

Methods

Quantitative assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon cycling

Nadejda A. Soudzilovskaia^{1,2,3}, Marcel G. A. van der Heijden^{4,5,6}, Johannes H. C. Cornelissen¹, Mikhail I. Makarov⁷, Vladimir G. Onipchenko⁸, Mikhail N. Maslov⁷, Asem A. Akhmetzhanova⁹ and Peter M. van Bodegom²

¹Systems Ecology, Department of Ecological Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, the Netherlands; ²Environmental Biology, Institute of Environmental Sciences, Leiden University, Einsteinweg 2, 2333CC Leiden, the Netherlands; ³Louis Bolk Instituut, Hoofdstraat 24, 3972 LA Driebergen, the Netherlands; ⁴Plant-Soil Interactions, Institute for Sustainability Sciences, Agroscope, 8046 Zürich, Switzerland; ⁵Institute of Evolutionary Biology and Environmental Studies, University of Zürich, 8057 Zürich, Switzerland; ⁶Plant–Microbe Interactions, Institute of Environmental Biology, Faculty of Science, Utrecht University, 3584 CH Utrecht, the Netherlands; ⁷Soil Science Department, Moscow State University, 119991 Moscow, Russia; ⁸Department of Geobotany, Moscow State University, 119991 Moscow, Russia; ⁹Teberda State Biosphere Reserve, 369210 Teberda, Russia

Summary

Author for correspondence:
Nadejda A. Soudzilovskaia
Tel: +31 20 5986988
Email: n.soudzilovskaia@gmail.com

Received: 16 December 2014
Accepted: 1 April 2015

New Phytologist (2015)
doi: 10.1111/nph.13447

Key words: arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (EM) fungi, extraradical mycelium, intraradical mycelium, plant trait, root length colonization, root tips, sub-arctic ecosystems.

- A significant fraction of carbon stored in the Earth's soil moves through arbuscular mycorrhiza (AM) and ectomycorrhiza (EM). The impacts of AM and EM on the soil carbon budget are poorly understood.
- We propose a method to quantify the mycorrhizal contribution to carbon cycling, explicitly accounting for the abundance of plant-associated and extraradical mycorrhizal mycelium. We discuss the need to acquire additional data to use our method, and present our new global database holding information on plant species-by-site intensity of root colonization by mycorrhizas. We demonstrate that the degree of mycorrhizal fungal colonization has globally consistent patterns across plant species. This suggests that the level of plant species-specific root colonization can be used as a plant trait.
- To exemplify our method, we assessed the differential impacts of AM : EM ratio and EM shrub encroachment on carbon stocks in sub-arctic tundra. AM and EM affect tundra carbon stocks at different magnitudes, and via partly distinct dominant pathways: via extraradical mycelium (both EM and AM) and via mycorrhizal impacts on above- and belowground biomass carbon (mostly AM).
- Our method provides a powerful tool for the quantitative assessment of mycorrhizal impact on local and global carbon cycling processes, paving the way towards an improved understanding of the role of mycorrhizas in the Earth's carbon cycle.

Introduction

According to recent estimates, soils store 500–3000 Pg carbon (C) globally, more than the atmosphere and all plants together (Todd-Brown *et al.*, 2013; Wieder *et al.*, 2013, 2014). Thus, in order to understand the processes of global C cycling and to predict the effect of environmental changes, we need to obtain a thorough understanding of the soil C economy (Chapin *et al.*, 2009). Despite most C transformations in soils being microbe driven (Fujita *et al.*, 2014), our understanding of belowground C transformation processes, and especially of the role of distinct groups of microorganisms therein, is poor (Fierer *et al.*, 2009; Treseder *et al.*, 2012; van der Putten *et al.*, 2013). Particularly important are mycorrhizal fungi (Treseder *et al.*, 2012; van der Heijden *et al.*, 2015), which live in a mutualistic

relationship with plants. Unraveling the role of mycorrhizal fungi in soil C transformations is important, given that 94% of vascular plant species feature mycorrhiza (Brundrett, 2009), and mycorrhizal fungi create by far the largest pool of soil microbiota and often the main source of belowground C (Godbold *et al.*, 2006; Talbot *et al.*, 2008; Cairney, 2012; Clemmensen *et al.*, 2013).

Depending on the fungal taxa involved, mycorrhiza may have different forms, among which arbuscular mycorrhiza (AM) and ectomycorrhiza (EM) are the most widespread, taxonomically (Brundrett, 2009) and geographically (Read, 1991). AM and EM differ fundamentally in morphology and physiology (Smith & Read, 2008). Accordingly, it has been suggested that ecosystem C cycling and storage may be strongly determined by the predominant mycorrhizal type of the ecosystem (Cornelissen *et al.*, 2001;

Read & Perez-Moreno, 2003; Averill *et al.*, 2014). Indeed, several correlative studies, in which established AM-dominated vegetation stands have been compared with EM-dominated ones, have found that EM association causes C accumulation in recalcitrant semi-decomposed litter in soil O horizons, whereas AM promotes more rapid C cycling and the development of more fertile humus-rich soils and deeper dark organic A horizons and thinner O horizons (Chuyong *et al.*, 2002; Read & Perez-Moreno, 2003; McGuire & Treseder, 2010; Phillips *et al.*, 2013; Averill *et al.*, 2014).

Until recently, the differential impacts of AM and EM in ecosystem C turnover have been mostly linked to the supporting role of mycorrhiza in plant nutrient uptake. Therefore, the differences among C cycling processes in ecosystems dominated by AM and EM vegetation have been traditionally attributed to the following factors: (1) AM-dominated ecosystems have higher gross and net plant primary production (GPP and NPP), which ultimately results in higher litter production (Read, 1991; Read & Perez-Moreno, 2003; Vargas *et al.*, 2010; Averill *et al.*, 2014); (2) EM plants allocate more C than AM plants to their fungal partner (Jones *et al.*, 1998; Leake *et al.*, 2004; Gehring *et al.*, 2006; Orwin *et al.*, 2011); and (3) litter of EM plants decomposes twice as slowly as that of AM plants (Cornelissen *et al.*, 2001; Langley & Hungate, 2003; Hobbie *et al.*, 2006; McGuire *et al.*, 2010; Vesterdal *et al.*, 2012; cf. Dickie *et al.*, 2014). This traditional concept coincides with the widely accepted view that NPP and litter quality are the main aspects of vegetation-mediated inputs to soil C stocks and to atmospheric CO₂ (Schimel *et al.*, 1994; Sitch *et al.*, 2008).

However, a rapidly growing body of recent research has suggested that the presence of AM and/or EM fungi in soil also directly (i.e. via their presence and activity beyond the supply of plants with nutrients) affects soil C sequestration processes, both in terms of sequestration rates and the fate of C added to the soil, in addition to the above-discussed mycorrhizal effects via NPP and litter quality (i.e. indirect effects, *sensu* Rillig (2004a)).

(1) EM fungi usually acquire more C than AM fungi from their host plants and, correspondingly, release more C into the soil, aiding the direct effects of mycorrhiza in addition to the indirect effect of less C being left for plants. The possible fates of this C (i.e. its utilization by fungi for enzyme production, biomass or respiration) are discussed below (points 2–4).

(2) Ectomycorrhizas release oxidative enzymes, facilitating nitrogen (N) uptake from litter (Aber *et al.*, 1998; Bödeker *et al.*, 2014), thereby increasing the recalcitrance of old, partially decomposed, litter (Gadgil & Gadgil, 1971; Bending, 2003; Read *et al.*, 2004) and promoting thicker organic surface horizons and larger humus C : N ratio through time (Clemmensen *et al.*, 2013).

(3) The external (extramatrical) mycelium of EM fungi has an order of magnitude higher standing biomass (Miller *et al.*, 1995; Anderson *et al.*, 2001; Sawyer *et al.*, 2003), and some studies have indicated that EM external mycelium has a several times slower turnover rate (Leake *et al.*, 2004; Olsson & Johnson, 2005; Ekblad *et al.*, 2013), than the external

(extraradical) mycelium of AM fungi. Accordingly, residues of external EM mycelium form a key (50–60%) source of C entering the belowground C pool, probably exceeding the input via leaf litter and fine root turnover (Read, 1991; Godbold *et al.*, 2006; Clemmensen *et al.*, 2013). For comparison, glomalin (a glycoprotein contained in residues of AM cell walls and in some other microbes) was estimated to constitute up to 5% of total soil C only (Rillig *et al.*, 2001; Rillig, 2004b; Treseder & Turner, 2007).

(4) EM fungi can also have a priming effect (defined as an addition of new easily available C, causing a release of old, more recalcitrant C) on saprotrophic fungi (Fontaine *et al.*, 2003, 2011; Subke *et al.*, 2011). This effect has not yet been found for AM fungi under ambient conditions (Burke *et al.*, 2002; Welch *et al.*, 2010; Leigh *et al.*, 2011; Nottingham *et al.*, 2013), although Cheng *et al.* (2012) reported priming effects of AM fungi under elevated CO₂. Further research is needed to clarify the priming ability of AM fungi.

The differences between AM and EM, summarized in Fig. 1, suggest that the extent of mycorrhizal impact on individual pools and fluxes of C turnover in AM- and EM-dominated ecosystems differs. However, the impacts of AM and EM on the total soil C pools have not yet been unraveled. Averill *et al.* (2014) estimated that, globally, EM ecosystems store 1.7 times more C per unit of soil N than do AM ecosystems. However, when comparing AM and EM estimates within the same biome, Vesterdal *et al.* (2012) found no differences in total C stocks between temperate AM and EM forests. Both Vesterdal *et al.* (2012) and Phillips *et al.* (2013) found slower C cycling in the O-horizon of EM-dominated forests compared with that in AM-dominated ones, but neither study assessed the individual C fluxes resulting in retarded C cycling. Thus, further in-depth investigations on the effects of AM and EM vegetation on total soil C stocks are essential.

Currently, mycorrhizal research tends to describe the functioning of AM and EM without specifying their abundance in a particular ecosystem. However, even purely AM or purely EM vegetations may vary considerably in actual biomass of mycorrhizal fungi, depending on soil type, soil fertility, vegetation type, climate and fungal community composition, making comparisons among studies difficult. Furthermore, purely AM or EM vegetation stands are rare in nature. Most ecosystems host both AM and EM plants in different proportions. Thus, AM and EM simultaneously affect biogeochemical cycling in such ecosystems, but the impacts of AM and EM may differ depending on their abundances.

Here, we propose that, to obtain a comprehensive understanding of the effects of AM vs EM on soil C cycling (Phillips *et al.*, 2013), we need to examine and integrate both direct and indirect effects of mycorrhizal fungi on processes involved in soil C stock formation in a quantitative manner. In order to do this, we need a quantitative measure of the involvement of each type of mycorrhiza in ecosystem functioning. The aims of this study are therefore: to propose a routine to quantitatively assess the differential involvement of AM and EM in soil C cycling and to demonstrate its advances utilizing data from a detailed field study; to provide a

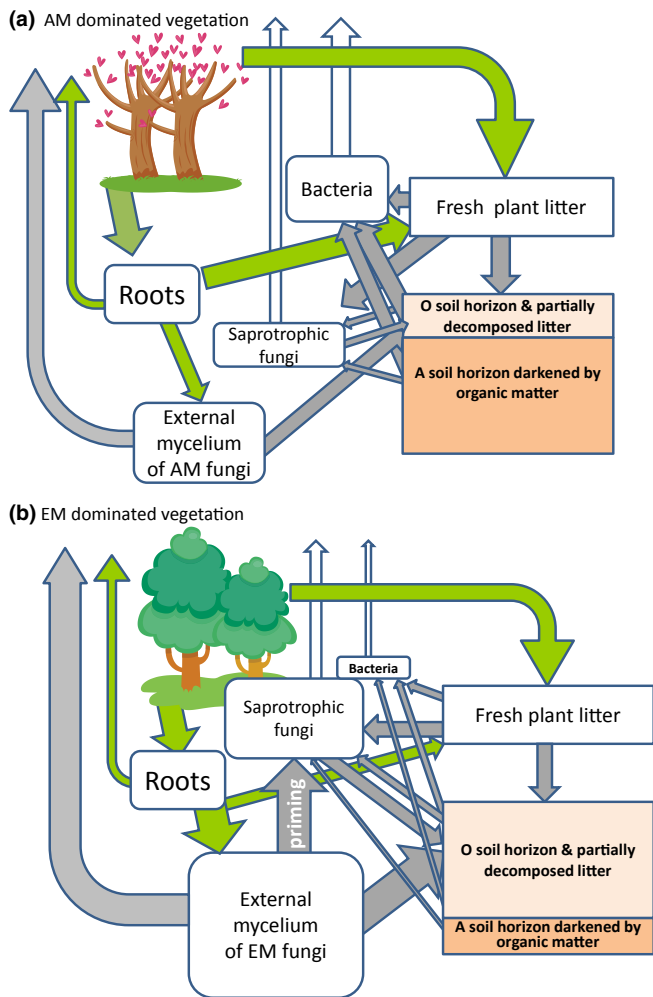


Fig. 1 Current view on individual pools and fluxes of belowground carbon (C) dynamics in (a) arbuscular mycorrhiza (AM)- and (b) ectomycorrhiza (EM)-dominated ecosystems. White blocks, living organisms and fresh litter; brown blocks, organic soil fractions; green arrows, plant-associated C fluxes, discussed in the text as indirect effects of mycorrhiza on C cycling; grey arrows, soil C pathways associated with direct effects of mycorrhiza on C cycling; white arrows, C losses via respiration of organisms not involved in mycorrhizal symbiosis. The sizes of the boxes/arrows reflect the magnitude of the pools/fluxes. The effects of AM and EM vegetation on the total soil C pool (amount of C stored in O and A soil horizons together) require further investigation (see the Introduction section for details).

perspective for the quantitative estimation of AM and EM involvement in C stocks at global scales; and to review the current data availability for such assessments.

Our concept has an important practical implication: changes in the abundances of AM and/or EM plants in an ecosystem as a result of introduction, invasion or expansion of plants featuring one of the mycorrhizal types (hereafter AM ↔ EM vegetation shifts) could strongly affect biogeochemical transformation processes relevant to ecosystem C cycling (Phillips *et al.*, 2013). Our concept may be applied to assess the impacts of shifts in abundance of AM and EM plants on C pools associated with functioning of arbuscular and ectomycorrhizas.

Materials and Methods

A quantitative assessment of the impacts of AM and EM fungi on soil carbon stocks

Our premise is, that, to assess the effects of mycorrhiza on ecosystem C pools and fluxes, the ‘effect of mycorrhiza’ should be examined in relation to the actual abundance of AM and/or EM in an ecosystem: that is, the abundance of each partner (plant and fungi) and the level of intimacy of the relationship between them need to be determined. Thus, we need to quantify the total amount of root-associated AM and EM fungi (i.e. total AM-colonized standing root length per soil mass unit and total number of root tips colonized by EM fungi per gram of soil) and the biomass of extraradical fungal mycelium (*sensu* Leake *et al.* 2004): that is, extraradical *sensu stricto* mycelium of AM fungi and extramatrical mycelium of EM fungi in the ecosystem. Changes in the abundances of AM and/or EM plants in an ecosystem will lead to changes in both of these aspects. The idea of taking into account the abundances of AM and EM fungi whilst examining the effects of mycorrhiza on C cycling is illustrated in Fig. 2(a).

To demonstrate this concept for ecosystem-level assessments, we have calculated the AM and EM fungal contributions to C pools in an AM- and EM-dominated sub-arctic alpine plant community. In addition, we show how the magnitude of this C stock and the ratio of fungi to plant C allocation can change on encroachment of the EM shrub *Betula nana* L. in a sub-arctic plant community (e.g. this causes a vegetation shift from AM towards EM dominance). This issue is highly relevant and urgent, because expansion of shrubs (which are often EM) is recognized as a major consequence of climate warming at high latitudes and altitudes (Myers-Smith *et al.*, 2011; Naito & Cairns, 2011; Cahoon *et al.*, 2012; Elmendorf *et al.*, 2012b; Heskell *et al.*, 2013).

We established seven and six 50 × 50-cm² plots in AM- and EM-dominated plant communities, respectively, in the alpine zone of sub-arctic Sweden (Abisko area, 68°22’N, 18°39’E). Both plant communities were situated within 50 m of each other, at the same elevation (800 m above sea level), on the same gneiss parent rock material. Both plant communities consisted of herbaceous and dwarf shrub vegetation, where EM plants were represented by the herbaceous dwarf shrubs *Salix herbacea* L., *Salix polaris* Wahlenb. and *Betula nana* L. Although some *Salix* species can feature both AM and EM symbioses (e.g. van der Heijden, 2000), we did not find AM in the examined *Salix* plants. In these plant communities, we assessed separately, for each plant species, the aboveground (for details, see Supporting Information Tables S1 and S2) and belowground biomass (the latter by separating rhizomes, coarse and fine roots), intensity of root mycorrhizal colonization, specific root length (root length per unit mass) and C concentration in above and belowground organs, and we estimated the amounts of AM and EM extraradical mycelium (Tables S1, S2). Based on these data, for both plant communities, we estimated the fraction of the total C pool stored in plant biomass as attributable to the impacts of mycorrhiza on plant nutrition and fitness (Fig. 3). In addition, we estimated the

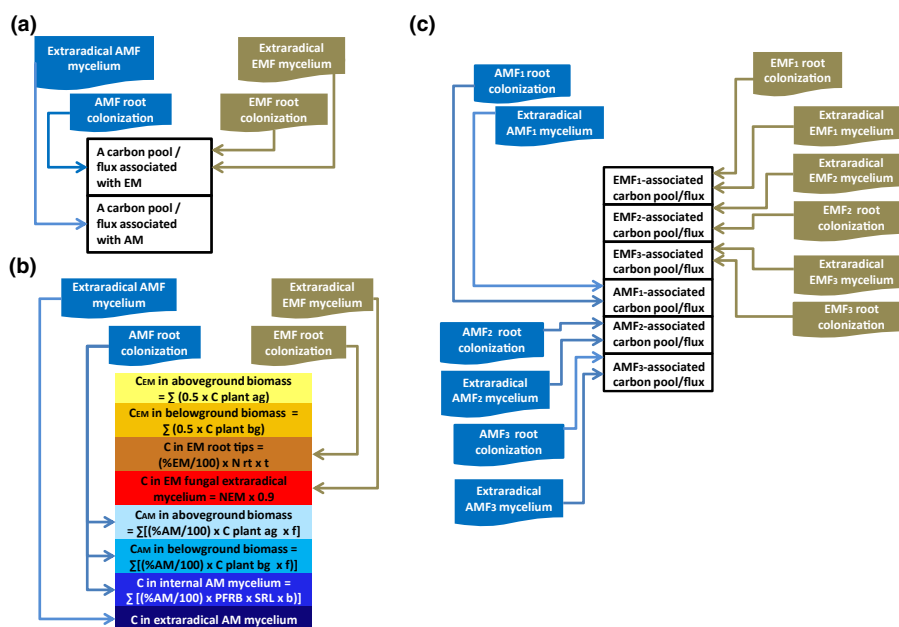


Fig. 2 Schematic illustration of the proposed method for quantitative assessment of involvement of AM and EM into soil carbon cycling. (a) General illustration of the proposed idea: assessments of the involvement of AM and EM into any type of soil carbon pools or fluxes should be conducted taking into consideration the actual abundance of AM and EM in the ecosystem; (b) implementation in the case study; (c) possible extension of the basic principle taking into account differences among individual species or functional groups of AM and EM fungi. For justification of formulas used in calculations, see Methods S3. Texts and abbreviations used in the figure: overall, Σ indicates summation over all vascular plants present in the ecosystem; extraradical AMF/EMF mycelium, biomass of AM/EM fungal extraradical mycelium present in the soil (total for the ecosystem in (a) and (b), or specific for individual fungal species or functional guilds in (c)). AMF/EMF root colonization, percentage of standing root length colonized by AM fungi and percentage of root tips colonized by EM fungi, respectively (ecosystem totals in (a) and (b), or specific for individual fungal species or functional guilds in (c)). C_{EM} in plant aboveground/belowground biomass, amount of carbon in plant aboveground/belowground biomass attributable to supporting role of EM fungi in plant nutrition; C plant ag/C plant bg, per plant species amount of carbon in above or belowground biomass. C in EM root tips, amount of carbon is EM fungi in plant root tips; %EM, percentage root tips colonized by EM fungi; Nrt, number of root tips per plant species, $Nrt = 8000 \times$ plant belowground biomass; t, C content in one root tip, $t = 0.016$ mg C per root tip; C in EM fungal extraradical mycelium, amount of carbon in fungal extraradical mycelium; N_{EM} , per plant species number of EM root tips, $N_{EM} = Nrt \times \%EM$; C_{AM} in aboveground/belowground biomass, amount of carbon in plant aboveground/belowground biomass attributable to supporting role of AM fungi in plant nutrition; %AM, per plant species percentage root length colonized by AM fungi; C plant ag/C plant bg, total carbon in plant species aboveground/belowground biomass; f, coefficient expressing plant species mycorrhizal benefit $f = 0.5$ for forbs, $f = 0.2$ for grasses; C in internal AM mycelium, amount of carbon in AM mycelium in plant roots; PlantFRB, plant species fine root biomass; SRL, Plant species specific root length; b, carbon content per 1 m of AM fungal mycelium in plant roots, $b = 1.03 \times 10^{-3}$ g C per m root colonized by AM for herbaceous plants; C in extraradical AM mycelium, amount of carbon in extraradical AM mycelium, estimated as total AM mycelium length multiplied by $k = 1.42 \times 10^{-6}$ μ g C per m AMF mycelium.

individual contributions of mycorrhiza-attributable C stocks in aboveground and belowground plant biomass, and C stocks in AM and EM fungal mycelium (Fig. 4). Fig. 2(b) illustrates the main points and the assumptions of the calculations. Details of calculations and the underlying data are shown in Tables S1 and S2. Justifications for the equations used, the reasoning underlying data estimations and literature references are given in Methods S1.

In short, the impacts of AM and EM on plant C pools (i.e. the amount of C in plant biomass accumulated as a result of the supportive role of mycorrhiza in plant nutrition and fitness) were estimated based on the results of experimental studies and meta-analyses of vascular plant biomass responses to mycorrhizal colonization. For AM, we used data from Lekberg & Koide (2005), Hoeksema *et al.* (2010) and Treseder (2013), and, for EM, from Hobbie & Hobbie (2006), Karst *et al.* (2008) and Simard *et al.* (2002). Using their proposed values, we estimated the impact of AM on the amount of C stored in biomass of each individual plant species as 50% of C stored in plant biomass multiplied by the fraction of root length colonized by AM fungi for forbs, and

20% of C stored in plant biomass multiplied by the fraction of root length colonized by AM fungi for grasses. We estimated the impact of EM on C stored in biomass of individual plant species as 50% of C stored in plant biomass, independent of EM colonization rate (Karst *et al.*, 2008). See Methods S1 for the reasoning underlying these estimates. The amount of C stored in root-associated and extraradical biomass of mycorrhizal fungi was estimated to be proportional to the respective biomasses of AM and EM fungal mycelium in plant roots or in soil (see Tables S1, S2 and Methods S1 for calculations), using values of 50% C for EM fungal tissues (Wallander *et al.*, 2011), 41% C for AM extraradical mycelium (Paul & Clark, 1996) and 1.03 μ g C per millimeter of root colonized by AM fungi for herbaceous plants (Treseder & Cross, 2006). It should be noted that several of these calculations and assumptions are based on meta-analyses, averaging results obtained from many studies. As such the values obtained must be treated with care and the outcome of further analysis (e.g. for different systems) might vary depending on ecosystem type, plant species and soil type.

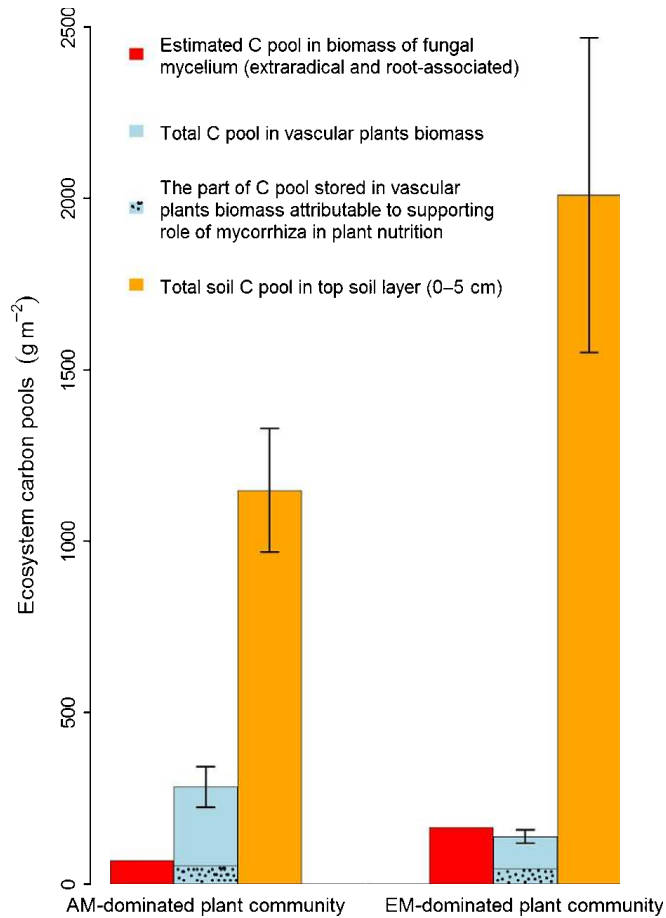


Fig. 3 Mycorrhiza-related carbon (C) pools, C pool in living plant above- and belowground biomass, and total soil C pool in the top 0–5-cm organic soil layer in arbuscular mycorrhiza (AM)- and ectomycorrhiza (EM)-dominated communities in subarctic–alpine Sweden. Mean values \pm SE are shown. $n = 7$, for AM; $n = 6$ for EM. Note that the light blue bar represents plant biomass, whereas the dotted section shows the fraction of the total plant biomass C gained as a result of the supporting role of mycorrhiza in plant nutrition.

We found that, in AM-dominated plant communities, the mycorrhiza-associated C pool in living plant and fungal biomass was similar to that in EM-dominated plant communities (Fig. 3). However, the C pool stored in mycorrhizal mycelium in EM-dominated plots was twice as large as the total C pool stored in above- and belowground plant biomass, whereas, in AM-dominated plots, the C pool stored in mycorrhizal mycelium was smaller than that of plant biomass (Figs 2, 3). This is reflected in the large differences between AM- and EM-dominated plots in the composition of the mycorrhiza-associated C pools (Fig. 4): in EM-dominated plots, 70% of the mycorrhiza-associated C pool was stored in EM mycelium, whereas, in AM-dominated plots, the AM-associated C stock in plant biomass was nearly equal to that in AM fungal mycelium.

Concurring with these differences, the top (0–5 cm) soil properties of AM- and EM-dominated ecosystems differ (Table 1; see Methods S2 for soil analysis; we also sampled soils at 5–10 cm depth, but found relatively little plant root mass there and no significant differences in soil characteristics; therefore, the data for

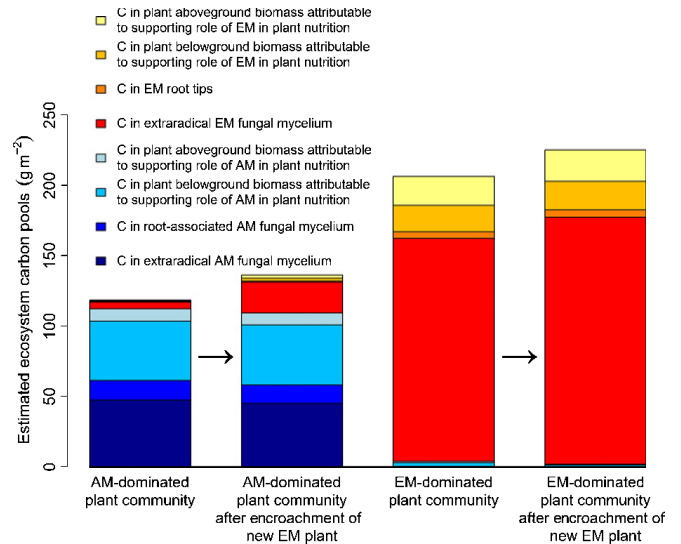


Fig. 4 Composition of mycorrhiza-related carbon (C) pools and simulated impacts of encroachment of the ectomycorrhizal plant *Betula nana* in arbuscular mycorrhiza (AM)- and ectomycorrhiza (EM)-dominated plots in subarctic–alpine Sweden.

the deeper soil layer are not discussed hereafter). Soils of EM-dominated plots showed syndromes of slower C cycling: a higher C : N ratio ($P = 0.04$), higher concentration of extractable organic C ($P = 0.03$) and lower soil respiration ($P < 0.001$). The mean total amount of soil C also appeared lower for EM-dominated plots, although this difference was insignificant as a result of large variations. In order to examine to what extent the differences in environmental conditions could underpin the differences in soil characteristics of AM- and EM-dominated plots, we conducted a 1-yr decomposition experiment in both types of plots, examining the decomposition of a standard plant material (tea; Keuskamp *et al.*, 2013; for details and justification, see Methods S2), and did not detect differences in the decomposition rate in the organic horizon (Table 1). Taking into consideration that the pH of the organic horizon in the two types of plant community also did not differ (Table 1), we suggest that the differences in C cycling syndromes between the soils of these plant communities are predominantly a result of the different composition of plant and microbial communities. However, further research needs to quantify the causal relationships between the size of mycorrhiza-associated C pools and soil C cycling processes, also accounting for differences in the turnover rate of the different pools. The turnover rate of EM mycelium is an order of magnitude higher than that of plant biomass (the dominant sink in AM-dominated ecosystems) (Leake *et al.*, 2004; Olsson & Johnson, 2005; Ekblad *et al.*, 2013). This might partly explain the smaller difference in total soil C pool between AM- and EM-dominated ecosystems than one would expect on the basis of the differential distribution of C in living biomass stocks.

Using the same calculation routine, we estimated how encroachment of an EM dwarf shrub *Betula nana* L. would affect mycorrhiza-associated C pools in both types of plant community. In this imaginary example, we simulated the situation in which *B. nana* would replace 5% of the biomass constituted by AM

Table 1 Properties of organic soil horizon (0–5 cm) of arbuscular mycorrhiza (AM)- and ectomycorrhiza (EM)-dominated plant communities in subarctic-alpine Sweden

	AM-dominated community			EM-dominated community			<i>P</i> (<i>t</i> -test)
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	
Total soil carbon (C) : nitrogen (N) ratio	11.75	0.34	7	14.80	1.05	6	0.04
Extractable organic C mg kg ⁻¹	537	22	6	854	157	5	0.03
Potential soil respiration (mg C-CO ₂ g ⁻¹ C d ⁻¹)	0.68	0.004	10	0.59	0.004	10	<0.001
Total soil C content (kg C m ⁻² soil)	1.15	0.18	6	2.01	0.46	5	0.14
Decomposition rate of standard material (tea bags), % mass loss during 1 yr of incubation	40	1	5	41	1	5	0.4
pH	4.99	0.18	7	5.04	0.15	5	0.8

For the details of the decomposition test using standard material, see Keuskamp *et al.* (2013).

plants in each community (substituting in each community the AM plant *Viola biflora* L.; Tables S3, S4). This example is simplified because, in a real ecosystem, invasion of a new plant would probably lead to complementary resource use (i.e. 5% increase in biomass of *B. nana* might lead to a smaller than 5% decrease in AM plants). However, even for this simplified example, Fig. 4 shows that, even such relatively small AM→EM vegetation shifts (compared with predictions made using climate manipulation experiments; Elmendorf *et al.*, 2012a) would alter the composition of mycorrhiza-associated C in living biomass pools of the AM-dominated plant community, decreasing the amount of plant-allocated C by 5% and increasing the amount of fungi-allocated C by 20%.

Such quantitative links between the changes in AM/EM abundance within an ecosystem and changes in one of the important ecosystem C pools can be used directly to model the role of AM/EM fungi in the soil C budget in a changing environment. We propose that further experimental assessments of connections between mycorrhiza and ecosystem soil C pools and fluxes could be performed in a similar manner, that is accounting for the quantitative abundance of mycorrhizas acting in the ecosystem. However, the calculations exemplified here use a number of assumptions and simplifications in cases in which the connections between the abundance of mycorrhizal fungi and ecosystem C pools are poorly understood. Methods S3 discusses the limitations of the exemplary data and the robustness of the case study analysis. For instance, in our study case, the abundance of extraradical mycelium was estimated based on current literature and the assumption that the extraradical mycelium abundance generally scales up with an increase in plant root colonization. This was performed purely for illustrative purposes. When using the method proposed here, the abundances of extraradical mycelium should be assessed in the field.

Results

Regional and global assessments of the role of AM and EM in carbon cycling using the proposed method

After the first phase of correlative comparisons of C cycling in AM- and EM-dominated biomes (Read & Perez-Moreno, 2003;

Averill *et al.*, 2014), our new method to explicitly determine the contributions of AM and EM to C pools may pave the way to a fully quantitative assessment of the effects of distinct mycorrhizas on regional or global C budgets, by including their individual direct effects in models of C turnover, for example (Liski *et al.*, 2005; Orwin *et al.*, 2011; Goll *et al.*, 2012). However, to achieve this, we need regional (or global) data on the components of AM and EM fungal abundance in soil (root-associated mycelium and extraradical mycelium) and knowledge about how alterations in these components affect soil C fluxes and pools. The latter issue requires experimental or observational data on the effects of mycorrhiza on C cycling to be related to the actual quantitative alterations in the abundance of AM or EM fungi (as exemplified above). For the first issue, we need to know the plant species-specific fraction of fine roots available for fungal colonization (a product of plant abundance and plant species-specific fine root length (AM plants) or number of root tips (EM plants)), *in situ* plant species-specific root colonization levels by mycorrhizal fungi, and abundance of extraradical mycelium of AM and EM fungi in soil. The data on the amounts of AM and EM fungal mycelium should be at the ecosystem level, whereas the data on fine root length and intensity of root colonization by AM and EM fungi could be presented as ecosystem-level means or, preferably, as weighted means derived from each of the plant species constituting the majority of ecosystem biomass. Ecosystem-scale root colonization is possible via the analysis of fungal biomarkers (specific fatty acids (Olsson *et al.*, 1998, 2003; Olsson & Wilhelmsson, 2000). However, the EM fungi for this analysis should be sampled using in-growth bags (Wallander *et al.*, 2011), because there is no fatty acid biomarker available that distinguishes between EM and saprotrophic fungi, or by quantitative PCR specifically targeting AM and EM fungi. Such analyses would be useful for comparisons between the roles of AM and EM in C cycling processes.

The use of per-plant species data of AM and EM fungal colonization would also allow the estimation of the impacts of particular vegetation shifts caused by invasions or introductions of new AM or EM plants in ecosystems dominated by EM or AM vegetation, respectively. Per-species data would also facilitate data coupling to other plant C economy traits available in large databases, such as TRY (Kattge *et al.*, 2011), and to species-by-site

aboveground plant abundance data, including publicly available Internet resources (GIVD, <http://www.givd.info>; GBIF, <http://www.gbif.org>; BIEN, <http://www.iplantcollaborative.org>).

Regional and global data on fine root biomass, root colonization by mycorrhizal fungi and abundance of extraradical mycelium of mycorrhizal fungi are available (Jackson *et al.*, 1997; Treseder & Cross, 2006; *Finer et al.*, 2011a,b; Kattge *et al.*, 2011; Akhmetzhanova *et al.*, 2012; Hempel *et al.*, 2013), as well as data on the global distributions of mycorrhizal fungal species (Tedesoo *et al.*, 2014). However, the data availability for each of these components varies considerably, as discussed below.

Plant fine root biomass Currently, comprehensive data on fine root biomass exist per biome, largely focusing on forests (Jackson *et al.*, 1997; *Finer et al.*, 2011a,b). To quantitatively predict impacts on C cycling and to account for, for example, changes in plant species composition, per-species estimations for plant fine root length would be preferable. Much information on species-specific standing root biomass or length exists, both in a direct form (e.g. Pregitzer *et al.*, 2002; Comas & Eissenstat, 2004, 2009; Wang *et al.*, 2006; Yuan & Chen, 2010; Birouste *et al.*, 2012; McCormack *et al.*, 2012; Beyer *et al.*, 2013; Tobner *et al.*, 2013; Gu *et al.*, 2014) and from root trait data stored in databases such as TRY (Kattge *et al.*, 2011). In addition, relationships between root biomass or length and their plastic responses to nutrient-rich environments have been established (Chapman *et al.*, 2012; Chen *et al.*, 2013; Valverde-Barrantes *et al.*, 2013), which may be used to refine database-derived estimates. However, to our knowledge, species root data have not yet been assembled into a single database accessible to a broad scientific community. Moreover, such data should distinguish between fine root and total root biomass or length, because mycorrhizal fungal colonization takes place primarily in fine roots (Guo *et al.*, 2008). Thus, the assembly of the existing data into a database, thorough data checks, quantitative assessment of root plasticity, and the identification of data gaps are the next necessary steps.

Intensity of root colonization by mycorrhizal fungi Recent published research has provided considerable detail on the type of mycorrhiza associated with each plant species (Wang & Qiu, 2006; Akhmetzhanova *et al.*, 2012; Hempel *et al.*, 2013). However, plant species-by-site data on mycorrhizal root colonization levels have, until now, been spread over a large number of scientific publications. Furthermore, the question of whether the intensity of plant root mycorrhizal infection can be used as a plant species-specific trait (*sensu* Lavorel & Garnier, 2002) in ecological analyses has, to our knowledge, never been properly examined. The intensity of plant root mycorrhizal infection is known to vary with plant age (Onipchenko, 2004), environmental conditions (Erland & Soderstrom, 1990; Nilsen *et al.*, 1998; Tuomi *et al.*, 2001; Treseder, 2004) and between seasons (Ruotsalainen *et al.*, 2002; Garcia & Mendoza, 2007; Mandyam & Jumpponen, 2008). These issues are typically seen as an inherent obstacle for the use of data on plant root colonization intensity by mycorrhizal fungi as a plant species-specific trait. However, similar problems are also recognized for other plant traits, and are solved

by the use of data collected following standardized protocols (Cornelissen *et al.*, 2003), and by the use of plant species trait mean values calculated over large sets of data, where the trait in question has been measured multiple times at distinct sites (Koele *et al.*, 2012; Reich, 2014). Evidence that the intensity of plant root mycorrhizal infection is plant species specific would allow the inclusion of these data into analyses aimed at the prediction of how vegetation influences global C cycling via the mycorrhizal pathway.

We assembled a global geographically referenced database of vascular plant root colonization intensities by mycorrhizal fungi, using published site-referenced surveys available via the ISI Web of Science up to 2013. The dataset holds information on the intensity of AM fungal root colonization of 4887 vascular plant species on 228 sites, and on EM fungal root colonization of 125 vascular plant species on 92 sites (Fig. 5; Tables S5, S6; Soudzilovskaia *et al.*, 2015). Using the largest study contained in the database (presented in Akhmetzhanova *et al.* (2012), which reports 7445 records on mycorrhizal infection type and intensity of 2970 plant species from 155 families in 154 sites, all assessed following the same protocol), we tested how much of the variation in the intensity of plant root colonization by AM and EM fungi could be explained by plant species identity, compared with intraspecific variation in AM and EM root colonization as indicated by site identity (see Methods S4 for details). Plant species identity was a much stronger predictor ($P < 0.001$, 53% of

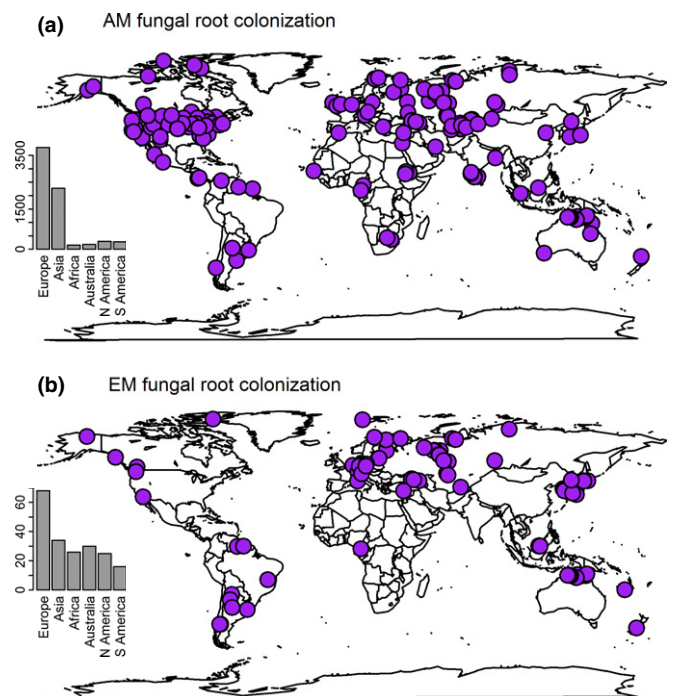


Fig. 5 Sites in which the plant root colonization data by (a) arbuscular mycorrhizal (AM) and (b) ectomycorrhizal (EM) fungi were collected. Bar graphs in the left corner of each map show the number of species-by-site data points per continent, for AM fungi ranging between 157 and 3790, and for EM fungi between 16 and 68. The smaller number of plant species examined for EM fungi corresponds with the overall lower number of EM plant species relative to AM plant species (2% vs 73% of all Earth plant species; Brundrett, 2009). Adapted from Soudzilovskaia *et al.* (2015).

variance explained) of the intensity of AM fungal root colonization relative to site identity ($P < 0.001$, 26% of variance explained), and we found no significant interactions between site and plant species as explanatory variables. The lower availability of EM fungal colonization data (see Fig. 5) did not allow us to conduct the same analysis for root colonization by EM fungi. Thus, we opted for testing only the significance of plant species identity as a predictor of plant root colonization intensity by EM fungi, and this factor was indeed highly significant ($P = 0.001$, 74% of variance explained). The proportion of variance in root colonization explained by plant species identity is similar to that of other plant traits commonly used in C cycling analyses, such as specific leaf area, leaf C and N content, photosynthesis rate per leaf dry mass and leaf litter decomposability (Wright *et al.*, 2004; Cornwell *et al.*, 2008; Kattge *et al.*, 2011), which are in the range of 40–80%. Such strong impacts of plant species identity on the intensity of root colonization by mycorrhizal fungi and the large differences in the mean values of intensity of root colonization of plant species by AM and EM fungi (Figs S1, S2) indicate that the intensity of mycorrhizal fungal root colonization can be used as a plant species-specific trait (*sensu* Lavorel & Garnier, 2002) in ecological analyses.

Biomass of extraradical mycelium of mycorrhizal fungi Our knowledge of the amount of mycorrhizal extraradical mycelium in distinct biomes is limited. Currently assembled global datasets (Öpik *et al.*, 2013, 2014; Tedersoo *et al.*, 2014) hold information on the genetic diversity of mycorrhizal fungi, but not on their biomass. Field studies of extraradical mycelium of EM fungi require the use of in-growth bags to distinguish between EM and saprotrophic fungi (Wallander *et al.*, 2011, 2013). Concerning AM fungi, it is possible to measure extraradical mycelium of AM fungi using various biochemical markers (see detailed discussion on this in the review of Leake *et al.* (2004)) or by visual discrimination on gridded membranes. However, currently, it is not clear how the amounts of extraradical mycelium and root colonization levels by mycorrhizal fungi are related at the ecosystem level. To date, only a few studies have investigated this problem for individual plant–fungi pairs, with contradicting results (Hart & Reader, 2002; Heinemeyer *et al.*, 2006; Powell *et al.*, 2009; Muriithi-Muchane, 2013). Furthermore, these studies covered only a handful of model plant species in laboratory set-ups, where one plant individual was inoculated by one fungus species, comparing the amounts of extraradical and root-associated mycelium. Such set-ups ignore the fact that, in the field, several fungal species are interconnected with many individuals of different plant species (Leake *et al.*, 2004), making the results from these studies of limited value for the question addressed here. Although we expect the amounts of root-associated and extraradical AM/EM fungal mycelium to be correlated at the community level (based on a comparison of the data of root-associated and extraradical mycelium presented in individual studies conducted in contrasting biomes; Staddon *et al.*, 2003; Gryndler *et al.*, 2006; Piotrowski *et al.*, 2008; Duan *et al.*, 2011), the extent to which these correlations vary among ecosystems and environmental settings needs further research.

Discussion

An understanding of the mechanisms and magnitudes of the differential involvement of AM and EM in soil C cycling processes requires the quantitative assessment of the involvement of AM and EM in ecosystem C cycling. We have shown the promise of such assessment in a data-rich case study and have set out an agenda for performing and improving such analyses at regional and global scales.

Recently, Phillips *et al.* (2013) and Moora (2014) proposed the use of the weighted aboveground abundance of plant species of each mycorrhizal type, possibly corrected for the ability of a plant species to grow with or without mycorrhiza (Moora, 2014), as a measure of the involvement of each type of mycorrhiza in ecosystem functioning. Such an approach is perfectly suitable for understanding the role of mycorrhizal symbiosis for vegetation pattern dynamics (Moora, 2014) and the associated C and nutrient cycling processes related to NPP and litter production (Phillips *et al.*, 2013), which are the indirect effects of mycorrhizal fungi. However, quantitative estimations of the involvement of AM and EM fungi in the broader spectrum of soil C sequestration processes, as proposed in this article, require more detailed measurements of the abundance of AM/EM fungi than simply the aboveground abundance of AM/EM plant species, for three reasons.

(1) The estimations of the involvement of AM/EM in C cycling based on data of aboveground plant biomass composition do not consider the amounts of extraradical mycelium of AM and EM fungi and differences in their decomposition.

(2) The estimation of AM and EM abundance based on the aboveground abundance of AM- or EM-associated plant species only presumes that, for a given plant species, the species-associated fraction in the total community-level aboveground plant biomass is a good predictor for the species-associated fraction in the total root biomass colonized by mycorrhizal fungi. This would be an acceptable assumption if mycorrhizal fungi colonized the entire belowground plant biomass. However, mycorrhizal fungal colonization takes place primarily, if not exclusively, in fine roots (Guo *et al.*, 2008), meaning that not the total root biomass but the fine root fraction needs to be examined in mycorrhizal studies. Unfortunately, plant species aboveground abundance is a poor predictor for the fraction of fine root biomass associated with the plant species (Finer *et al.*, 2011a), and for the associated microbial processes (Mariotte, 2014).

(3) There is growing evidence that there are interspecific differences among mycorrhizal fungi, especially EM fungi, in the chemical composition of cell walls triggering mycelium decomposition (Malik & Haider, 1982; Dahlberg *et al.*, 1997; Koide *et al.*, 2014) and enzymatic capabilities (Bödeker *et al.*, 2014). These traits are important for processes such as organic matter decomposition (Bödeker *et al.*, 2014; Koide *et al.*, 2014) as well as plant nutrition (Thonar *et al.*, 2011). Therefore, fluxes of C through the fungal biomass and the way in which C is utilized depend on the fungal community composition. Although our method is currently based on total root-associated and extraradical biomasses of AM and EM fungi, it principally allows for differentiation among distinct fungal species or functional

types within the groups of AM and EM fungi, as soon as we have reliable techniques to assess the abundance of each functional type. Figure 2(c) illustrates how the method proposed here could be extended to take into consideration fungal interspecific differences.

Global upscaling of our routine requires considerably more data than are currently available. Moreover, we do not know whether all functionalities of mycorrhiza scale with the abundance of mycorrhizal fungi. Following the logic of the biomass ratio hypothesis (Grime, 1998), we consider that the abundance of mycorrhizas in roots and soil is probably related to mycorrhizal functions, but some relationships may be non-linear, or the essence of 'mycorrhizal functions' may be more complex than we currently know. Several factors need to be taken into account to implement a model that incorporates all mycorrhizal fungal effects on C cycling. First, we lack data on the effects of specific plant–fungal combinations on NPP. Second, we still need to determine whether and how plant litter quality is related to the activity and abundance of mycorrhizal fungi colonizing the litter-producing plant species (Dickie *et al.*, 2014). Third, we need to better understand how extraradical mycorrhizal fungal mycelium affects soil C turnover. Biomass of AM fungi in soil is known to be a proxy for soil aggregation rate (Rillig & Mummey, 2006; Leifheit *et al.*, 2014), with positive knock-on effects on soil C and nutrient turnover (Wilson *et al.*, 2009). EM fungi also affect soil aggregation (Zheng *et al.*, 2014), but their impacts have never been compared with those of AM fungi. In addition, although the biomass of extraradical EM fungal mycelium appears to be a good predictor for the direct effects of EM on soil C cycling (Leake *et al.*, 2004; Cairney, 2012; Ekblad *et al.*, 2013; Wallander *et al.*, 2013), we still need to further improve our understanding of the impacts of extraradical mycelium on C cycling via particular pathways, such as organic matter decomposition, competition with and priming of saprotrophic organisms, and the decomposability of the extraradical mycelium itself. There is growing evidence that distinct species of mycorrhizal fungi differ in both the ability to acquire nutrients from distinct organic sources (with knock-on effects on the rates of decomposition of soil organic matter) and the decomposability of extraradical mycelium. These interspecific differences seem to be especially strong among EM fungi (Hobbie & Agerer, 2010; Hobbie *et al.*, 2013; Bödeker *et al.*, 2014; Koide *et al.*, 2014). EM fungi differ in their capacity to degrade distinct types of organic matter as well as to utilize the released C. For example, *Laccaria bicolor* lacks carbohydrate-active enzymes involved in the degradation of plant cell walls, although it possesses enzymes able to degrade non-plant cell wall polysaccharides (Martin *et al.*, 2008); *Cortinarius glaucopus* can produce a large number of peroxidases, comparable with white-rot saprotrophic wood-decomposing fungi (Bödeker *et al.*, 2014); and *Paxillus involutus* produces a set of enzymes similar to those involved in the oxidative degradation of wood by saprotrophic brown-rot fungi, but lacks mechanisms for metabolizing the released C (Rineau *et al.*, 2012). A potentially large source of variation in EM impact on soil C turnover may be related to differences among EM fungi in mycelium biomass turnover.

There are two main potential drivers of interspecific differences in mycelium biomass turnover among EM fungi (Koide *et al.*, 2014): the ability to produce rhizomorphs, that is long thread-like aggregations of hyphae, and melanization levels of cell walls. Rhizomorph-producing species, mostly found among *Basidiomycota*, grow more rapidly and create larger biomass than the EM fungi producing short-distance exploration types of hyphae (Hobbie, 2006; Weigt *et al.*, 2012) with a longer life span (Treseder *et al.*, 2005), but many of such species also show more rapidly decomposing litter (Clemmensen *et al.*, 2015), probably as a result of their ability to produce enzymes able to recycle their own necromass (Boddy, 1999; Falconer *et al.*, 2007, but see Treseder *et al.*, 2005; Koide & Malcolm, 2009). The concentration and type of melanin (a group of complex compounds composed of phenolic and indolic monomers) in the cell walls are other important determinants of resistance of EM fungi litter to decomposition (Malik & Haider, 1982; Robinson, 2001; Koide *et al.*, 2014). In particular, the litter of highly melanized *Cenococcum geophilum* is known to contain high concentrations of C, causing the litter of *C. geophilum* to be recalcitrant and to contribute significantly to stabilization of the soil C pool (Fogel & Hunt, 1983; Dahlberg *et al.*, 1997; Watanabe *et al.*, 2007; Koide *et al.*, 2014).

The decomposition of AM and EM abundance measures into individual components will allow the direct inclusion of existing data into global C cycling models. At the current state of our knowledge, the method proposed here might be more useful for AM than for EM systems, because of the larger (in comparison with AM) uncertainty about the relationship between the root colonization levels by EM fungi and the EM impacts on plant biomass, and significant interspecific differences between EM fungi. However, the key feature of the routine proposed here is that it allows easy extensions to account for differences between species of mycorrhizal fungi, or to account for a presence/absence effect of a specific component of mycorrhiza on a C turnover process (as carried out here to account for the effects of EM root colonization intensity on plant biomass, see Methods S1).

Conclusions

As a result of fundamental differences in morphology and physiology, AM and EM fungi are differently involved in principal aspects of belowground C cycling. Therefore, increased abundance of AM plants in EM-dominated ecosystems and vice versa may lead to profound changes in soil C budgets. We suggest that these potential impacts must be assessed quantitatively and differences in the effects of AM and EM fungi on global C cycling should be compared with other vegetation-mediated effects on C turnover. To conduct such assessments, we need a quantitative measure for the amounts of distinct types of mycorrhizal fungi present within and outside plant roots in an ecosystem. We propose a routine to obtain such a quantitative measure and, for the first time, provide a quantitative assessment of AM and EM impacts on an important ecosystem C pool. Our data-rich case study suggests that AM fungi mostly affect the C pool in living plant biomass, whereas EM fungi mostly directly affect the soil C

stock. For this analysis, and for the first time, we consider the intensity of plant root colonization by mycorrhizal fungi as a plant functional trait, and we demonstrate that this is a valid approach, that is, at the global level, the interspecific variability in root colonization by mycorrhizal fungi exceeds the intraspecific (i.e. site-driven) variation. Our study shows that a comprehensive understanding of the various components of mycorrhizal abundance and their direct and indirect impacts on C turnover is essential for the full quantification of the role of mycorrhiza in biogeochemical cycling.

Acknowledgements

We are thankful to Kathleen Treseder and Esther Moens, who supplied a considerable part of the literature data for our database. Our thanks also go to Thom Kuyper, Mari Moora and Ivano Brunner for discussions on the subject of this paper. The establishment of the field plots, and the ecological analyses based on them, were supported by grant 047.018.003 from the Netherlands Organization for Scientific Research (NWO) to J.H.C.C., and by grants 14-04-00214 from the Russian Foundation for Basic Research (RFBR) and 14-50-00029 from the Russian Science Foundation (RNF) to V.G.O.

References

- Aber J, McDowell W, Nadelhoffer K, Magill A, Berntson G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I. 1998. Nitrogen saturation in temperate forest ecosystems – hypotheses revisited. *BioScience* 48: 921–934.
- Akhmetzhanova AA, Soudzilovskaia NA, Onipchenko VG, Cornwell WK, Agafonov VK, Selivanov IA, Cornelissen JHC. 2012. A rediscovered treasure: mycorrhizal intensity database for 3000 vascular plant species across the former Soviet Union. *Ecology* 93: 689–690.
- Anderson IC, Chambers SM, Cairney JWG. 2001. Distribution and persistence of Australian *Pisolithus* species genets at native sclerophyll forest field sites. *Mycological Research* 105: 971–976.
- Averill C, Turner BL, Finzi AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505: 543–545.
- Bending GD. 2003. Litter decomposition, ectomycorrhizal roots and the 'Gadgil' effect. *New Phytologist* 158: 228–229.
- Beyer F, Hertel D, Leuschner C. 2013. Fine root morphological and functional traits in *Fagus sylvatica* and *Fraxinus excelsior* saplings as dependent on species, root order and competition. *Plant and Soil* 373: 143–156.
- Birouste M, Kazakou E, Blanchard A, Roumet C. 2012. Plant traits and decomposition: are the relationships for roots comparable to those for leaves? *Annals of Botany* 109: 463–472.
- Boddy L. 1999. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia* 91: 13–32.
- Bödeker ITM, Clemmensen KE, de Boer W, Martin F, Olson A, Lindahl BD. 2014. Ectomycorrhizal *Cortinarius* species participate in enzymatic oxidation of humus in northern forest ecosystems. *New Phytologist* 203: 245–256.
- 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 and Soil* 320: 37–77.
- Burke DJ, Hamerlynck EP, Hahn D. 2002. Effect of arbuscular mycorrhizae on soil microbial populations and associated plant performance of the salt marsh grass *Spartina patens*. *Plant and Soil* 239: 141–154.
- Cahoon SMP, Sullivan PF, Shaver GR, Welker JM, Post E. 2012. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters* 15: 1415–1422.
- Cairney JWG. 2012. Extramatrical mycelia of ectomycorrhizal fungi as moderators of carbon dynamics in forest soil. *Soil Biology & Biochemistry* 47: 198–208.
- Chapin FS, McFarland J, McGuire AD, Euskirchen ES, Ruess RW, Kielland K. 2009. The changing global carbon cycle: linking plant–soil carbon dynamics to global consequences. *Journal of Ecology* 97: 840–850.
- Chapman N, Miller AJ, Lindsey K, Whalley WR. 2012. Roots, water, and nutrient acquisition: let's get physical. *Trends in Plant Science* 17: 701–710.
- Chen W, Zeng H, Eissenstat DM, Guo D. 2013. Variation of first-order root traits across climatic gradients and evolutionary trends in geological time. *Global Ecology and Biogeography* 22: 846–856.
- Cheng L, Booker FL, Tu C, Burke KO, Zhou LS, Shew HD, Rufty TW, Hu SJ. 2012. Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO₂. *Science* 337: 1084–1087.
- Chuyong GB, Newbery DM, Songwe NC. 2002. Litter breakdown and mineralization in a central African rain forest dominated by ectomycorrhizal trees. *Biogeochemistry* 61: 73–94.
- Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339: 1615–1618.
- Clemmensen KE, Finlay RD, Dahlberg A, Stenlid J, Wardle DA, Lindahl BD. 2015. Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. *New Phytologist* 205: 1525–1536.
- Comas LH, Eissenstat DM. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* 18: 388–397.
- Comas LH, Eissenstat DM. 2009. Patterns in root trait variation among 25 co-existing North American forest species. *New Phytologist* 182: 919–928.
- Cornelissen JHC, Aerts R, Cerabolini B, Werger MJA, van der Heijden MGA. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* 129: 611–619.
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA *et al.* 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Perez-Harguindeguy N *et al.* 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065–1071.
- Dahlberg A, Jonsson L, Nylund JE. 1997. Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old-growth Norway spruce forest in south Sweden. *Canadian Journal of Botany. Journal Canadien de Botanique* 75: 1323–1335.
- Dickie IA, Koele N, Blum JD, Gleason JD, McGlone MS. 2014. Mycorrhizas in changing ecosystems. *Botany-Botanique* 92: 149–160.
- Duan T, Facelli E, Smith SE, Smith FA, Nan Z. 2011. Differential effects of soil disturbance and plant residue retention on function of arbuscular mycorrhizal (AM) symbiosis are not reflected in colonization of roots or hyphal development in soil. *Soil Biology & Biochemistry* 43: 571–578.
- Ekblad A, Wallander H, Godbold DL, Cruz C, Johnson D, Baldrian P, Bjork RG, Epron D, Kieliszewska-Rokicka B, Kjoller R *et al.* 2013. The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling. *Plant and Soil* 366: 1–27.
- Elmendorf SC, Henry GHR, Hollister RD, Bjork RG, Bjorkman AD, Callaghan TV, Collier LS, Cooper EJ, Cornelissen JHC, Day TA *et al.* 2012a. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* 15: 164–175.
- Elmendorf SC, Henry GHR, Hollister RD, Bjork RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA, Dorrepaal E, Elumeeva TG *et al.* 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2: 453–457.
- Erland S, Soderstrom B. 1990. Effects of liming on ectomycorrhizal fungi infecting *Pinus sylvestris* L. 1. Mycorrhizal infection in limed humus in the laboratory and isolation of fungi from mycorrhizal roots. *New Phytologist* 115: 675–682.

- Falconer RE, Bown JL, White NA, Crawford JW. 2007. Biomass recycling: a key to efficient foraging by fungal colonies. *Oikos* 116: 1558–1568.
- Fierer N, Strickland MS, Liptzin D, Bradford MA, Cleveland CC. 2009. Global patterns in belowground communities. *Ecology Letters* 12: 1238–1249.
- Finer L, Ohashi M, Noguchi K, Hirano Y. 2011a. Factors causing variation in fine root biomass in forest ecosystems. *Forest Ecology and Management* 261: 265–277.
- Finer L, Ohashi M, Noguchi K, Hirano Y. 2011b. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* 262: 2008–2023.
- Fogel R, Hunt G. 1983. Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. *Canadian Journal of Forest Research. Journal Canadien de la Recherche Forestière* 13: 219–232.
- Fontaine S, Henault C, Aamor A, Bdioui N, Bloor JMG, Maire V, Mary B, Revallot S, Maron PA. 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. *Soil Biology & Biochemistry* 43: 86–96.
- Fontaine S, Mariotti A, Abbadie L. 2003. The priming effect of organic matter: a question of microbial competition? *Soil Biology & Biochemistry* 35: 837–843.
- Fujita Y, Witte JPM, van Bodegom PM. 2014. Incorporating microbial ecology concepts into global soil mineralization models to improve predictions of carbon and nitrogen fluxes. *Global Biogeochemical Cycles* 28: 223–238.
- Gadgil RL, Gadgil PD. 1971. Mycorrhiza and litter decomposition. *Nature* 233: 133.
- Garcia IV, Mendoza RE. 2007. Arbuscular mycorrhizal fungi and plant symbiosis in a saline-sodic soil. *Mycorrhiza* 17: 167–174.
- Gehring CA, Mueller RC, Whitham TG. 2006. Environmental and genetic effects on the formation of ectomycorrhizal and arbuscular mycorrhizal associations in cottonwoods. *Oecologia* 149: 158–164.
- Godbold DL, Hoosbeek MR, Lukac M, Cotrufo MF, Janssens IA, Ceulemans R, Polle A, Velthorst EJ, Scarascia-Mugnozza G, De Angelis P *et al.* 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant and Soil* 281: 15–24.
- Goll DS, Brovkin V, Parida BR, Reick CH, Kattge J, Reich PB, van Bodegom PM, Niinemets U. 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. *Biogeosciences* 9: 3547–3569.
- Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Gryndler M, Larsen J, Hrselova H, Rezacova V, Gryndlerova H, Kubat J. 2006. Organic and mineral fertilization, respectively, increase and decrease the development of external mycelium of arbuscular mycorrhizal fungi in a long-term field experiment. *Mycorrhiza* 16: 159–166.
- Gu J, Xu Y, Dong X, Wang H, Wang Z. 2014. Root diameter variations explained by anatomy and phylogeny of 50 tropical and temperate tree species. *Tree Physiology* 34: 415–425.
- Guo DL, Xia MX, Wei X, Chang WJ, Liu Y, Wang ZQ. 2008. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytologist* 180: 673–683.
- Hart MM, Reader RJ. 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist* 153: 335–344.
- van der Heijden L. 2000. Mycorrhizal symbioses of *Salix repens*: diversity and functional significance. PhD thesis, Wageningen University, Wageningen, the Netherlands.
- van der Heijden MGA, Martin F, Selosse MA, Sanders IR. 2015. Mycorrhizal ecology and evolution: the past, the present and the future. *Tansley Review. New Phytologist* 205: 1406–1423.
- Heinemeyer A, Ineson P, Ostle N, Fitter AH. 2006. Respiration of the external mycelium in the arbuscular mycorrhizal symbiosis shows strong dependence on recent photosynthates and acclimation to temperature. *New Phytologist* 171: 159–170.
- Hempel S, Gotzenberger L, Kuhn I, Michalski SG, Rillig MC, Zobel M, Moora M. 2013. Mycorrhizas in the Central European flora – relationship with plant life history traits and ecology. *Ecology* 94: 1389–1399.
- Heskel M, Greaves H, Kornfeld A, Gough L, Atkin OK, Turnbull MH, Shaver G, Griffin KL. 2013. Differential physiological responses to environmental change promote woody shrub expansion. *Ecology and Evolution* 3: 1149–1162.
- Hobbie EA. 2006. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. *Ecology* 87: 563–569.
- Hobbie EA, Agerer R. 2010. Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. *Plant and Soil* 327: 71–83.
- Hobbie EA, Ouimette AP, Schuur EAG, Kierstead D, Trappe JM, Bendiksen K, Ohenoja E. 2013. Radiocarbon evidence for the mining of organic nitrogen from soil by mycorrhizal fungi. *Biogeochemistry* 114: 381–389.
- Hobbie JE, Hobbie EA. 2006. N-15 in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. *Ecology* 87: 816–822.
- Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowski R, Hale C, Karolewski P. 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* 87: 2288–2297.
- Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC *et al.* 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* 13: 394–407.
- Jackson RB, Mooney HA, Schulze ED. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, USA* 94: 7362–7366.
- Jones MD, Durall DM, Tinker PB. 1998. Comparison of arbuscular and ectomycorrhizal *Eucalyptus coccifera*: growth response, phosphorus uptake efficiency and external hyphal production. *New Phytologist* 140: 125–134.
- Karst J, Marczak L, Jones MD, Turkington R. 2008. The mutualism–parasitism continuum in ectomycorrhizas: a quantitative assessment using meta-analysis. *Ecology* 89: 1032–1042.
- Kattge J, Diaz S, Lavorel S, Prentice C, Leadley P, Bonisch G, Garnier E, Westoby M, Reich PB, Wright IJ *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935.
- Keuskamp JA, Dingemans BJJ, Lehtinen T, Sarneel JM, Hefting MM. 2013. Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution* 4: 1070–1075.
- Koele N, Dickie IA, Oleksyn J, Richardson SJ, Reich PB. 2012. No globally consistent effect of ectomycorrhizal status on foliar traits. *New Phytologist* 196: 845–852.
- Koide RT, Fernandez C, Malcolm G. 2014. Determining place and process: functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytologist* 201: 433–439.
- Koide RT, Malcolm GM. 2009. N concentration controls decomposition rates of different strains of ectomycorrhizal fungi. *Fungal Ecology* 2: 197–202.
- Langley JA, Hungate BA. 2003. Mycorrhizal controls on belowground litter quality. *Ecology* 84: 2302–2312.
- Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- Leake JR, Johnson D, Donnelly DP, Muckle GE, Boddy L, Read DJ. 2004. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Canadian Journal of Botany. Journal Canadien de Botanique* 82: 1016–1045.
- Leifheit EF, Veresoglou SD, Lehmann A, Morris EK, Rillig MC. 2014. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation – a meta analysis. *Plant and Soil* 374: 523–537.
- Leigh J, Fitter AH, Hodge A. 2011. Growth and symbiotic effectiveness of an arbuscular mycorrhizal fungus in organic matter in competition with soil bacteria. *Fems Microbiology Ecology* 76: 428–438.
- Lekberg Y, Koide RT. 2005. Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytologist* 168: 189–204.
- Liski J, Palosuo T, Peltoniemi M, Sievanen R. 2005. Carbon and decomposition model Yasso for forest soils. *Ecological Modelling* 189: 168–182.
- Malik KA, Haider K. 1982. Decomposition of C-14-labeled melanoid fungal residues in a marginally sodic soil. *Soil Biology & Biochemistry* 14: 457–460.
- Mandyam K, Jumpponen A. 2008. Seasonal and temporal dynamics of arbuscular mycorrhizal and dark septate endophytic fungi in a tallgrass prairie

- ecosystem are minimally affected by nitrogen enrichment. *Mycorrhiza* 18: 145–155.
- Mariotte P. 2014. Do subordinate species punch above their weight? Evidence from above- and below-ground. *New Phytologist* 203: 16–21.
- Martin F, Aerts A, Ahren D, Brun A, Danchin EGJ, Duchaussoy F, Gibon J, Kohler A, Lindquist E, Pereda V *et al.* 2008. The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. *Nature* 452: 88–92.
- McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist* 195: 823–831.
- McGuire KL, Treseder KK. 2010. Microbial communities and their relevance for ecosystem models: decomposition as a case study. *Soil Biology & Biochemistry* 42: 529–535.
- McGuire KL, Zak DR, Edwards IP, Blackwood CB, Upchurch R. 2010. Slowed decomposition is biotically mediated in an ectomycorrhizal, tropical rain forest. *Oecologia* 164: 785–795.
- Miller RM, Reinhardt DR, Jastrow JD. 1995. External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* 103: 17–23.
- Moora M. 2014. Mycorrhizal traits and plant communities: perspectives for integration. *Journal of Vegetation Science* 25: 1126–1132.
- Muriithi-Muchane M. 2013. Influences of agricultural management practices on arbuscular mycorrhizal fungal symbioses in Kenyan agro-ecosystems. PhD thesis, Wageningen University, Wageningen, the Netherlands.
- Myers-Smith IH, Hik DS, Kennedy C, Cooley D, Johnstone JF, Kenney AJ, Krebs CJ. 2011. Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. *Ambio* 40: 610–623.
- Naito AT, Cairns DM. 2011. Patterns and processes of global shrub expansion. *Progress in Physical Geography* 35: 423–442.
- Nilsen P, Borja I, Knutsen H, Breun R. 1998. Nitrogen and drought effects on ectomycorrhizae of Norway spruce *Picea abies* L. (Karst.). *Plant and Soil* 198: 179–184.
- Nottingham AT, Turner BL, Winter K, Chamberlain PM, Stott A, Tanner EVJ. 2013. Root and arbuscular mycorrhizal mycelial interactions with soil microorganisms in lowland tropical forest. *Fems Microbiology Ecology* 85: 37–50.
- Olsson PA, Francis R, Read DJ, Soderstrom B. 1998. Growth of arbuscular mycorrhizal mycelium in calcareous dune sand and its interaction with other soil microorganisms as estimated by measurement of specific fatty acids. *Plant and Soil* 201: 9–16.
- Olsson PA, Johnson NC. 2005. Tracking carbon from the atmosphere to the rhizosphere. *Ecology Letters* 8: 1264–1270.
- Olsson PA, Larsson L, Bago B, Wallander H, van Aarle IM. 2003. Ergosterol and fatty acids for biomass estimation of mycorrhizal fungi. *New Phytologist* 159: 7–10.
- Olsson PA, Wilhelmsson P. 2000. The growth of external AM fungal mycelium in sand dunes and in experimental systems. *Plant and Soil* 226: 161–169.
- Onipchenko VG. 2004. Mycorrhiza. In: Onipchenko VG, ed. *Alpine ecosystems in the Northwestern Caucasus*. Dordrecht, the Netherlands: Kluwer, 284–296.
- Öpik M, de Bello F, Price JN, Fraser LH. 2014. New insights into vegetation patterns and processes. *New Phytologist* 201: 383–387.
- Öpik M, Zobel M, Cantero JJ, Davison J, Facelli JM, Hiiesalu I, Jairus T, Kalwij JM, Koorem K, Leal ME *et al.* 2013. Global sampling of plant roots expands the described molecular diversity of arbuscular mycorrhizal fungi. *Mycorrhiza* 23: 411–430.
- Orwin KH, Kirschbaum MUF, St John MG, Dickie IA. 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. *Ecology Letters* 14: 493–502.
- Paul EA, Clark FE. 1996. *Soil microbiology and biochemistry*. San Diego, CA, USA: Academic Press.
- Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* 199: 41–51.
- Piotrowski JS, Lekberg Y, Harner MJ, Ramsey PW, Rillig MC. 2008. Dynamics of mycorrhizae during development of riparian forests along an unregulated river. *Ecography* 31: 245–253.
- Powell JR, Parrent JL, Hart MM, Klironomos JN, Rillig MC, Maherali H. 2009. Phylogenetic trait conservatism and the evolution of functional trade-offs in arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B: Biological Sciences* 276: 4237–4245.
- Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL. 2002. Fine root architecture of nine North American trees. *Ecological Monographs* 72: 293–309.
- van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA *et al.* 2013. Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology* 101: 265–276.
- Read DJ. 1991. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.
- Read DJ, Leake JR, Perez-Moreno J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany. Journal Canadien de Botanique* 82: 1243–1263.
- Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* 157: 475–492.
- Reich PB. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.
- Rillig MC. 2004a. Arbuscular mycorrhizae and terrestrial ecosystem processes. *Ecology Letters* 7: 740–754.
- Rillig MC. 2004b. Arbuscular mycorrhizae, glomalin, and soil aggregation. *Canadian Journal of Soil Science* 84: 355–363.
- Rillig MC, Mummey DL. 2006. Mycorrhizas and soil structure. *New Phytologist* 171: 41–53.
- Rillig MC, Wright SF, Kimball BA, Pinter PJ, Wall GW, Ottman MJ, Leavitt SW. 2001. Elevated carbon dioxide and irrigation effects on water stable aggregates in a Sorghum field: a possible role for arbuscular mycorrhizal fungi. *Global Change Biology* 7: 333–337.
- Rineau F, Roth D, Shah F, Smits M, Johansson T, Canback B, Olsen PB, Persson P, Grell MN, Lindquist E *et al.* 2012. The ectomycorrhizal fungus *Paxillus involutus* converts organic matter in plant litter using a trimmed brown-rot mechanism involving Fenton chemistry. *Environmental Microbiology* 14: 1477–1487.
- Robinson CH. 2001. Cold adaptation in Arctic and Antarctic fungi. *New Phytologist* 151: 341–353.
- Ruotsalainen AL, Vare H, Vestberg M. 2002. Seasonality of root fungal colonization in low-alpine herbs. *Mycorrhiza* 12: 29–36.
- Sawyer NA, Chambers SM, Cairney JWG. 2003. Distribution of *Amanita* spp. genotypes under eastern Australian sclerophyll vegetation. *Mycological Research* 107: 1157–1162.
- Schimel DS, Braswell BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend AR. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* 8: 279–293.
- Simard SW, Durall D, Jones M. 2002. Carbon and nutrient fluxes within and between mycorrhizal plants. In: Van der Heijden MGA, Sanders IR, eds. *Mycorrhizal ecology*. Berlin, Germany: Springer, 456.
- Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P *et al.* 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate–carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology* 14: 2015–2039.
- Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis*. London, UK: Academic Press.
- Soudzilovskaia NA, Douma JC, Akhmetzhanova AA, van Bodegom PM, Cornwell WK, Moens EJ, Treseder KK, Tibbett M, Wang YP, Cornelissen JHC. 2015. Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Global Ecology and Biogeography* 24: 371–382.
- Staddon PL, Thompson K, Jakobsen I, Grime JP, Askew AP, Fitter AH. 2003. Mycorrhizal fungal abundance is affected by long-term climatic manipulations in the field. *Global Change Biology* 9: 186–194.

- Subke JA, Voke NR, Leronni V, Garnett MH, Ineson P. 2011. Dynamics and pathways of autotrophic and heterotrophic soil CO₂ efflux revealed by forest girdling. *Journal of Ecology* 99: 186–193.
- Talbot JM, Allison SD, Treseder KK. 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Functional Ecology* 22: 955–963.
- Tedersoo L, Bahram M, Polme S, Koljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A *et al.* 2014. Global diversity and geography of soil fungi. *Science* 346: 1078–1090.
- Thonar C, Schnepf A, Frossard E, Roose T, Jansa J. 2011. Traits related to differences in function among three arbuscular mycorrhizal fungi. *Plant and Soil* 339: 231–245.
- Tobner CM, Paquette A, Messier C. 2013. Interspecific coordination and intraspecific plasticity of fine root traits in North American temperate tree species. *Frontiers in Plant Science* 4: 242.
- Todd-Brown KEO, Randerson JT, Post WM, Hoffman FM, Tarnocai C, Schuur EAG, Allison SD. 2013. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences* 10: 1717–1736.
- Treseder KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164: 347–355.
- Treseder KK. 2013. The extent of mycorrhizal colonization of roots and its influence on plant growth and phosphorus content. *Plant and Soil* 371: 1–13.
- Treseder KK, Allen MF, Ruess RW, Pregitzer KS, Hendrick RL. 2005. Lifespans of fungal rhizomorphs under nitrogen fertilization in a pinyon–juniper woodland. *Plant and Soil* 270: 249–255.
- Treseder KK, Balsler TC, Bradford MA, Brodie EL, Dubinsky EA, Eviner VT, Hofmockel KS, Lennon JT, Levine UY, MacGregor BJ *et al.* 2012. Integrating microbial ecology into ecosystem models: challenges and priorities. *Biogeochemistry* 109: 7–18.
- Treseder KK, Cross A. 2006. Global distributions of arbuscular mycorrhizal fungi. *Ecosystems* 9: 305–316.
- Treseder KK, Turner KM. 2007. Glomalin in ecosystems. *Soil Science Society of America Journal* 71: 1257–1266.
- Tuomi J, Kytöviita MM, Hardling R. 2001. Cost efficiency of nutrient acquisition and the advantage of mycorrhizal symbiosis for the host plant. *Oikos* 92: 62–70.
- Valverde-Barrantes OJ, Smemo KA, Feinstein LM, Kershner MW, Blackwood CB. 2013. The distribution of below-ground traits is explained by intrinsic species differences and intraspecific plasticity in response to root neighbours. *Journal of Ecology* 101: 933–942.
- Vargas R, Baldocchi DD, Querejeta JI, Curtis PS, Hasselquist NJ, Janssens IA, Allen MF, Montagnani L. 2010. Ecosystem CO₂ fluxes of arbuscular and ectomycorrhizal dominated vegetation types are differentially influenced by precipitation and temperature. *New Phytologist* 185: 226–236.
- Vesterdal L, Elberling B, Christiansen JR, Callesen I, Schmidt IK. 2012. Soil respiration and rates of soil carbon turnover differ among six common European tree species. *Forest Ecology and Management* 264: 185–196.
- Wallander H, Ekblad A, Bergh J. 2011. Growth and carbon sequestration by ectomycorrhizal fungi in intensively fertilized Norway spruce forests. *Forest Ecology and Management* 262: 999–1007.
- Wallander H, Ekblad A, Godbold DL, Johnson D, Bahr A, Baldrian P, Björk RG, Kieliszewska-Rokicka B, Kjoller R, Kraigher H *et al.* 2013. Evaluation of methods to estimate production, biomass and turnover of ectomycorrhizal mycelium in forests soils – a review. *Soil Biology & Biochemistry* 57: 1034–1047.
- Wang B, Qiu YL. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16: 299–363.
- Wang Z, Guo D, Wang X, Gu J, Mei L. 2006. Fine root architecture, morphology, and biomass of different branch orders of two Chinese temperate tree species. *Plant and Soil* 288: 155–171.
- Watanabe M, Sato H, Matsuzaki H, Kobayashi T, Sakagami N, Maejima Y, Ohta H, Fujitake N, Hiradate S. 2007. C-14 ages and delta C-13 of sclerotium grains found in forest soils. *Soil Science and Plant Nutrition* 53: 125–131.
- Weigt RB, Raidl S, Verma R, Agerer R. 2012. Exploration type-specific standard values of extramatrical mycelium – a step towards quantifying ectomycorrhizal space occupation and biomass in natural soil. *Mycological Progress* 11: 287–297.
- Wele M, Ravnskov S, Kieliszewska-Rokicka B, Larsen J. 2010. Suppression of other soil microorganisms by mycelium of arbuscular mycorrhizal fungi in root-free soil. *Soil Biology & Biochemistry* 42: 1534–1540.
- Wieder WR, Boehnert J, Bonan GB. 2014. Evaluating soil biogeochemistry parameterizations in Earth system models with observations. *Global Biogeochemical Cycles* 28: 211–222.
- Wieder WR, Bonan GB, Allison SD. 2013. Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change* 3: 909–912.
- Wilson GWT, Rice CW, Rillig MC, Springer A, Hartnett DC. 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecology Letters* 12: 452–461.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Yuan ZY, Chen HYH. 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. *Critical Reviews in Plant Sciences* 29: 204–221.
- Zheng W, Morris EK, Rillig MC. 2014. Ectomycorrhizal fungi in association with *Pinus sylvestris* seedlings promote soil aggregation and soil water repellency. *Soil Biology & Biochemistry* 78: 326–331.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Data frequency distribution for plant species-specific arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) root colonization.

Fig. S2 Intraspecific variability in plant species-specific arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) root colonization values.

Table S1 Calculations of the involvement of arbuscular mycorrhiza and ectomycorrhiza in the total ecosystem carbon pool of living plants and mycorrhizal fungi in an arbuscular mycorrhiza plant-dominated alpine plant community

Table S2 Calculations of the involvement of arbuscular mycorrhiza and ectomycorrhiza in the total ecosystem carbon pool of living plants and mycorrhizal fungi in an ectomycorrhiza plant-dominated alpine plant community

Table S3 Calculations of changes in the involvement of arbuscular mycorrhiza and ectomycorrhiza in the total ecosystem carbon pool of living plants and mycorrhizal fungi

Table S4 Calculations of changes in the involvement of arbuscular mycorrhiza and ectomycorrhiza in the total ecosystem carbon pool of living plants and mycorrhizal fungi

Table S5 Sources of arbuscular mycorrhiza data in the global database of plant root colonization intensity by mycorrhizal fungi

Table S6 Sources of ectomycorrhiza data in the global database of plant root colonization intensity by mycorrhizal fungi

Methods S1 Data sources and calculation methods used in Supporting Information Tables S1–S4 for the estimation of the involvement of arbuscular mycorrhiza and ectomycorrhiza in the total ecosystem carbon pool of living plants and mycorrhizal fungi.

Methods S2 Soil analysis methods.

Methods S3 Robustness analysis of the case study data and data limitations caused by adopted estimations and simplifications.

Methods S4 Statistical analysis of interspecific differences in mycorrhizal root colonization levels among vascular plant species.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.



About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <26 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**