Read and Perez-Moreno 2003), including some recalcitrant forms. More recently it has been suggested that arbuscular mycorrhizal fungi can also enhance the uptake of organic N and P (Tarafdar and Marschner 1994; Cheng et al. 2012; Veresoglou et al. 2012) although Hodge and Fitter (2010) suggest that arbuscular mycorrhizal fungi use organic N predominantly for their own nutrition and do not transport it to the host plant, unlike ectomycorrhizal and ericoid mycorrhizal fungi. Because most mycorrhizal fungi obtain carbon from hosts, nutrient uptake by mycorrhizas from organic matter can influence soil nutrient stoichiometry by removing N, P or other nutrients decoupled from C. Using a modelling approach, Orwin et al. (2011) suggested that mycorrhizal fungal uptake of nutrients depletes the residual organic matter and generates a poorer-quality substrate for decomposition by saprotrophs and other free-living microorganisms. This is in line with observations of decreased litter decomposition when ectomycorrhizal roots are present (Gadgil and Gadgil 1975), although Koide and Wu (2003) note that these field observations may be driven by plant water uptake as well. Furthermore, the accumulation of mycorrhizal exudates, biomass, and necromass over time can form a major part of the organic carbon and nutrient pools in retrogressive ecosystems (Rillig et al. 2001; Wallander et al. 2009; Turner et al. 2012a, b). This accumulation is potentially augmented by the relative recalcitrance of fungal tissue to decomposition (Wallander et al. 2009). Better incorporation of mycorrhizal stoichiometric relationships, particularly the decoupling of C and soil nutrients, may be critical in understanding the role of mycorrhizas in soil organic matter development (Orwin et al. 2011).

In mineral soil, fungal hyphae and exudates bind soil particles and play a key role in soil aggregation (Jehne and Thompson 1981; Rillig et al. 2003; Rillig and Mummey 2006). Mycorrhizal fungi, together with

plant roots, soil microorganisms and decaying organic matter, release organic acids, acidifying the soil and increasing mineral weathering (Bormann et al. 1998; Chadwick and Chorover 2001). As soils develop, some mineral grains develop tunnel-like dissolution pits over a period of several thousand years (Jongmans et al. 1997; Smits et al. 2005; van Schöll et al. 2006). These tunnels have been attributed to the hyphae of ectomycorrhizal fungi, and the excretion of organic acids and dissolution of the mineral structure (Hoffland et al. 2004, 2005; van Schöll et al. 2008; Gazzè et al. 2012). Ectomycorrhizal fungal weathering of minerals has the potential to be an important source of plant nutrients (e.g., Paris et al. 1996; Landeweert et al. 2001; Blum et al. 2002; Glowa et al. 2003; Hoffland et al. 2004, 2005; Smits et al. 2012), although tunnels are likely to be quantitatively much less important than mineral surface weathering (Smits et al. 2005). Most mycorrhizal weathering experiments are lab-based (e.g., Paris et al. 1996; Adeleke et al. 2012; Smits et al. 2012) and give contrasting results. Field-based experiments, particularly those involving substrate bag incubations, show that fungal biomass increases in the presence of apatite particularly when plants are nutrient limited, but suggest that fungal responses are not sensitive to fungal species (Hagerberg et al. 2003; Wallander and Thelin 2008; Berner et al. 2012). Most studies have assumed that fungal tunnelling only occurs in ectomycorrhizal fungi; nonetheless, similar tunnels have been reported in areas where ectomycorrhizal fungi are absent, suggesting non-ectomycorrhizal or even non-fungal explanations in some instances (Sverdrup 2009). Similarly, whether localised weathering by mycorrhizal fungi contributes substantively to the total weathering budget induced by plant growth, organic matter decomposition and associated acidification of the the soil is not known. It is also worth noting that mycorrhizal helper bacteria, which have high mineral weathering capability (Koele et al. 2009; Uroz et al. 2009), may be particularly important in mineral tunnelling.

Tunnelling of primary minerals is a transient phenomenon in ecosystem development. The first tunnels appear in mineral grains coinciding with the depletion of the initial pool of available mineral nutrients, at around 2000 years but vary with parent material, climate, hydrology and vegetation (Hoffland et al. 2002; Smits et al. 2005). After this initial period, mineral tunnelling could increase mineral nutrient availability. However, eventually all primary minerals will have been weathered from the soil leaving no substrate for further weathering. The implications of this for long-term ecosystem development are unclear. By increasing the speed of weathering, mineral tunnelling could increase peak plant biomass, but could also ultimately increase the rate of nutrient loss from the ecosystem. Alternatively, the active use of mineral nutrients by ectomycorrhizal plants could inhibit leaching of these nutrients, thus decreasing the depletion of mineral nutrients and delaying retrogression. Curiously, two of the best-studied chronosequences in terms of P limitation, Franz Josef and Hawaii, both lack ectomyorrhizal fungi. Comparison of the dynamics of these sequences with sequences where ectomycorrhizal fungi are present could be informative, although any direct comparison is confounded by climate and parent material differences. A modelling approach may be better suited to address this question. For instance the model of Orwin et al. (2011) could be used to incorporate ectomycorrhizal weathering to predict shifts in mineral, recalcitrant and organic nutrient pools. A further advantage of the modelling approach would be to allow differentiation of mineral weathering effects from differences in organic nutrient cycling between mycorrhizal types.

Apart from the role of mycorrhizal fungi in nutrient cycling at the surface, many of the important mineral-nutrient pedogenic effects of mycorrhizal fungi occur deep in the soil profile. For example, in a temperate grassland chronosequence, Moore et al. (2010) reported that biological and geochemical cycling of nutrients was spatially separated: biological cycling occurred at the soil surface in a tightly coupled cycle, whereas geochemical nutrient cycles (weathering) occurred at >1 m depth. Unfortunately, most studies of mycorrhizal ecology do not sample below c. 30 cm depth (e.g., Dickie et al. 2002b), leaving deeper soil processes obscure. However, we know that ectomycorrhizal and arbuscular mycorrhizal fungi occur to at least 2–4 m depth in soils (Egerton-Warburton et al. 2003; Bornyasz et al. 2005) and that mycorrhizal effects on soil organic C may extend to at least 1 m depth (Chapela et al. 2001). Unravelling the role of mycorrhizal weathering deep in the soil profile should be a key priority for chronosequence research.

Mycorrhizal fungi – plant community interactions

Mycorrhizal fungal communities can be important determinants of plant community composition and

drivers of plant–soil biota feedbacks (Bever et al. 2010; Klironomos et al. 2011). During early succession or transitions between mycorrhizal types (e.g., ectomycorrhizal tree succession into arbuscular mycorrhizal grasslands), positive plant–soil biota feedback appears common (Dickie et al. 2002a). Most of the evidence for positive biotic feedback involves established plants increasing the local density of compatible symbionts in a site where symbionts would otherwise be limiting (e.g., Dickie et al. 2002a; Ashkannejhad and Horton 2006; Nara 2006a, 2006b; Spence et al. 2011). Nonetheless, Mangan et al. (2010) found positive feedback in arbuscular mycorrhizal forest trees on Barro Colorado Island, Panama, suggesting that positive feedback can also occur within mature, relatively stable ecosystems. Further positive feedback may occur if mycorrhizal fungi serve as conduits for the transfer of nutrients, water or carbon between plants through hyphal linkages. Inter-plant transfer is clearly important in some achlorophyllous plants, but evidence for the ecological significance of hyphal-network resource transfers between photosynthetic plants remains equivocal (reviewed in Bever et al. 2010), perhaps due to the very small size of such transfers (Teste et al. 2010) relative to larger effects of seedling genetics and environment (Bingham and Simard 2013). Regardless of mechanism, where positive feedback occurs it has the potential to contribute to reduced plant diversity (Bever et al. 1997, 2010).

Negative plant–soil biota feedback occurs where plants modify soil communities such that other plant species have increased relative competitiveness. Negative plant–soil biota feedback can occur through increased populations of pathogens. Somewhat counter-intuitively, negative plant–soil feedback can also be driven by beneficial mycorrhizal symbionts (Bever 1999, 2002). This reflects the species-specific interaction between fungi and plants, with plant response to the symbiosis depending on the identity of both plant species and fungal species. Negative feedback does not necessarily require a negative symbiotic interaction, as feedbacks are due to the effect of soil on the relative growth of competing plant species. Negative plant–soil feedbacks can be important for maintaining plant diversity, but can also contribute to species turnover and successional change at larger spatial and temporal scales, particularly in early-successional communities (Kardol et al. 2006).

The extent to which specific plant–fungal interactions can be considered a mutualism rather than parasitism depends on environmental context (Hoeksema et al. 2010). Although no studies to date have examined the nature of this interaction along a chronosequence, previous work on soil nutrient availability suggests that interactions may become less parasitic and more mutualistic as nutrients (particularly P) decline along the sequence and greater nutrient limitation increases the relative benefits to the plant (Graham and Eissenstat 1994). Plants can respond to nutrient conditions by limiting carbon allocation to non-beneficial arbuscular mycorrhizal fungi (Bever et al. 2009; Kiers et al. 2011), thereby reducing the benefit of the association to both partners. However, plant species differ in their ability to adjust allocation in this way, probably related to differences in their root structures and associated capacity to access different nutrient pools (Grman 2012). Host-specific fungi may also be able to demand more resources from their hosts (Bruns et al. 2002), potentially explaining their frequency in early- to mid-succession.

A relatively new development in understanding interactions between mycorrhizal fungal communities and plant communities has been the application of network theory (Bascompte 2009). Network theory is a framework for the study of relationships (links) between objects (nodes). It is applied to a variety of network types, including neural, computer, social, and ecological networks, with the latter normally describing the architecture of interactions among species irrespective of their identity (Bascompte 2009). In ecology, this has expanded from earlier work on food webs to include a wider range of interactions, such as mutualism (Bascompte and Jordano 2007) and parasitism (Tylianakis et al. 2007). Community-wide plant–mycorrhizal fungus association networks have only recently begun to be quantified (Chagnon et al. 2012; Montesinos-Navarro et al. 2012), though practical constraints on identification have meant that these have not yet been studied in a replicated way (e.g., along chronosequences). Despite some potential caveats about the interpretation of these networks (Caruso et al. 2012), they provide a potentially valuable tool in understanding how the structure of mycorrhizal interactions between plant and fungal communities changes through ecosystem development.

Networks of interactions among mutualists tend to have a nested structure, whereby specialists interact with symbionts that also interact with generalists (Bascompte and Jordano 2007). Not only is this pattern widespread across regions and types of organisms, but it is known to be important for maintaining network stability (Bastolla et al. 2009; Thebault and Fontaine 2010). Therefore, association networks between plants and mycorrhizal mutualists would be predicted to have a nested structure, and this is supported by recent empirical work on plant–arbuscular mycorrhizal networks (Chagnon et al. 2012; Montesinos-Navarro et al. 2012).

Both mycorrhizal fungi and mycorrhizal plants vary strongly in their specificity, with fungi ranging from ultra-generalist species such as *Cenococcum geophilum* (Dickie 2007), to fungi specific to particular plant genera (e.g., *Alnicola*), and plants ranging from a few with extremely broad receptivity to fungi (e.g., arbutoid mycorrhizal *Arctostaphylos uva-ursi*; Krpata et al. 2007) to plants that associate with only a very few species of fungi (e.g., *Pisonia* spp.; Suvi et al. 2010; Hayward and Horton 2012). Smith and Read (2008) suggested that plant–mycorrhizal fungi associations become increasingly specialised through time, in keeping with Odum's (1969) suggestion that niches become narrower as ecosystems develop. However, examples of ectomycorrhizal fungi specialising on early-successional species (see *Ectomycorrhizal fungi along chronosequences* and Fig. 1), and increasing evidence of host specificity in some arbuscular mycorrhizal fungi, suggest that plant compositional changes may drive turnover in the presence or absence of certain mycorrhizal fungi, rather than a consistent shift in specialisation along the chronosequence.

We suggest that application of network theory to mycorrhizal fungi across resource gradients has strong potential to enhance both our understanding of network theory and our understanding of mycorrhizal ecology. The outcome of network interactions can be highly dependent on the nature of the interaction (Thebault and Fontaine 2010). By grading from mutualism to parasitism depending on environmental context (Hoeksema et al. 2010), mycorrhizas provide a unique system that can help us to understand whether different interaction types among the same organisms can produce different network structures, as well as whether mutualistic network structure theory developed largely in the context of motile organisms (e.g.,

pollinators) can also be applied to non-motile mutualists. Recent empirical plant–mycorrhizal fungus networks (Chagnon et al. 2012; Montesinos-Navarro et al. 2012) suggest patterns consistent with those of mutualist networks involving mobile animals, though simulation studies have demonstrated that declining mobility of species leads to lower connectedness of interaction networks, higher asymmetries of interaction strengths between partners, and less predictable interaction patterns (Morales and Vázquez 2008). Therefore, as more plant–fungal networks are studied, important differences between their structure and those of other mutualist networks may emerge.

Conclusions

Despite the critical role of mycorrhizas in nutrient acquisition by plants, mycorrhizal fungi remain poorly integrated within the ecosystem development and retrogression paradigm. In part, this may reflect a widespread view of predictable shifts in mycorrhizal status over ecosystem development, despite evidence such shifts are not predictable (Table 1). Instead we find that single mycorrhizal types can dominate over very long periods and strong gradients of soil N and P. Chronosequences therefore present an ideal system for testing hypotheses about the role of mycorrhizas and mycorrhizal fungal community composition in ecosystems (Klironomos et al. 2011) and, conversely, the role of soil nutrients in fungal community composition and mutualistic interactions.

Across different mycorrhizal types there are striking differences in the types of ecosystems that have been studied. For example, an extensive literature has developed on ectomycorrhizal fungi and dark septate endophytes in early primary succession, yet virtually nothing is known of ericoid mycorrhizal fungi in primary succession. Conversely, ericoid mycorrhizal fungi are frequently studied in high soil organic matter, potentially retrogressive sites, where relatively little work has been done on arbuscular mycorrhiza or ectomycorrhizal fungi. Indeed, across most mycorrhizal types there is a lack of information on retrogressive sequences. Despite these limitations, some overarching conclusions emerge:

1. Existing models of predictable trajectories of mycorrhizal types over ecosystem development do not adequately describe the observed trajectories on

well-described retrogressive sequences. Instead, we find that single mycorrhizal types can dominate over most or all of ecosystem development.

2. In early succession, dispersal limitation is an important factor shaping fungal communities. For ectomycorrhizal fungi, which have effective long-distance dispersal, this results in a predictable suite of fungi adapted to early succession. Arbuscular mycorrhizal fungi appear less predictable in early succession, perhaps due to less effective long-distance dispersal leading to a greater stochasticity and larger role of the regional species pool.

3. Pedogenesis is an important factor in shaping fungal communities through development of organic horizons, changing pH and altered nutrient availability. Although a literature has developed around vertical niche differentiation by ectomycorrhizal fungi, little is known of how soil pedogenesis influences arbuscular or ericoid mycorrhizal fungal communities. Even within ectomycorrhizal fungal ecology there has been no integration of vertical niche studies with pedogenesis, which is surprising given how closely pedogenesis and vertical profile development are linked.

4. Mycorrhizal fungi are important drivers of pedogenic processes, through physical binding of soil particles, exudation of organic compounds, shifting soil nutrient stoichiometry, and weathering of minerals. This suggests that the absence of major mycorrhizal types along some chronosequences (e.g., ectomycorrhizas at Franz Josef, NZ, and Hawaii, USA) could have important consequences for the way that ecosystems develop, and potentially limit generalisations across chronosequences, if differences in mycorrhizal type are not considered.

5. The interactions between fungal communities and plant species have been studied primarily in the context of plant–soil feedbacks and mainly for arbuscular mycorrhizal plants. Recent application of network theory to these complex community interactions shows promise as a technique for elucidating emergent properties, as well as for testing network theory itself.

Retrogressive sequences provide a unique opportunity to improve our understanding of how mycorrhizal communities respond to gradients of soil nutrient availability and physical structure. We hope that one outcome of this review may be to encourage mycorrhizal researchers and chronosequence researchers to look for ways to unify and integrate findings between the two fields of research. In particular, we suggest that chronosequences represent an underutilised natural experiment for mycorrhizal ecology. This is especially important for those mycorrhizal symbioses that are difficult to manipulate ex situ, including most arbuscular mycorrhizal fungi, some ectomycorrhizal fungi (e.g., *Cortinarius*, *Russula*), and orchid mycorrhizas. Better utilisation of these sequences will advance both mycorrhizal science and our understanding of ecosystem development and retrogression.

References

Adeleke RA, Cloete TE, Bertrand A, Khasa DP (2012) Iron ore weathering potentials of ectomycorrhizal plants. Mycorrhiza 22:535–544

Agerer R (2001) Exploration types of ectomycorrhizae; a proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. Mycorrhiza 11:107–114

Alfredsen G, Hoiland K (2001) Succession of terrestrial macrofungi along a deglaciation gradient at Glacier Blaisen, South Norway. Nord J Bot 21:19–37

Allen MF (1987) Re-establishment of mycorrhizas on Mount St Helens: migration vectors. Trans Br Mycol Soc 88:413–417

Allen MF, MacMahon JA (1988) Direct VA mycorrhizal inoculation of colonizing plants by pocket gophers (*Thomomys talpoides*) on Mount St. Helens. Mycologia 80:754–756

Allen MF, Crisafulli C, Friese CF, Jeakins SL (1992) Re-formation of mycorrhizal symbioses on Mount St Helens, 1980-1990—interactions of rodents and mycorrhizal fungi. Mycol Res 96:447–453

Arveby AS, Granhall U (1998) Occurrence and succession of mycorrhizas in *Alnus incana*. Swed J Agric Res 28:117–127

Ashford AE, Allaway WG, Reed ML (1996) A possible role for the thick-walled epidermal cells in the mycorrhizal hair roots of *Lysinema ciliatum* R. Br. and other Epacridaceae. Ann Bot 77:375–381

Ashkannejhad S, Horton TR (2006) Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. New Phytol 169:345–354

Avis PG (2012) Ectomycorrhizal iconoclasts: the ITS rDNA diversity and nitrophilic tendencies of foetid *Russula*. Mycologia. doi:10.3852/11-399

Bascompte J (2009) Disentangling the web of life. Science 325:416–419

Bascompte J, Jordano P (2007) Plant–animal mutualistic networks: the architecture of biodiversity. Annu Rev Ecol Evol Syst 38:567–593

Bastolla U, Fortuna MA, Pascual-Garcia A, Ferrera A, Luque B, Bascompte J (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1020

Bellei MD, Garbaye J, Gil M (1992) Mycorrhizal succession in young *Eucalyptus viminalis* plantations in Santa-Catarina (Southern Brazil). For Ecol Manag 54:205–213

Berendsen RL, Pieterse CMJ, Bakker PAHM (2012) The rhizosphere microbiome and plant health. Trends Plant Sci 17:478–486

Bergero R, Perotto S, Girlanda M, Vidano G, Luppi AM (2000) Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). Mol Ecol 9:1639–1649

Berner C, Johansson T, Wallander H (2012) Long-term effect of apatite on ectomycorrhizal growth and community structure. Mycorrhiza. doi:10.1007/s00572-012-0438-y

Bever JD (1999) Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. Ecol Lett 2:52–61

Bever JD (2002) Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. Proc R Soc Lond B Biol Sci 269:2595–2601

Bever JD, Westover KM, Antonovics J (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. J Ecol 85:561–573

Bever JD, Schultz PA, Pringle A, Morton JB (2001) Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. Bioscience 51:923–931

Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M (2009) Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol Lett 12:13–21

Bever JD, Dickie IA, Facelli E, Facelli JM, Klironomos J, Moora M, Rillig MC, Stock WD, Tibbett M, Zobel M (2010) Rooting theories of plant community ecology in microbial interactions. Trends Ecol Evol 25:468–478

Bidartondo MI, Read DJ, Trappe JM, Merckx V, Ligrone R, Duckett JG (2011) The dawn of symbiosis between plants and fungi. Biol Lett 7:574–577

Bingham MA, Simard SW (2013) Seedling genetics and life history outweigh mycorrhizal network potential to improve conifer regeneration under drought. For Ecol Manag 287:132–139

Blaalid R, Carlsen T, Kumar S, Halvorsen R, Ugland KI, Fontana G, Kauserud H (2012) Changes in the root-associated fungal communities along a primary succession gradient analysed by 454 pyrosequencing. Mol Ecol 21:1897–1908

Blum JD, Klaue A, Nezat CA, Driscoll CT, Johnson CE, Siccama TG, Eagar C, Fahey TJ, Likens GE (2002) Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. Nature 417:729–731

Bormann BT, Wang D, Snyder MC, Bormann FH, Benoit G, April R (1998) Rapid, plant-induced weathering in an aggrading experimental ecosystem. Biogeochemistry 43:129–155

Bornyasz MA, Graham RC, Allen MF (2005) Ectomycorrhizae in a soil-weathered granitic bedrock regolith: linking matrix resources to plants. Geoderma 126:141–160

Bougoure DS, Parkin PI, Cairney JWG, Alexander IJ, Anderson IC (2007) Diversity of fungi in hair roots of Ericaceae varies along a vegetation gradient. Mol Ecol 16:4624–4636

Brenner DL, Amundson R, Baisden WT, Kendall C, Harden J (2001) Soil N and 15N variation with time in a California annual grassland ecosystem. Geochim Cosmochim Acta 65:4171–4186

Brundrett MC (2002) Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304

Brundrett MC (2004) Diversity and classification of mycorrhizal associations. Biol Rev 79:473–495

Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77

Bruns TD (1995) Thoughts on the processes that maintain local species diversity of ectomycorrhizal fungi. Plant Soil 170:63–73

Bruns TD, Shefferson RP (2004) Evolutionary studies of ectomycorrhizal fungi: recent advances and future directions. Can J Bot 82:1122–1132

Bruns TD, Bidartondo MI, Taylor DL (2002) Host specificity in ectomycorrhizal communities: what do the exceptions tell us? Integr Comp Biol 42:352–359

Bruns TD, Peay KG, Boynton PJ, Grubisha LC, Hynson NA, Nguyen NH, Rosenstock NP (2009) Inoculum potential of *Rhizopogon* spores increases with time over the first 4 year of a 99-year spore burial experiment. New Phytol 181:463–470

Cairney JWG, Meharg AA (2003) Ericoid mycorrhiza: a partnership that exploits harsh edaphic conditions. Eur J Soil Sci 54:735–740

Calvaruso C, Turpault M-P, Leclerc E, Frey-Klett P (2007) Impact of ectomycorrhizosphere on the functional diversity of soil bacterial and fungal communities from a forest stand in relation to nutrient mobilization processes. Microb Ecol 54:567–577

Caruso T, Rillig MC, Garlaschelli D (2012) On the application of network theory to arbuscular mycorrhizal fungi–plant interactions: the importance of basic assumptions. New Phytol 194:891–894

Cázares E, Trappe JM, Jumpponen A (2005) Mycorrhiza-plant colonization patterns on a subalpine glacier forefront as a

model system of primary succession. Mycorrhiza 15:405–416

Chadwick OA, Chorover J (2001) The chemistry of pedogenic thresholds. Geoderma 100:321–353

Chagnon PL, Bradley RL, Klironomos JN (2012) Using ecological network theory to evaluate the causes and consequences of arbuscular mycorrhizal community structure. New Phytol. doi:10.1111/j.1469-8137.2011.04044.x

Chapela IH, Osher LJ, Horton TR, Henn MR (2001) Ectomycorrhizal fungi introduced with exotic pine plantations induce soil carbon depletion. Soil Biol Biochem 33:1733–1740

Chapin FS III, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecol Monogr 64:149–175

Cheng L, Brooker FL, Cong T, Burkey KO, Zhou L, Shew HD, Rufty TW, Hu S (2012) Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO_2. Science 337:1084–1087

Courty P-E, Buée M, Diedhiou AG, Le Frey-Klett FPT, Rineau F, Turpault M-P, Uroz S, Garbaye J (2010) The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. Soil Biol Biochem 42:679–698

Cox F, Barsoum N, Lilleskov EA, Bidartondo MI (2010) Nitrogen availability is a primary determinant of conifer mycorrhizas across complex environmental gradients. Ecol Lett 13:1103–1113

Crocker RL, Major J (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J Ecol 43:427–448

Dahlberg A, Stenlid J (1994) Size, distribution and biomass of genets in populations of Suillus bovinus (L.: Fr.) Roussel revealed by somatic incompatibility. New Phytol 128:225–234

Day MJ, Currah RS (2011) Role of selected dark septate endophyte species and other hyphomycetes as saprobes on moss gametophytes. Botany 89:349–359

del Moral R, Saura JM, Emenegger JN (2010) Primary succession trajectories on a barren plain, Mount St. Helens, Washington. J Veg Sci 21:857–867

den Bakker HC, Zuccarello GC, Kuyper TH, Noordeloos ME (2004) Evolution and host specificity in the ectomycorrhizal genus Leccinum. New Phytol 163:201–215

Dhillion SS (1994) Ectomycorrhizae, arbuscular mycorrhizae, and rhizoctonia sp. of alpine and boreal Salix spp. in Norway. Arct Alp Res 26:304–307

Dickie IA (2007) Host preference, niches and fungal diversity. New Phytol 174:230–233

Dickie IA, Moyersoen B (2008) Towards a global view of ectomycorrhizal ecology. New Phytol 180:263–265

Dickie IA, Reich PB (2005) Ectomycorrhizal fungal communities at forest edges. J Ecol 93:244–255

Dickie IA, Koide RT, Fayish AC (2001) Vesicular-arbuscular mycorrhizal infection of Quercus rubra seedlings. New Phytol 151:257–264

Dickie IA, Koide RT, Steiner KC (2002a) Influences of established trees on mycorrhizas, nutrition, and growth of Quercus rubra seedlings. Ecol Monogr 72:505–521

Dickie IA, Xu B, Koide RT (2002b) Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. New Phytol 156:527–535

Dickie IA, Guza RC, Krazewski SE, Reich PB (2004) Shared ectomycorrhizal fungi between a herbaceous perennial (Helianthemum bicknellii) and oak (Quercus) seedlings. New Phytol 164:375–382

Dickie IA, Richardson SJ, Wiser SK (2009) Ectomycorrhizal fungal communities in two temperate Nothofagus rainforests respond to changes in soil chemistry after small-scale timber harvesting. Can J For Res 39:1069–1079

Diez JM (2007) Hierarchical patterns of symbiotic orchid germination linked to adult proximity and environmental gradients. J Ecol 95:159–170

Doblas-Miranda E, Wardle DA, Peltzer DA, Yeates GW (2008) Changes in the community structure and diversity of soil invertebrates across the Franz Josef Glacier chronosequence. Soil Biol Biochem 40:1069–1108

Egerton-Warburton LM, Graham RC, Hubbert KR (2003) Spatial variability in mycorrhizal hyphae and nutrient and water availability in a soil-weathered bedrock profile. Plant Soil 249:331–342

Finlay R (2008) Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. J Exp Bot 59:1115–1126

Fiore-Donno AM, Martin F (2001) Populations of ectomycorrhizal Laccaria amethystina and Xerocomus spp. show contrasting colonization patterns in a mixed forest. New Phytol 152:533–542

Fitzsimons MS, Miller RM, Jastrow JD (2008) Scale-dependent niche axes of arbuscular mycorrhizal fungi. Oecologia 158:117–127

Fleming LV (1984) Effects of soil trenching and coring on the formation of ectomycorrhizas on birch seedlings grown around mature trees. New Phytol 98:143–153

Fleming LV, Deacon JW, Last FT, Donaldson SJ (1984) Influence of propagating soil on the mycorrhizal succession of birch seedlings transplanted to a field site. Trans Br Mycol Soc 82:707–711

Fleming LV, Deacon JW, Last FT (1986) Ectomycorrhizal succession in a Scottish birch wood. In: Gianinazzi-Pearson V (ed) Physiological and genetical aspects of Mycorrhizae. INRA, Dijon, pp 259–264

Frey-Klett P, Chavatte M, Clausse M-L, Courrier S, le Roux C, Raaijmakers J, Martinotti MG, Pierrat J-C, Garbaye J (2005) Ectomycorrhizal symbiosis affects functional diversity of rhizosphere fluorescent pseudomonads. New Phytol 165:317–328

Frey-Klett P, Garbaye J, Tarkka M (2007) The mycorrhiza helper bacteria revisited. New Phytol 176:22–36

Fujiyoshi M, Yoshitake S, Watanabe K, Murota K, Tsuchiya Y, Uchida M, Nakatsubo T (2011) Successional changes in ectomycorrhizal fungi associated with the polar willow Salix polaris in a deglaciated area in the High Arctic, Svalbard. Polar Biol 34:667–673

Gadgil RL, Gadgil PD (1975) Suppression of litter decomposition by mycorrhizal roots of Pinus radiata. N Z J For Sci 5:33–41

Galante TE, Horton TR, Swaney DP (2011) 95 % of basidiospores fall within 1 m of the cap: a field- and modeling-based study. Mycologia 103:1175–1183

Gao Q, Yang ZL (2010) Ectomycorrhizal fungi associated with two species of *Kobresia* in an alpine meadow in the eastern Himalaya. Mycorrhiza 20:281–287

Garbaye J (1994) Helper bacteria: a new dimension to the mycorrhizal symbiosis. New Phytol 128:197–210

Gassibe PV, Fabero RF, Hernandez-Rodriguez M, Oria-de-Rueda JA, Martin-Pinto P (2011) Fungal community succession following wildfire in a Mediterranean vegetation type dominated by *Pinus pinaster* in Northwest Spain. For Ecol Manag 262:655–662

Gazzè SA, Saccone L, Vala Ragnarsdottir K, Smits MM, Duran AL, Leake JR, Banwart SA, McMaster TJ. (2012) Nanoscale channels on ectomycorrhizal-colonized chlorite: evidence for plant-driven fungal dissolution. J Geophys Res 117:G00N09, doi:10.1029/2012JG002016

Genney DR, Anderson IC, Alexander IJ (2006) Fine-scale distribution of pine ectomycorrhizas and their extramatrical mycelium. New Phytol 170:381–390

George E, Marschner H, Jakobsen I (1995) Role of arbuscular mycorrhizal fungi in uptake of phosphorus and nitrogen from soil. Crit Rev Biotech 15:257–270

Gherbi H, Delaruelle C, Selosse MA, Martin F (1999) High genetic diversity in a population of the ectomycorrhizal basidiomycete *Laccaria amethystina* in a 150–year–old beech forest. Mol Ecol 8:2003–2013

Gibson F, Deacon JW (1990) Establishment of ectomycorrhizas in aseptic culture: effects of glucose, nitrogen and phosphorus in relation to successions. Mycol Res 94:166–172

Glowa K, Arocena J, Massicotte H (2003) Extraction of potassium and/or magnesium from selected soil minerals by Piloderma. Geomicrobiol J 20:99–111

Graham JH, Eissenstat DM (1994) Host genotype and the formation and function of VA mycorrhizae. Plant Soil 159:179–185

Grau O, Rautio P, Heikkinen J, Saravesi K, Kozlov MV, Markkola A (2010) An ericoid shrub plays a dual role in recruiting both pines and their fungal symbionts along primary succession gradients. Oikos 119:1727–1734

Grelet G-A, Meharg AA, Alexander IJ (2005) Carbon availability affects nitrogen source utilisation by *Hymenoscyphus ericae*. Mycol Res 109:469–477

Grelet G-A, Meharg AA, Duff EI, Anderson IC, Alexander IJ (2009) Small genetic differences between ericoid mycorrhizal fungi affect nitrogen uptake by *Vaccinium*. New Phytol 181:708–718

Grelet G-A, Johnson D, Vrålstad T, Alexander IJ, Anderson IC (2010) New insights into the mycorrhizal *Rhizoscyphus ericae* aggregate: spatial structure and co-colonization of ectomycorrhizal and ericoid roots. New Phytol 188:210–222

Grman E (2012) Plant species differ in their ability to reduce allocation to non-beneficial arbuscular mycorrhizal fungi. Ecology 93:711–718

Grünig CR, Queloz V, Sieber TN, Holdenrieder O (2008) Dark septate endophytes (DSE) of the *Phialocephala fortinii* sl-*Acephala applanata* species complex in tree roots: classification, population biology, and ecology. Botany 86:1355–1369

Hagerberg D, Thelin G, Wallander H (2003) The production of ectomycorrhizal mycelium in forests: Relation between forest nutrient status and local mineral sources. Plant Soil 252:279–290

Hambleton S, Sigler L (2005) *Meliniomyces*, a new anamorph genus for root-associated fungi with phylogenetic affinities to *Rhizoscyphus ericae* (≡ *Hymenoscyphus ericae*), Leotiomycetes. Stud Mycol 53:1–27

Harden JW (1982) A quantitative index of soil development from field descriptions: examples from a chronosequence in central California. Geoderma 28:1–28

Hart MM, Reader RJ (2002) Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytol 153:335–344

Hayward JA, Horton TR (2012) Edaphic factors do not govern the ectomycorrhizal specificity of *Pisonia grandis* (Nyctaginaceae). Mycorrhiza 22:647–652

Helm DJ, Allen EB, Trappe JM (1996) Mycorrhizal chronosequence near Exit Glacier, Alaska. Can J Bot 74:1496–1506

Helm DJ, Allen EB, Trappe JM (1999) Plant growth and ectomycorrhiza formation by transplants on deglaciated land near Exit Glacier, Alaska. Mycorrhiza 8:297–304

Hobbie EA (2006) Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. Ecology 87:563–569

Hobbie EA, Jumpponen A, Trappe J (2005) Foliar and fungal (15) N :(14) N ratios reflect development of mycorrhizae and nitrogen supply during primary succession: testing analytical models. Oecologia 146:258–268

Hodge A, Fitter AH (2010) Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. Proc Natl Acad Sci U S A 107:13754–13759

Hodge A, Campbell CD, Fitter AH (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature 413:297–299

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GW, Klironomos JN, Umbanhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407

Hoffland E, Giesler R, Jongmans T, van Breemen N (2002) Increasing feldspar tunneling by fungi across a north Sweden podzol chronosequence. Ecosystems 5:11–22

Hoffland E, Kuyper TW, Wallander H, Plassard C, Gorbushina AA, Haselwandter K, Holmström S, Landeweert R, Lundström US, Rossling A, Sen R, Smits MM, van Hees PAW, van Breemen N (2004) The role of fungi in weathering. Front Ecol Environ 2:258–264

Hoffland E, Smits MM, van Schöll L, Landeweert R (2005) Rock-eating mycorrhizas: Mobilizing nutrients from minerals? In: Li CJ, Zhang FS, Doberman A, Hinsinger P, Oenema O, Peng SB, Rengel Z, Shen QR, Welch R, von Wirén N, Yan XL, Zhu YG (eds) Plant nutrition for food security, human health and environmental protection. Tsinghua University Press, Beihing, pp 802–803

Hogberg P, Read DJ (2006) Towards a more plant physiological perspective on soil ecology. Trends Ecol Evol 21:548–554

Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA (2011) Species- and community-level patterns in fine root traits along a 120 000-year soil

chronosequence in temperate rain forest. J Ecol 99:954–963

Horton TR (2006) The number of nuclei in basidiospores of 63 species of ectomycorrhizal Homobasidiomycetes. Mycologia 98:233–238

Horton TR, Cázares E, Bruns TD (1998) Ectomycorrhizal, vesicular-arbuscular and dark septate fungal colonization of bishop pine (*Pinus muricata*) seedlings in the first 5 months of growth after wildfire. Mycorrhiza 8:11–18

Horton TR, Bruns TD, Parker VT (1999) Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. Can J Bot 77:93–102

Hutton J, Dixon KW, Sivasithamparam K, Pate JS (1997) Effect of habitat disturbance on inoculum potential of Ericoid endophytes of Western Australian heaths (Epacridaceae). New Phytol 135:739–744

Ishida TA, Nara K, Tanaka M, Kinoshita A, Hogetsu T (2008) Germination and infectivity of ectomycorrhizal fungal spores in relation to their ecological traits during primary succession. New Phytol 180:491–500

Jehne W, Thompson CH (1981) Endomycorrhizae in plant colonization on coastal sand–dunes at Cooloola, Queensland. Aust J Ecol 6:221–230

Jenny H (1958) Role of the plant factor in the pedogenic functions. Ecology 39:5–16

Jenny H (1980) The soil resource, origin and behaviour. Springer, New York

Johnson NC, Zak DR, Tilman D, Pfleger FL (1991) Dynamics of vesicular-arbuscular mycorrhizae during old field succession. Oecologia 86:349–358

Johnston VR (1994) California forests and woodlands: A natural history. University of California Press, Berkeley and Los Angeles, California, USA, 222

Jongmans AG, van Breemen N, Lundström U, van Hees PAW, Finlay RD, Srinivasan M, Unestam T, Giesler R, Melkerud P-A, Olsson M (1997) Rock-eating fungi. Nature 389:682–683

Jumpponen A (2003) Soil fungal community assembly in a primary successional glacier forefront ecosystem as inferred from rDNA sequence analyses. New Phytol 158:569–578

Jumpponen A, Trappe JM (1998) Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytol 140:295–310

Jumpponen A, Trappe JM, Cazares E (1999) Ectomycorrhizal fungi in Lyman Lake Basin: a comparison between primary and secondary successional sites. Mycologia 91:575–582

Jumpponen A, Trappe JM, Cazares E (2002) Occurrence of ectomycorrhizal fungi on the forefront of retreating Lyman Glacier (Washington, USA) in relation to time since deglaciation. Mycorrhiza 12:43–49

Kardol P, Bezemer TM, Van der Putten WH (2006) Temporal variation in plant–soil feedback controls succession. Ecol Lett 9:1080–1088

Kennedy PG, Bruns TD (2005) Priority effects determine the outcome of ectomycorrhizal competition between two *Rhizopogon* species colonizing *Pinus muricata* seedlings. New Phytol 166:631–638

Kennedy PG, Peay KG, Bruns TD (2009) Root tip competition among ectomycorrhizal fungi: are priority effects a rule or an exception? Ecology 90:2098–2107

Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A, Palmer TM, West SA, Vandenkoornhuyse P, Jansa J, Bucking H (2011) Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333:880–882

Kipfer T, Moser B, Egli S, Wohlgemuth T, Ghazoul J (2011) Ectomycorrhiza succession patterns in *Pinus sylvestris* forests after stand-replacing fire in the Central Alps. Oecologia 167:219–228

Kitayama K, Mueller-Dombois D (1995) Vegetation changes along gradients of long-term soil development in the Hawaiian montane rainforest zone. Plant Ecol 120:1–20

Kjøller R, Olsrud M, Michelsen A (2010) Co-existing ericaceous plant species in a subarctic mire community share fungal root endophytes. Fungal Ecol 3:205–214

Klironomos J, Zobel M, Tibbett M, Stock WD, Rillig MC, Parrent JL, Moora M, Koch AM, Facelli JM, Facelli E, Dickie IA, Bever JD (2011) Forces that structure plant communities: quantifying the importance of the mycorrhizal symbiosis. New Phytol 189:366–370

Koele N, Turpault M-P, Hildebrand EE, Uroz S, Frey-Klett P (2009) Interactions between mycorrhizal fungi and mycorrhizosphere bacteria during mineral weathering: budget analysis and bacterial quantification. Soil Biol Biochem 41:1935–1942

Koele N, Dickie IA, Oleksyn J, Richardson SJ, Reich PB (2012) No globally consistent effect of ectomycorrhizal status on foliar traits. New Phytol 196:845–852

Kohout P, Sýkorová Z, Bahram M, Hadincová V, Albrechtová J, Tedersoo L, Vohník M (2011) Ericaceous dwarf shrubs affect ectomycorrhizal fungal community of the invasive *Pinus strobus* and native *Pinus sylvestris* in a pot experiment. Mycorrhiza 21:403–412

Koide RT, Wu T (2003) Ectomycorrhizas and retarded decomposition in a *Pinus resinosa* plantation. New Phytol 158:401–407

Kropp BR, Fortin JA (1988) The incompatibility system and relative ectomycorrhizal performance of monokaryons and reconsitituted dikaryons of *Laccaria bicolor*. Can J Bot 66:289–294

Krpata D, Muhlmann O, Kuhnert R, Ladurner H, Gobl F, Peintner U (2007) High diversity of ectomycorrhizal fungi associated with *Arctostaphylos uva-ursi* in subalpine and alpine zones: potential inoculum for afforestation. For Ecol Manag 250:167–175

Kruger M, Kruger C, Walker C, Stockinger H, Schussler A (2012) Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level. New Phytol 193:970–984

Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103

Landeweert R, Hoffland E, Finlay RD, Kuyper TW, van Breemen N (2001) Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. Trends Ecol Evol 16:248–254

Last FT, Mason PA, Ingleby K, Fleming LV (1984) Succession of fruitbodies of sheathing mycorrhizal fungi associated with *Betula pendula*. For Ecol Manag 9:229–234

Leake JR, Johnson D, Donnelly D, Muckle G, Boddy L, Read D (2004) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Can J Bot 82:1016–1045

Leigh J, Hodge A, Fitter AH (2009) Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. New Phytol 181:199–207

Lekberg Y, Koide RT, Rohr JR, Aldrich-Wolfe L, Morton JB (2007) Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. J Ecol 95:95–105

Lekberg Y, Meadow J, Rohr JR, Redecker D, Zabinski CA (2011) Importance of dispersal and thermal environment for mycorrhizal communities: lessons from Yellowstone National Park. Ecology 92:1292–1302

Li D-W (2005) Release and dispersal of basidiospores from Amanita muscaria var. alba and their infiltration into a residence. Mycol Res 109:1235–1242

Lilleskov EA, Bruns TD (2005) Spore dispersal of a resupinate ectomycorrhizal fungus, Tomentella sublilacina, via soil food webs. Mycologia 97:762–769

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM (2002) Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83:104–115

Lindahl BD, Ihrmark K, Boberg J, Trumbore SE, Högberg P, Stenlid J, Finlay RD (2007) Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytol 173:611–620

Maherali H, Klironomos JN (2012) Phylogenetic and trait-based assembly of arbuscular mycorrhizal fungal communities. PLoS One 7:e36695

Mangan SA, Herre EA, Bever JD (2010) Specificity between neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. Ecology 91:2594–2603

Mark AF, Grealish G, Ward CM, Wilson JB (1988) Ecological studies of a marine terrace sequence in the Waitutu Ecological District of southern New Zealand. Part 1: the vegetation and soil patterns. J R Soc N Z 18:29–58

Martínez-García LB, Armas C, Miranda JD, Padilla FM, Pugnaire FI (2011) Shrubs influence arbuscular mycorrhizal fungi communities in a semi-arid environment. Soil Biol Biochem 43:682–689

Massicotte HB, Melville LH, Peterson RL (2005) Structural features of mycorrhizal associations in two members of the Monotropoideae, Monotropa uniflora and Pterospora andromedea. Mycorrhiza 15:101–110

McCormick MK, Lee Taylor D, Juhaszova K, Burnett RKJ, Whigham DF, O'Neill JP (2012) Limitations on orchid recruitment: not a simple picture. Mol Ecol 21:1511–1523

Molina R (1981) Ectomycorrhizal specificity in the genus Alnus. Can J Bot 59:325–334

Molina R, Massicotte H, Trappe JM (1992) Specificity phenomena in mycorrhizal symbioses: Community-ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning. Chapman and Hall, New York, pp 357–423

Montesinos-Navarro A, Segarra-Moragues JG, Valiente-Banuet A, Verdu M (2012) The network structure of plant-arbuscular mycorrhizal fungi. New Phytol 194:536–547

Moore J, Macalady JL, Schulz MS, White AF, Brantley SL (2010) Shifting microbial community structure across a marine terrace grassland chronosequence, Santa Cruz, California. Soil Biol Biochem 42:21–31

Morales JM, Vázquez DP (2008) The effect of space in plant–animal mutualistic networks: insights from a simulation study. Oikos 117:1362–1370

Moreau PA, Peintner U, Gardes M (2006) Phylogeny of the ectomycorrhizal mushroom genus Alnicola (Basidiomycota, Cortinariaceae) based on rDNA sequences with special emphasis on host specificity and morphological characters. Mol Phylogenet Evol 38:794–807

Moyersoen B, Fitter AH (1999) Presence of arbuscular mycorrhizas in typically ectomycorrhizal host species from Cameroon and New Zealand. Mycorrhiza 8:247–253

Moyersoen B, Beever RE, Martin F (2003) Genetic diversity of Pisolithus in New Zealand indicates multiple long-distance dispersal from Australia. New Phytol 160:569–579

Muhlmann O, Peintner U (2008) Mycobionts of Salix herbacea on a glacier forefront in the Austrian Alps. Mycorrhiza 18:171–180

Muhlmann O, Bacher M, Peintner U (2008) Polygonum viviparum mycobionts on an alpine primary successional glacier forefront. Mycorrhiza 18:87–95

Nara K (2006a) Ectomycorrhizal networks and seedling establishment during early primary succession. New Phytol 169:169–178

Nara K (2006b) Pioneer dwarf willow may facilitate tree succession by providing late colonizers with compatible ectomycorrhizal fungi in a primary successional volcanic desert. New Phytol 171:187–198

Nara K, Nakaya H, Hogetsu T (2003) Ectomycorrhizal sporocarp succession and production during early primary succession on Mount Fuji. New Phytol 158:193–206

Navarro-Ródenas A, Pérez-Gilabert M, Torrente P, Morete A (2012) The role of phosphorus in the ectendomycorrhiza coninuum of desert truffle mycorrhizal plants. Mycorrhiza 22:565–575

Newsham KK (2011) A meta-analysis of plant responses to dark septate root endophytes. New Phytol 190:783–793

Newsham KK, Upson R, Read DJ (2009) Mycorrhizas and dark septate root endophytes in polar regions. Fungal Ecol 2:10–20

Northup RR, Dahlgren RA, McColl JG (1998) Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback? Biogeochemistry 42:189–220

Oba H, Shinozaki N, Oyaizu H, Tawaraya K, Wagatsuma T, Barraquio WL, Saito M (2004) Arbuscular mycorrhizal fungal communities associated with some pioneer plants in the Lahar area of Mt. Pinatubo, Philippines. Soil Sci Plant Nutr 50:1195–1203

Obase K, Tamai Y, Yajima T, Miyamoto T (2007) Mycorrhizal associations in woody plant species at the Mt. Usu volcano, Japan. Mycorrhiza 17:209–215

Odum EP (1969) The strategy of ecosystem development. Science 164:262–279

Oehl F, Sieverding E, Ineichen K, Ris E-A, Boller T, Wiemken A (2005) Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. New Phytol 165:273–283

Oehl F, Schneider D, Sieverding E, Burga CA (2011a) Succession of arbuscular mycorrhizal communities in the foreland

of the retreating Morteratsch glacier in the Central Alps. Pedobiologia 54:321–331

Oehl F, Sieverding E, Palenzuela J, Ineichen K, Alves da Silva G (2011b) Advances in Glomeromycota taxonomy and classification. IMA Fungus 2:191–199

Öpik M, Moora M, Liira J, Zobel M (2006) Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. J Ecol 94:778–790

Öpik M, Metsis M, Daniell TJ, Zobel M, Moora M (2009) Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. New Phytol 184:424–437

Orwin KH, Kirschbaum MU, St John MG, Dickie IA (2011) Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. Ecol Lett 14:493–502

Paris F, Botton B, Lapeyrie F (1996) In vitro weathering of phlogopite by ectomycorrhizal fungi. Plant Soil 179:141–150

Peay KG, Garbelotto M, Bruns TD (2010a) Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91:3631–3640

Peay KG, Kennedy PG, Davies SJ, Tan S, Bruns TD (2010b) Potential link between plant and fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. New Phytol 185:529–542

Peay KG, Kennedy PG, Bruns TD (2011) Rethinking ectomycorrhizal succession: are root density and hyphal exploration types drivers of spatial and temporal zonation? Fungal Ecol 4:233–240

Peay KG, Schubert MG, Nguyen NH, Bruns TD (2012) Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. Mol Ecol 21:4122–4136

Peintner U, Dammrich F (2012) Tomentella alpina and other tomentelloid taxa fruiting in a glacier valley. Mycol Prog 11:109–119

Peltzer DA, Wardle DA, Allison VJ, Baisden WT, Bardgett RD, Chadwick OA, Condron LM, Parfitt RL, Porder S, Richardson SJ (2010) Understanding ecosystem retrogression. Ecol Monogr 80:509–529

Pezzani F, Montana C, Guevara R (2006) Associations between arbuscular mycorrhizal fungi and grasses in the successional context of a two-phase mosaic in the Chihuahuan Desert. Mycorrhiza 16:285–295

Piercey MM, Thormann MN, Currah RS (2002) Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of Rhododendron groenlandicum and Picea mariana in culture. Mycorrhiza 12:175–180

Porder S, Vitousek PM, Chadwick OA, Chamberlain CP, Hilley GE (2007) Uplift, erosion, and phosphorus limitation in terrestrial ecosystems. Ecosystems 10:159–171

Read DJ (1974) Pezizella ericae sp. nov., the perfect state of a typical mycorrhizal endophyte of Ericaceae. Trans Br Mycol Soc 63:381–419

Read DJ (1993) Mycorrhiza in plant communities. Adv Plant Pathol 9:1–31

Read DJ, Perez-Moreno J (2003) Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? New Phytol 157:475–492

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005) Linking tree species, litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8:811–818

Reiners WA, Worley IA, Lawrence DB (1971) Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52:55–69

Reverchon F, Ortega-Larrocea MD, Perez-Moreno J, Pena-Ramirez VM, Siebe C (2010) Changes in community structure of ectomycorrhizal fungi associated with Pinus montezumae across a volcanic soil chronosequence at Sierra Chichinautzin, Mexico. Can J For Res 40:1165–1174

Reynolds HL, Hartley AE, Vogelsang KM, Bever JD, Schultz PA (2005) Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. New Phytol 167:869–880

Richardson SJ, Peltzer DA, Allen RB, McGlone MS, Parfitt RL (2004) Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. Oecologia 139:267–276

Richardson SJ, Peltzer DA, Allen RB, McGlone MS (2005) Resorption proficiency along a chronosequence: responses among communities and within species. Ecology 86:20–25

Rillig MC, Mummey DL (2006) Mycorrhizas and soil structure. New Phytol 171:41–53

Rillig MC, Wright SF, Nichols KA, Schmidt WF, Torn MS (2001) Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. Plant Soil 233:167–177

Rillig MC, Maestre FT, Lamit LJ (2003) Microsite differences in fungal hyphal length, glomalin, and soil aggregate stability in semiarid Mediterranean steppes. Soil Biol Biochem 35:1257–1260

Rodriguez-Cabal MA, Barrios-Garcia MN, Nuñez MA (2012) Positive interactions in ecology: filling the fundamental niche. Ideas Ecol Evol 5:36–41

Rosling A, Landeweert R, Lindahl B, Larsson KH, Kuyper TW, Taylor AFS, Finlay RD (2003) Vertical distribution of ectomycorrhizal fungal taxa in a podzol soil profile. New Phytol 159:775–783

Sanders IR (2004) Plant and arbuscular mycorrhizal fungal diversity – are we looking at the relevant levels of diversity and are we using the right techniques? New Phytol 164:415–418

Scattolin L, Montecchio L, Mosca E, Agerer R (2008) Vertical distribution of the ectomycorrhizal community in the top soil of Norway spruce stands. Eur J For Res 127:347–357

Selmants PC, Hart SC (2008) Substrate age and tree islands influence carbon and nitrogen dynamics across a retrogressive semiarid chronosequence. Global Biogeochem Cycles 22: GB1021, doi:10.1029/2007GB003062

Selosse M, Setaro S, Glatard F, Richard F, Urcelay C, Weiß M (2007) Sebacinales are common mycorrhizal associates of Ericaceae. New Phytol 174:864–878

Sikes BA, Maherali H, Klironomos JN (2012) Arbuscular mycorrhizal fungal communities change among three stages of

primary sand dune succession but do not alter plant growth. Oikos. doi:10.1111/j.1600-0706.2012.20160.x

Simard SW, Perry DA, Smith JE, Molina R (1997) Effects of soil trenching on occurrence of ectomycorrhizas on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol 136:327–340

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis. 3rd edn. Academic Press, London, 787

Smith ME, Henkel TW, Aime MC, Fremier AK, Vilgalys R (2011) Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest. New Phytol 192:699–712

Smits MM, Hoffland E, Jongmans AG, van Breemen N (2005) Contribution of mineral tunnelling to total feldspar weathering. Geoderma 125:59–69

Smits MM, Bonneville S, Benning LG, Banwart SA, Leake JR (2012) Plant-driven weathering of apatite – the role of an ectomycorrhizal fungus. Geobiology 10:445–456

Spence LA, Dickie IA, Coomes DA (2011) Arbuscular mycorrhizal inoculum potential: a mechanism promoting positive diversity–invasibility relationships in mountain beech forests in New Zealand? Mycorrhiza 21:309–314

Stevens PR, Walker TW (1970) The chronosequence concept and soil formation. Q Rev Biol 45:333–350

Suvi T, Tedersoo L, Abarenkov K, Beaver K, Gerlach J, Kõljalg U (2010) Mycorrhizal symbionts of *Pisonia grandis* and *P. sechellarum* in Seychelles: identification of mycorrhizal fungi and description of new *Tomentella* species. Mycologia 102:522–533

Sverdrup H (2009) Chemical weathering of soil minerals and the role of biological processes. Fungal Biol Rev 23:94–100

Tarafdar JC, Marschner H (1994) Phosphatase activity in the rhizosphere and hyphosphere of VA mycorrhizal wheat supplied with inorganic and organic phosphorus. Soil Biol Biochem 26:387–395

Taylor DL, Bruns TD (1999) Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. Mol Ecol 8:1837–1850

Tedersoo L, Suvi T, Beaver K, Kõljalg U (2007) Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpiniaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). New Phytol 175:321–333

Tedersoo L, Sadam A, Zambrano M, Valencia R, Bahram M (2010) Low diversity and high host preference of ectomycorrhizal fungi in western Amazonia, a neotropical biodiversity hotspot. ISME J 4:465–471

Tejesvi MV, Ruotsalainen AL, Markkola AM, Pirttila AM (2010) Root endophytes along a primary succession gradient in northern Finland. Fungal Divers 41:125–134

Terwilliger J, Pastor J (1999) Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83–94

Teste FP, Simard SW, Durall DM, Guy RD, Berch SG (2010) Net carbon transfer between *Pseudotsuga menzeisii* var.

glauca seedlings in the field is influenced by soil disturbance. J Ecol 98:429–439

Thebault E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856

Treseder KK (2004) A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol 164:347–355

Trocha LK, Oleksyn J, Turzanska E, Rudawska M, Reich PB (2007) Living on the edge: Ecology of an incipient *Betula*-fungal community growing on brick walls. Trees – Struct Funct 21:239–247

Trowbridge J, Jumpponen A (2004) Fungal colonization of shrub willow roots at the forefront of a receding glacier. Mycorrhiza 14:283–293

Turnbull MH, Tissue DT, Griffin KL, Richardson SJ, Peltzer DA, Whitehead D (2005) Respiration characteristics in temperate rainforest tree species differ along a long-term soil-development chronosequence. Oecologia 143:271–279

Turner BL, Wells A, Andersen KM, Condron LM (2012a) Patterns of tree community composition along a coastal dune chronosequence in lowland temperate rain forest in New Zealand. Plant Ecol 213:1525–1541

Turner BL, Lambers H, Condron LM, Cramer MD, Leake JR, Richardson AE, Smith SE (2012) Soil microbial biomass and the fate of phosphorus during long-term ecosystem development. Plant Soil: in press

Twieg BD, Durall DM, Simard SW (2007) Ectomycorrhizal fungal succession in mixed temperate forests. New Phytol 176:437–447

Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445:202–205

Uroz S, Calvaruso C, Turpault M-P, Frey-Klett P (2009) Mineral weathering by bacteria: ecology, actors and mechanisms. Trends Microbiol 17:378–387

Usuki F, Narisawa K (2005) Formation of structures resembling ericoid mycorrhizas by the root endophytic fungus *Heteroconium chaetospira* within roots of *Rhododendron obtusum* var. *kaempferi*. Mycorrhiza 15:61–64

van der Heijden EW, Vosatka M (1999) Mycorrhizal associations of *Salix repens* L. communities in succession of dune ecosystems. II. Mycorrhizal dynamics and interactions of ectomycorrhizal and arbuscular mycorrhizal fungi. Can J Bot 77:1833–1841

van Schöll L, Smits MM, Hoffland E (2006) Ectomycorrhizal weathering of the soil minerals muscovite and hornblende. New Phytol 171:805–814

van Schöll L, Kuyper TW, Smits MM, Landeweert R, Hoffland E, van Breemen N (2008) Rock-eating mycorrhizas: their role in plant nutrition and biogeochemical cycles. Plant Soil 303:35–47

Veresoglou SD, Chen B, Rillig MC (2012) Arbuscular mycorrhiza and soil nitrogen cycling. Soil Biol Biochem 46:53–62

Villarreal-Ruiz L, Anderson IC, Alexander IJ (2004) Interaction between an isolate from the *Hymenoscyphus ericae* aggregate and roots of *Pinus* and *Vaccinium*. New Phytol 164:183–192

Villarreal-Ruiz L, Neri-Luna C, Anderson IC, Alexander IJ (2012) In vitro interactions between ectomycorrhizal fungi and ericaceous plants. Symbiosis 56:67–75

Vitousek PM (1998) Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. Ecosystems 1:401–407

Vohník M, Albrechtová (2011) The co-occurence and morphological continuum between ericoid mycorrhiza and dark septate endophytes in roots of six European *Rhododendron* species. Folia Geobot 46:373–386

Vralstad R, Fossheim T, Schumacher T (2000) *Piceirhiza bicolorata* – the ectomycorrhizal expression of the *Hymenoscyphus ericae* aggregate? New Phytol 145:549–563

Walker LR, Chapin FS (1987) Interactions among processes controlling successional change. Oikos 50:131–135

Walker LR, del Moral R (2003) Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15:1–19

Walker J, Thompson CH, Fergus IF, Tunstall BR (1981) Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. In: West DC, Shugart HH, Botkin DB (eds) Forest succession: Concepts and application. Springer, New York, pp 107–131

Walker JF, Aldrich-Wolfe L, Riffel A, Barbare H, Simpson NB, Trowbridge J, Jumpponen A (2011) Diverse Helotiales associated with the roots of three species of Arctic Ericaceae provide no evidence for host specificity. New Phytol 191:515–527

Wallander H, Thelin G (2008) The stimulating effect of apatite on ectomycorrhizal growth diminishes after PK fertilization. Soil Biol Biochem 40:2517–2522

Wallander H, Morth CM, Giesler R (2009) Increasing abundance of soil fungi is a driver for (15)N enrichment in soil profiles along a chronosequence undergoing isostatic rebound in northern Sweden. Oecologia 160:87–96

Wardle DA (2002) Communities and ecosystems: Linking the aboveground and belowground components. Princeton University Press, Princeton

Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305:509–513

Wardle DA, Bardgett RD, Walker LR, Peltzer DA, Lagerström A (2008) The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. Oikos 117:93–107

Wardle DA, Jonsson M, Bansal S, Bardgett RD, Gundale MJ, Metcalfe DB (2012) Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. J Ecol 100:16–30

Warner NJ, Allen MF, MacMahon JA (1987) Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. Mycologia 79:721–730

Weijtmans K, Davis M, Clinton P, Kuyper TW, Greenfield L (2007) Occurrence of arbuscular mycorrhiza and ectomycorrhizas on *Leptospermum scoparium* from the Rakia catchment, Caterbury. N Z J Ecol 31:255–260

Weiß M, Sýkorová Z, Garnica S, Riess K, Martos F, Krause C, Oberwinkler F, Bauer R, Redecker D (2011) Sebacinales everywhere: previously overlooked ubiquitous fungal endophytes. PLoS One 6:e16793

Westman WE (1975) Edaphic climax pattern of the pygmy forest region of California. Ecol Monogr 45:109–135

Whitehead D, Boelman NT, Turnbull MH, Griffin KL, Tissue DT, Barbour MM, Hunt JE, Richardson SJ, Peltzer DA (2005) Photosynthesis and reflectance indices for rainforest species in ecosystems undergoing progression and retrogression along a soil fertility chronosequence in New Zealand. Oecologia 144:233–244

Williamson WM, Wardle DA, Yeates GW (2005) Changes in soil microbial and nematode communities during ecosystem decline across a long-term chronosequence. Soil Biol Biochem 37:1289–1301

Wright SH, Berch SM, Berbee ML (2009) The effect of fertilization on the below-ground diversity and community composition of ectomycorrhizal fungi associated with western hemlock (*Tsuga heterophylla*). Mycorrhiza 19:267–276

Wu BY, Hogetsu T, Isobe K, Ishii R (2007) Community structure of arbuscular mycorrhizal fungi in a primary successional volcanic desert on the southeast slope of Mount Fuji. Mycorrhiza 17:495–506

Wurzburger N, Higgins BP, Hendrick RL (2012) Ericoid mycorrhizal root fungi and their multicopper oxidases from a temperate forest shrub. Ecol Evol 2:65–79

Yu TEJ-C, Egger KN, Peterson RL (2001) Ectendomycorrhizal associations—characteristics and functions. Mycorrhiza 11:167–177

Zaffarano PL, Queloz V, Duó A, Grünig CR (2011) Sex in the PAC: a hidden affair in dark septate endophytes? BMC Evol Biol 11:282

Zangaro W, Alves RA, Lescano LE, Ansanelo AP, Nogueira MA (2012) Investment in fine roots and arbuscular mycorrhizal fungi decrease during succession in three Brazilian ecosystems. Biotropica 44:141–150