Methods

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

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Summary

- 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 CO_2 (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; Welc *et al.*, 2010; Leigh *et al.*, 2011; Nottingham *et al.*, 2013), although Cheng *et al.* (2012) reported priming effects of AM fungi under elevated CO_2. 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

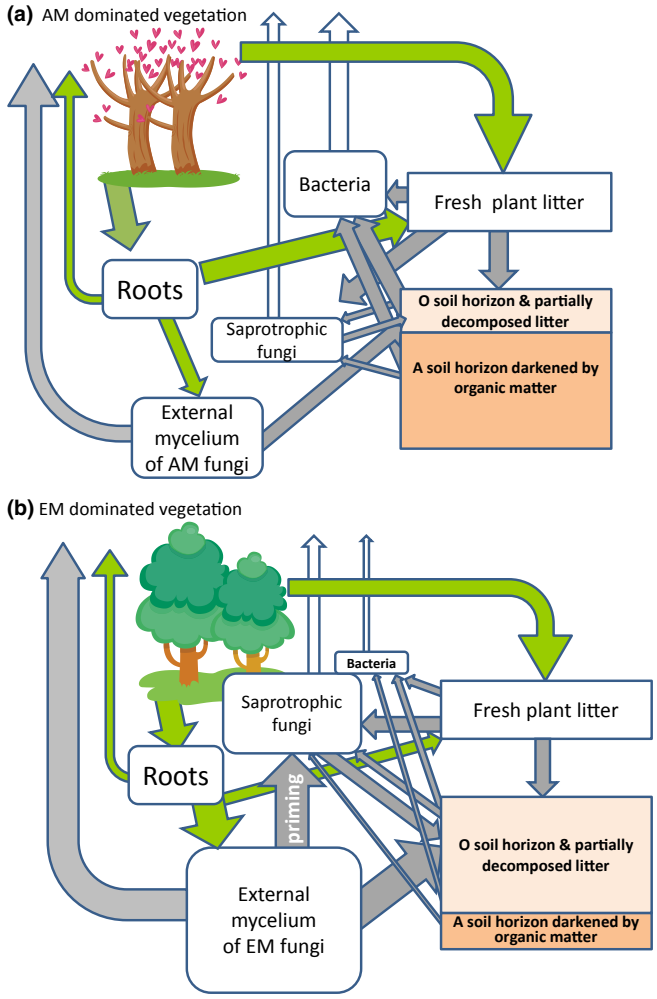

Fig. 1 Current view on individual pools and fluxes of belowground carbon (C) dynamics in (a) arbuscular mycorrhiza (AM)- and (b) ectomycorrhiza (EM)-dominated ecosystems. White blocks, living organisms and fresh litter; brown blocks, organic soil fractions; green arrows, plant-associated C fluxes, discussed 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 funtioning 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; Heskel *et al.*, 2013).

We established seven and six 50 × 50-cm^2 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

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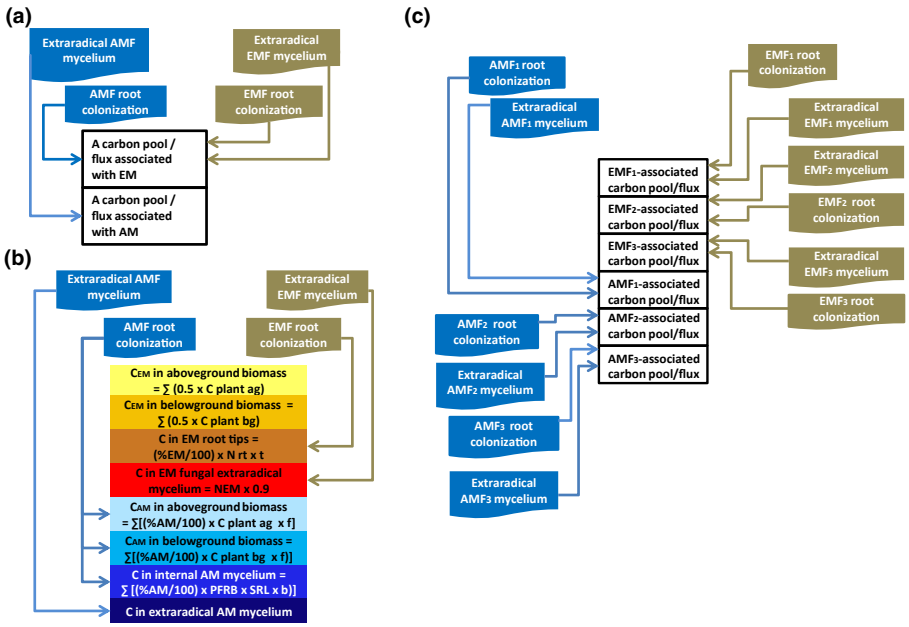

Fig. 2 Schematic illustration of the proposed method for quantitative assessment of involvement of AM and EM into soil carbon cycling. (a) General illustration of the proposed idea: assessments of the involvement of AM and EM into any type of soil carbon pools or fluxes should be conducted taking into 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, ∑ 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 × 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 × %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 $k = 1.42 \times 10^{-6}$ μg 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 μg 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.

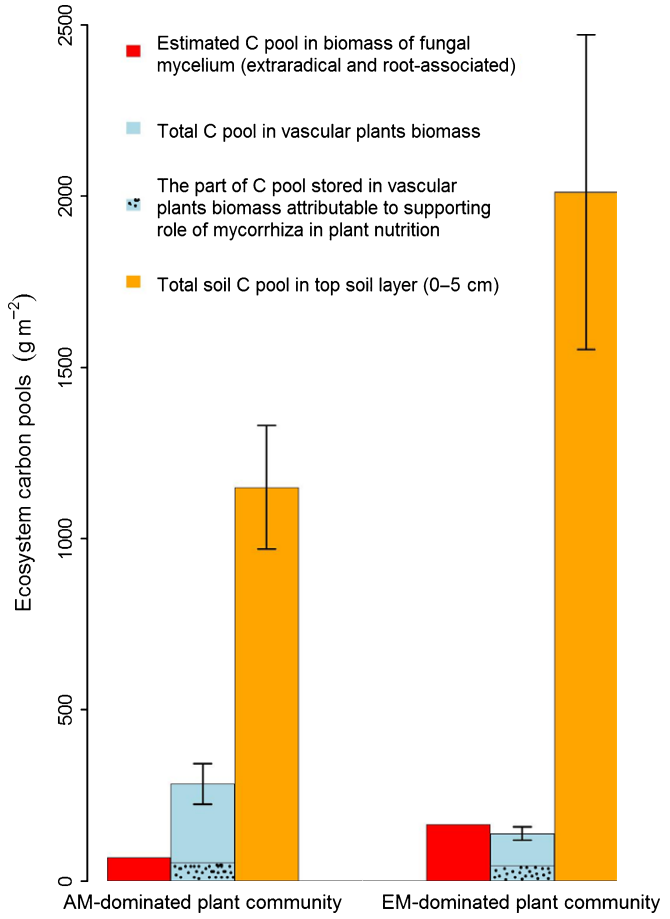

Fig. 3 Mycorrhiza-related carbon (C) pools, C pool in living plant above- and belowground biomass, and total soil C pool in the top 0–5-cm organic soil layer in arbuscular mycorrhiza (AM)- and ectomycorrhiza (EM)-dominated communities in subarctic–alpine Sweden. Mean values ± SE are shown. $n = 7$, for 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.

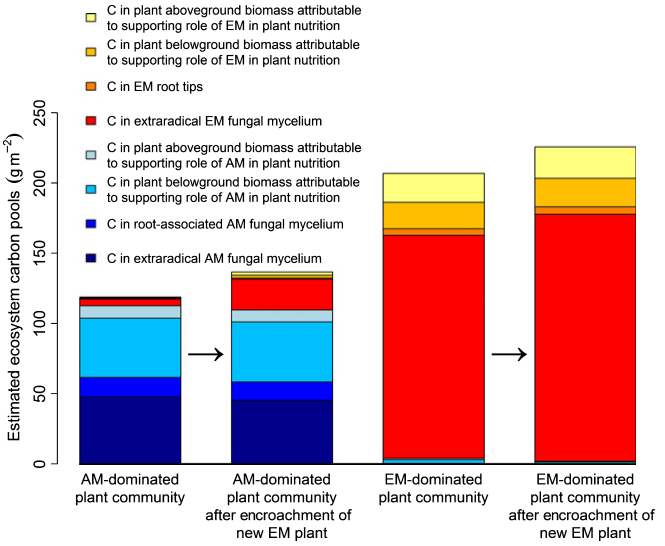

Fig. 4 Composition of mycorrhiza-related carbon (C) pools and simulated impacts of encroachment of the ectomycorrhizal plant *Betula nana* in arbuscular mycorrhiza (AM)- and ectomycorrhiza (EM)-dominated plots in subarctic–alpine Sweden.

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 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			
	Mean	SE	*n*	Mean	SE	*n*	*P* (*t*-test)
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 publically 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 (Tedersoo *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

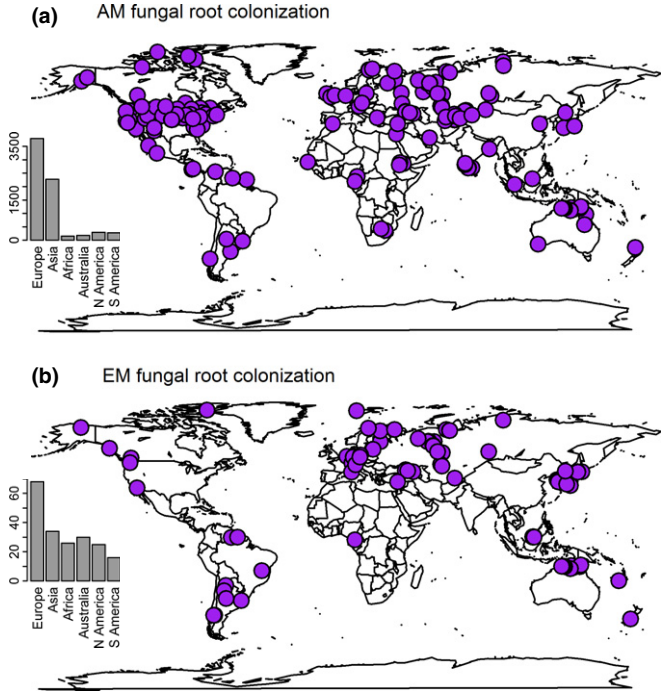

Fig. 5 Sites in which the plant root colonization data by (a) arbuscular mycorrhizal (AM) and (b) ectomycorrhizal (EM) fungi were collected. Bar graphs in the left corner of each map show the number of species-by-site data points per continent, for AM fungi ranging between 157 and 3790, and for EM fungi 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 geophillum* is known to contain high concentrations of C, causing the litter of *C. geophillum* 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.

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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.

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