Global mycorrhizal plants distribution linked to terrestrial carbon stocks

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Abstract

Vegetation impacts on ecosystem functioning are mediated by mycorrhiza, a plant-fungal association formed by most plant species. Ecosystems dominated by distinct mycorrhizal types differ strongly in biogeochemical cycles. Quantitative analyses of mycorrhizal impacts of ecosystem functioning are hindered by the absence of information on mycorrhizal distribution. We present the first global high-resolution maps of vegetation biomass distribution among main types of mycorrhizal associations. Arbuscular, ecto-, ericoid and non-mycorrhizal vegetation store, respectively, 242, 98, 7 and 31 GT carbon in aboveground biomass. Soil carbon stocks in both topsoil and subsoil are positively related to the biomass fraction of ectomycorrhizal plants in the community, though the strength of this relationship varies across biomes. We show that human-induced transformations of Earth's ecosystems reduced ectomycorrhizal vegetation, with potential knock-on effects on terrestrial carbon stocks. Our work provides a benchmark for spatially explicit global quantitative assessments of mycorrhizal impacts on ecosystem functioning and biogeochemical cycles.

Short title: Global distribution of mycorrhizal plants

One Sentence Summary: First maps of the global distribution of mycorrhizal plants reveal global losses of ectomycorrhizal vegetation, and quantitative links between mycorrhizal vegetation patterns and terrestrial carbon stocks.

Mycorrhizas are mutualistic relationships between plants and fungi, in which fungi supply plants with nutrients and plants provide carbon to fungi[1]. Among known mycorrhizal types, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), and ericoid mycorrhiza (ErM) are geographically the most widespread, colonizing over 85% of vascular plants across vegetated terrestrial biomes[1-4]. Due to the enhancement of plant nutrient acquisition[1] and the large biomass of fungal networks in soil[5], the presence and type of mycorrhiza is among the key determinants of ecosystem functioning[6-9] and biogeochemical cycling[10-13].

Differential biogeochemical processes among ecosystems dominated by plants hosting distinct types of mycorrhizas[12] likely also affect the global patterns of topsoil vs subsoil carbon stocks[14]. There is growing evidence that ecosystems dominated by EcM and ErM vegetation exhibit higher topsoil carbon to nitrogen ratios (C/N) compared to ecosystems dominated by AM plants[11,12,15,16], although in temperate forests the pattern may be reversed in deeper soil layers[17]. The mechanisms of these differences are heavily debated in current literature, with distinct physiological traits of the mycorrhizal fungi most likely playing a critical role[14,17-20]. A full understanding of the global carbon and nitrogen stocks demands quantitative models on the distribution of mycorrhizal types in ecosystems. Despite the existence of regional maps of current[21,22] and past[23] mycorrhizal vegetation, we still lack global information on the distribution of mycorrhizal types. While current terrestrial biosphere models simulate feedbacks between the carbon cycle and vegetation distribution[24], such models ignore mycorrhizal types and their effects on nutrient cycling. Integration of such information is a promising way towards a more realistic simulation of carbon and nutrient fluxes associated with plant nutrition[17,18,25] and soil carbon cycles[16,26]. Quantitative models of the distribution of mycorrhizal vegetation constitute an important missing link between known effects of mycorrhiza in biogeochemical cycles and their global impacts[27].

Human activities such as forest logging, urbanization, and agricultural practices have altered 50-75% of the Earth's terrestrial ecosystems[28], transforming areas with previously natural EcM and ErM vegetation into AM and non-mycorrhizal (NM) vegetation. So far, the impact of anthropogenic land use shifts on biogeochemical cycles associated with mycorrhizas have remained poorly known due to the lack of appropriate spatial information.

Based on a comprehensive quantitative evaluation of plant-mycorrhizal associations and the distribution of vascular plant species across biomes and continents, we assembled the first high-resolution digital maps of the global distribution of biomass fractions of AM, EcM, ErM, and NM plants. Building on these maps, we assessed (i) the amount of aboveground biomass carbon currently stored in each type of mycorrhizal vegetation, (ii) the impact of conversion of natural ecosystems to croplands on the distribution of mycorrhizal types globally, and (iii) the relation between ecosystem soil carbon content and the relative abundance of AM, EcM and ErM plants in topsoil (0-20cm), medium (20-60) and deep (60-100 cm) subsoil layers.

Assembly of mycorrhizal vegetation maps

Based on data accumulated over the past three decades, we established the largest dataset to date containing information about the presence and type of mycorrhizal colonisation of vascular plant species, which is comprised of 27,736 records for 12,702 plant species obtained from 1,565 data sources including published reviews, data compilations and previously neglected or recent case studies (Supplementary Table 1). We assigned the abundance of mycorrhizal types to all available combinations of continents, 98 ecological regions (as defined by Bailey[29]; Supplementary Table 2), and 38 land cover types (as defined by ESA CCI land cover map[30]; Supplementary Table 3) based on information about vegetation composition, dominant plant species and their growth forms provided by vegetation surveys obtained from 2,169 sources (Supplementary Table 4) and the data about plant species growth forms obtained from the TRY database[31]. By combining these sources of information, we constructed global maps of mycorrhizal type distribution. Extended Data Figure 1 shows the flowchart of the data assembly processes employed for map construction.

Our maps (Figure 1) provide quantitative estimates of the distribution of aboveground biomass fractions among AM, EcM and ErM plants within areal units of 10 arcmin. The use of a detailed map of ecoregions[29] provides much greater resolution compared to the biome-based patterns of mycorrhizal distributions reported by Read[3] >25 years ago, whereas the land cover map[30] enabled us to provide accurate spatial positioning of ecosystem boundaries based on satellite-derived data, explicitly taking into account human-driven transformations of vegetation.

We evaluated the accuracy of our maps using four independent datasets: (i) forest biomass structure for Eurasia[32], (ii) a global dataset of forest biomass structure used for an analysis of mycorrhizal impacts on carbon *vs* nitrogen dynamics[19], (iii) estimates of mycorrhizal associations in the USA based on remote sensing[33], and (iv) West Australian map of mycorrhizal root abundance[21] (Extended Data Figure 2). This validation revealed that the vast majority of the data (87% of the AM data points and 89% of the EcM data points) deviate by <25% from the measurements[19,32,33] (Extended Data Figure 3) when excluding ESA land use classes comprising poorly resolved combinations (i.e. mixed classes of land cover types[30], such as “Tree cover, broadleaved, evergreen, closed to open (>15%)”, see methods for details) that were difficult to couple to our classification scheme.

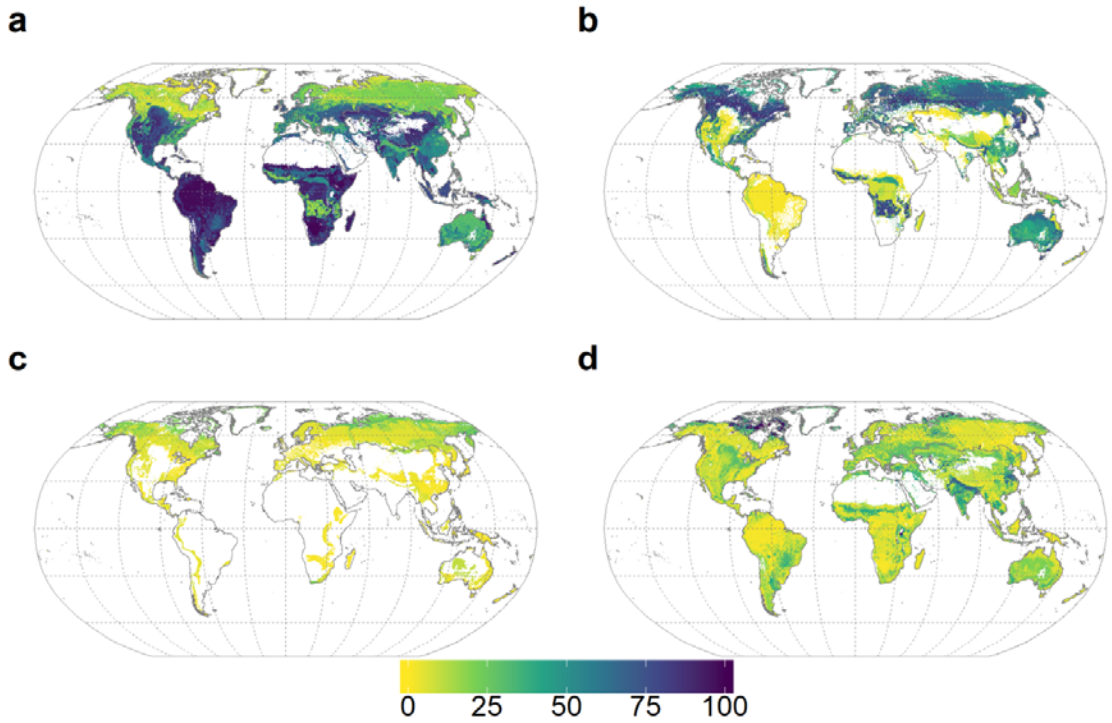

Figure 1. Percentage of aboveground plant biomass of a - arbuscular mycorrhizal plants, b - ectomycorrhizal plants, c - ericoid mycorrhizal plants, and d -non-mycorrhizal plants. The map resolution is 10 arcmin.

Mycorrhizal vegetation and aboveground carbon stocks

Linking our maps to the global data on distribution of aboveground biomass carbon[34] we estimated the amount of aboveground biomass carbon stored in arbuscular, ecto-, ericoid and non-mycorrhizal vegetation as 242, 98, 7 and 31 GT, respectively (Figure 2). In this analysis, the data were scaled to a resolution of 15 arcmin to match the aboveground plant biomass information[34]. Most of the aboveground carbon stock stored in arbuscular mycorrhizal vegetation is situated in tropical forests (Figure 3). Extended Data Table 1 shows per biome distribution of the carbon stocks among mycorrhizal types.

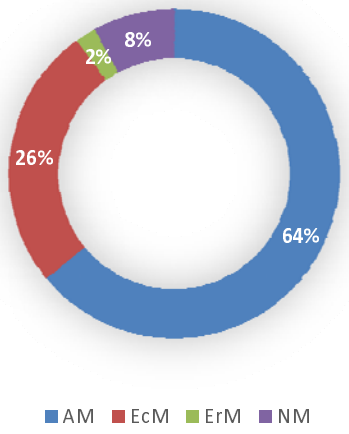

Figure 2. Aboveground biomass carbon globally stored in terrestrial vegetation featuring arbuscular mycorrhizal vegetation (AM), ectomycorrhizal vegetation (EcM), ericoid mycorrhizal vegetation (ErM) and nom-mycorrhizal vegetation (NM).

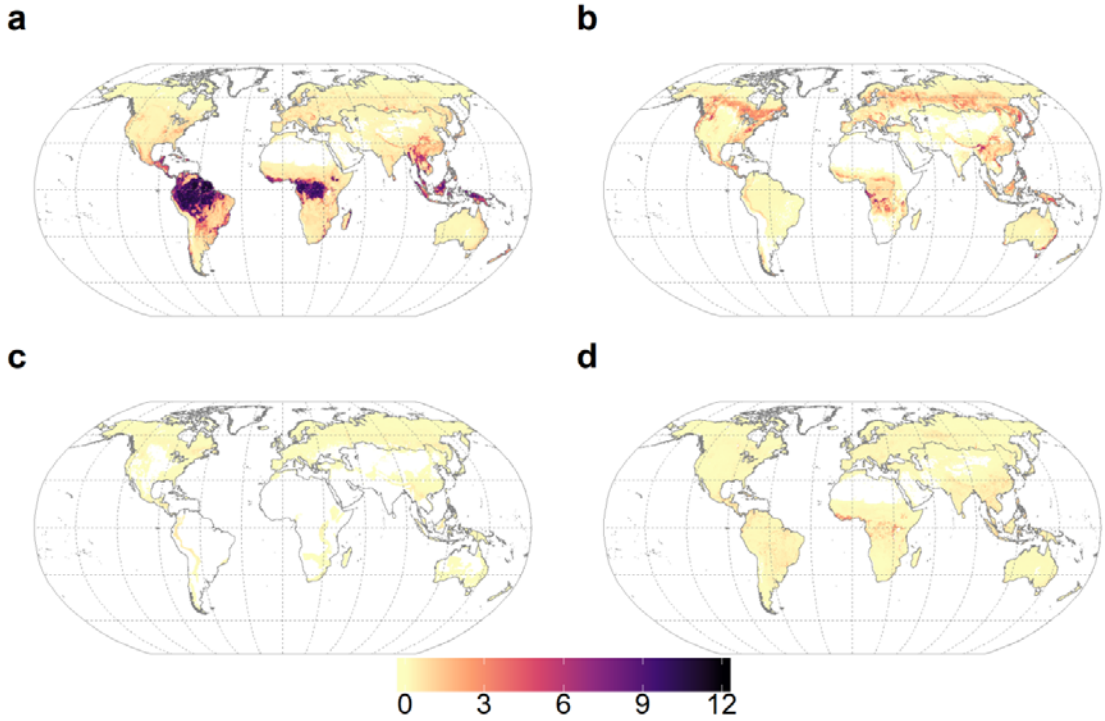

Figure 3. Amount of carbon (Mt per grid cell of 15 arcmin) stored in plant biomass of (a) arbuscular mycorrhizal plants, (b) ectomycorrhizal plants, (c) ericoid mycorrhizal plants, (d) non-mycorrhizal plants.

Impacts of human-induced land transformations on distribution patterns of mycorrhizal vegetation

Agricultural practices drive the replacement of natural vegetation by non-mycorrhizal and facultative AM crops[1,35], which are often *de-facto* non-mycorrhizal due to destruction of hyphal networks by ploughing and excess fertilisation[36,37]. Using past vegetation estimates, Swaty and co-workers[23] showed that across conterminous USA, agriculture has reduced the relative abundance of ectomycorrhizal plants compared to other mycorrhizal types. However, global quantifications of agricultural impacts on distribution of mycorrhizas have not been possible until now. Based on the current land use data underlying our maps (Supplementary Table 4), we assessed mycorrhizal distributions on Earth in the absence of croplands. For each ecoregion-continent-land cover combination that contained croplands, we replaced current biomass fractions by estimates of per-grid cell biomass fractions in AM, EcM, ErM and NM plants that were *expected* at these locations based on natural vegetation types (see Methods for details). Based on these data, we generated maps presenting *potential natural* distributions of biomass fraction of AM, EcM, ErM, and NM plants in a cropland-free world (Extended Data Figure 3). The current biomass fractions of AM plants have increased in Europe, parts of Asia, and North America, but declined in Africa, Asia (mostly India) and South America, coinciding with increase of non-mycorrhizal vegetation due to cultivation of effectively non-mycorrhizal crops (Figure 4, Extended Data Figure 4). The models predict that EcM biomass fractions have decreased in all continents, mostly due to replacement of natural forests by agricultural lands, whereas ErM biomass has remained unchanged.

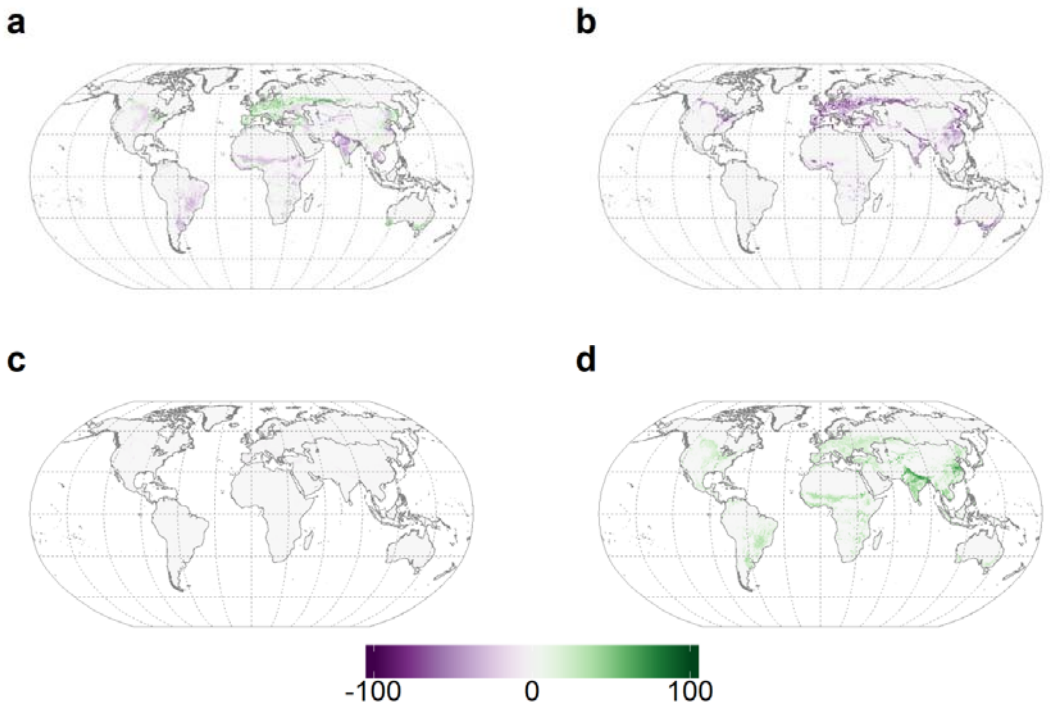

Figure 4. Changes in biomass fractions of mycorrhizal vegetation induced by crop cultivation and pastures. a - arbuscular mycorrhizal plants, b - ectomycorrhizal plants, c - ericoid mycorrhizal plants, d - non-mycorrhizal plants. Purple colors indicate losses, green colors indicate gains.

Relationships between biomass fractions of mycorrhizal types and soil carbon stocks

Recent field research in temperate forests in the USA[14] suggests that the positive impact of greater abundance of EcM relative to AM trees on soil carbon content declines with increasing soil depth, with a positive effect of AM on subsoil carbon. This is in agreement with the Microbial Efficiency-Matrix Stabilization hypothesis, which predicts that ecosystems with rapid decomposition, such as most AM-dominated forests[19], enhance soil organic matter (SOM) stabilization by accelerating the production and deposition of microbial residues[38,39]. However, the relationships between mycorrhizal types and topsoil vs subsoil carbon stocks have been never assessed quantitatively across the entire Earth's vegetation. So far, biome

type (a compound variable combining impacts of climate, and dominant plant growth forms) has been regarded as the principal driver of soil carbon stocks[40], cf [11].

To disentangle the effects of biomes vs mycorrhizal types within biomes, we modelled the global relationships between soil carbon content, biome type[41], and (1) biomass fractions of AM and EcM plants (the data presented in Figure 1), and (2) absolute amount of carbon stored in the above ground biomass of different vegetation types (the data presented in Figure 3) . We did not analyse the relationship between ErM plant cover and soil C content, due to a small proportion of the ErM plant biomass in the majority of ecosystems.

We conducted separate analyses for the topsoil (uppermost 20 cm soil layer) and subsoil (20-60, and 60-100cm soil layers), as obtained from the ISRIC WISE Soil Property Databases, at a resolution of 30 arcsec[42]. The data sources used for these analyses are independent: the ecoregion classification and hence mycorrhizal type distribution does not account for edaphic parameters, whereas our soil C data is unrelated to that of vegetation. Model comparisons were based on the Akaike information criterion (AIC). The relative importance of each predictor was examined using the Lindemann-Merenda-Gold (LMG) metric, providing the fraction of variance explained by each predictor.

Our analysis revealed a moderate positive relationship between the biomass fractions of EcM plants, and both topsoil and subsoil carbon (Figure 5, Extended Data Figure 5). Consistent with the current paradigm[40], cf[11], biome is the main predictor of soil carbon stocks. Even so, the grid cell biomass fraction of EcM plants still accounted for one third of the explained variation in both topsoil carbon and in subsoil (Table 1). The interaction between biome and EcM biomass fractions was significant ($P<0.001$) but only marginally important (LMG=1%),

suggesting that the increase in topsoil carbon along with an increase in EcM plant biomass is mostly independent from the environment. The relationship between EcM biomass fraction and soil C stocks had steepest slopes in temperate forests, mountain grasslands and shrublands and coniferous forests. Despite explaining a large proportion of data variance, the shallowest correlation slopes were evident in tropical and subtropical broadleaved forests (Figure 5, Extended Data Figures 5,6, Extended Data Table 2). The total aboveground carbon stock stored in the EcM plants was a relatively worse predictor of soil carbon stocks compared to the EcM relative biomass fraction, showing in all cases higher AIC (ΔAIC=5404, 3141, 2144, for 0-20, 20-60, 60-100cm soil depth, respectively) and slightly lower R^2 (ΔR^2 = 0.03, 0.03, 0.02 for 0-20 cm, 20-60 cm and 60-100 cm soil depth, respectively).

In contrast to EcM, AM biomass fractions per grid cell showed negative but inconsistent relationships to soil carbon, with a contrasting positive trend in tundra (Figure 5, Extended Data Figure 6). The latter relationship explained only a small amount of variance in tundra soil carbon stocks, (12% in top 0-20cm, 1.7% in 20-60 cm layer and 0.2% in 60-100 cm layer) and could arise from less accurate data of soil C in tundra[42] due to local landscape heterogeneity and prevalence of facultative AM plants with no or extremely low mycorrhizal colonization[43].

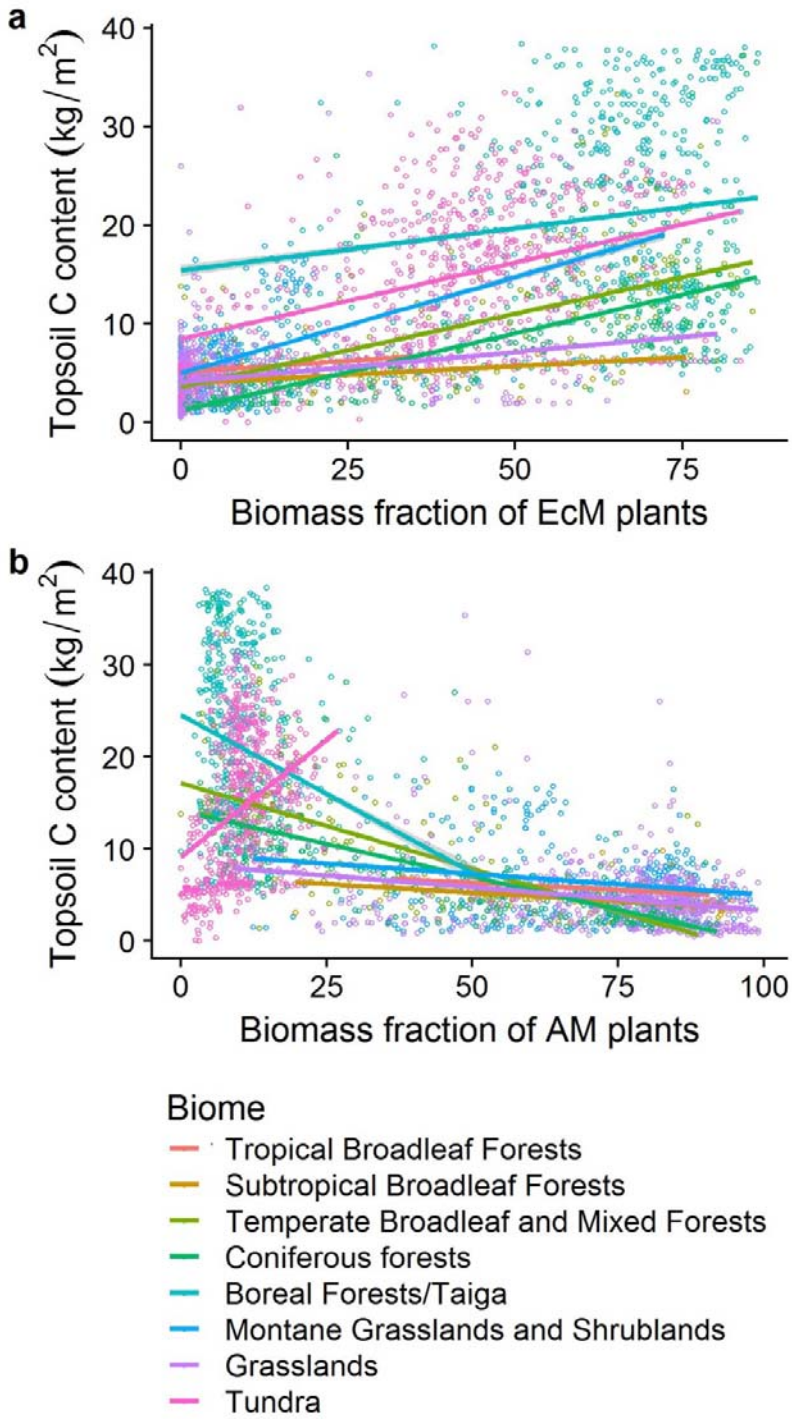

Figure 5. Quantitative relationships between topsoil (0-20cm) C and biomass fraction of a – EcM plants and b - AM plants in natural ecosystems. The outcomes of individual models are presented in the Extended Table 2. Croplands were excluded from the analysis. Per-biome predictions are shown in different colours.

Implications

Our work provides the first quantitative estimates of the global biomass distribution of arbuscular, ecto-, ericoid and non-mycorrhizal plants, accounting for human-induced transformation of habitats. Previous research has shed light onto the distribution patterns of species richness of mycorrhizal types in selected regions[44]. In contrast, our maps directly reflect the global distribution of biomass fractions across all biomes. All maps were derived at spatial resolutions allowing identification of the global patterns of mycorrhizal distributions and are most appropriate for global and large-geographical scale analyses of mycorrhizal impacts on ecosystem functioning and global drivers thereof. Recent estimates suggest that the total soil carbon loss due to agricultural practices accounts for 133 GT, with great acceleration of losses during the past 200 years[45]. Our analyses accounting for pre-agricultural patterns in EcM plant distribution point to large-scale losses of ectomycorrhizal vegetation, with potentially strong effect on the amount of C stored in soils.

The question whether increased domination of EcM plants in an ecosystem is associated with higher soil carbon content across both top- and subsoil is heavily debated (see above). However the studies thereof are based on a limited number of observations[11] or regional-scale analyses[11,12,14,46,47]. Our analysis demonstrates that across large geographical scales, higher cover of EcM vegetation is broadly associated with greater soil C stocks in both topsoil and subsoil, while AM vegetation has more variable, weaker and mostly negative relationships. Although it can be argued that high abundance of EcM plants is a consequence rather than a driver of soil C accumulation, a large body of recent findings provides evidence that EcM symbionts may be the key drivers of topsoil carbon accumulation through two interacting mechanisms. First, EcM fungi produce greater biomass of more recalcitrant mycelium compared to AM fungi[5]. Second, while EcM fungi are more efficient in taking up N in N-poor

soils than AM fungi or roots[10,25], EcM fungi immobilize most of the N in their own biomass. This suppresses saprotrophic decomposition processes[48] and reinforces the competitive advantage of the EcM and ErM plants via enhanced N limitation[48,49].

Our estimates of the carbon stocks in AM and EcM aboveground biomass together with the quantitative relationships between soil carbon stocks and AM or EcM plant dominance in ecosystems provide new insights into the global carbon cycle, highlighting the substantial role of mycorrhizas therein. Tropical forests, usually dominated by AM symbiosis (Figure 3), contain 162 GT (44%) of global aboveground biomass[34] whereas the predominately EcM temperate and boreal forests altogether store only 21% of global aboveground biomass carbon[34], indicating that contribution of EcM vegetation to the aboveground biomass carbon is relatively small. In contrast, belowground carbon stocks are positively correlated to the proportion of EcM plant biomass, suggesting that mycorrhizal contribution to large carbon stocks in these regions occurs primarily through the carbon supply to belowground organs and mycorrhizal fungi, which is further emphasized with slowed decomposition processes[48]. Furthermore, our analyses revealed relatively stronger relationship between soil C and EcM plant biomass fraction (%) than between soil C and the amount of carbon stored in EcM plants. These findings suggest that belowground carbon allocation by plants through mycorrhizal pathways is not directly proportional to the aboveground plant biomass, supporting the view of the importance of mutualism-parasitism trade-off in ectomycorrhizal associations[50] across biomes.

Taken together, this study provides a benchmark for relating ecosystem processes to the functioning of distinct types of mycorrhiza on a global scale. So far, quantitative global information about mycorrhizal distribution was virtually absent in spite of high demand for

such data [12,13,27]. Our mycorrhizal distribution maps provide an essential basis for detailed and systematic analyses of mycorrhizal biogeography and the environmental drivers thereof. Inclusion of mycorrhizal distribution into vegetation models allows testing hypotheses about mycorrhizal impacts on ecosystem functioning and related ecosystem services. Our integrated models enable quantifying relationships between mycorrhizal abundances in ecosystems as well as soil and vegetation carbon content in global-scale analyses of biogeochemical cycles. In particular, the results of our study suggest that restoration of native vegetation especially in abandoned agricultural and barren land may help alleviate anthropogenic soil carbon losses and ameliorate increase in atmospheric greenhouse gases.

Methods

To construct the maps of mycorrhizal biomass fraction distributions, we assembled a global database on plant mycorrhizal type associations and combined it with information about dominant plant species and their growth form across distinct combinations of Bailey's ecoregions[29] and European Space Agency (ESA) landcover categories[30]. Here we defined a species or a set of species with a similar mycorrhizal strategy and growth form as 'dominant' if it constituted more than 20% of a community biomass. Extended Data Figure 1 shows a flowchart of the map assembly process.

Global data sets of mycorrhizal types

We integrated information about the plant mycorrhizal types from multiple sources into currently the largest and the most comprehensive data set containing information about the type of mycorrhizal colonisation of vascular plants. First, we combined all currently available large compilations of data on the mycorrhizal type and geographical records of individual plant species and genera[2,22,27,35,44,51,52]. We examined these data, excluded duplicate references, and traced each data set back to the original articles for geographical location (based on site descriptions) and the reports of plant mycorrhizal status. We performed an additional literature search in the most-comprehensive and extensive non-English scientific literature (Spanish, Portuguese, Russian, Chinese, German, French) searching for reports of plant mycorrhizal status in regions where these languages are spoken using Google Scholar key words 'mycorrhiza' AND /name of the country/ or region where the respective language is spoken. The data obtained from these references were added to the data set that included 2,169 studies and 27,736 species-by-site records for 12,702 plant species (the number exceeding the previously reported total number of plant species for which the type of mycorrhizal colonization has ever been assessed[2]. Supplementary Table 1 provides a list of the literature sources included in the data set.

Information about the plant species being unable to form mycorrhizal infection was derived from the work of Brundrett[2,53]. Though many crops are able to form mycorrhizas[1], intensive agricultural practices often lead to loss of mycorrhizal infection due to disturbances of mycorrhizal networks introduced by ploughing, excess of nutrients due to fertilization, and fungicide treatments aimed to reduce pathogen infections [36,37]. Therefore, we considered croplands to be effectively non-mycorrhizal, with the exception of Solanaceae and perennial crops.

All Diapensiaceae and Ericaceae were considered ericoid mycorrhizal[54], except for *Enkianthus* (AM), *Arbuteae*, *Pyroleae*, *Monotropeae* and *Pterosporeae* (all subtypes of EcM). We critically re-evaluated the literature[22,35] about the EcM habit and potential dual colonisation with AM fungi. Because of multiple incorrect reports and alternative definitions for EcM, we took a conservative approach by considering plants to be EcM only when this was supported by multiple independent studies and the proportion of conflicting reports was <50%[55].

<u>Biomass fractions of mycorrhizal plants within ecoregions per land cover type</u>

We selected the global ecoregion map of Bailey (2014) [29] with 98 ecoregions (Supplementary Table 2), provided by the Oak Ridge National Laboratory Distributed Active Archive Center[56] (spatial resolution 10 arcmin), as a basis for mapping of global-scale distribution of mycorrhizal types. This map was preferred over that of biomes provided by Olson and co-workers[41] and others because of higher level of detail for ecoregions and because the boundaries of ecoregions were more strongly related to the distribution of mycorrhiza types. Ecoregions spanning across multiple continents were considered separately within each

continent. Hereto we used the continent division based upon the FAO Global Administrative Unit Layers (http://www.fao.org/geonetwork/srv/en/). Finally, we have detected which landcover types are present within each combination of ecoregions and continents. Hereto we used an up-to-date satellite observation-based land cover map for the year 2015 (38 land cover categories including land transformations such as croplands and urban areas, spatial resolution of 300 m), generated by the European Space Agency [30] (see Supplementary Table 3 for the list of land cover categories)

Based on 1,568 data sources (Supplementary Table 4) we examined the vegetation descriptions of ecoregions by continent and by landcover type. We assessed species composition and species dominance level in each ecoregion by continent by landcover combination and linked this data to species mycorrhizal types (AM, EcM, and ErM, using the datasources listed in Supplementary Table 1), and plant growth forms (trees, shrubs, herbaceous plants) obtained from vegetation descriptions (Supplementary Table 4) and publically available part of the TRY database (www.try-db.org).

Combining these data, we estimated the fractions of living biomass (hereafter 'biomass') of EcM, AM, ErM and non-mycorrhizal plants in each ecoregion by continent by landcover combination. In these estimates, we used the following coefficients to translate information of plant growth forms into biomass fractions of plants: in forests that consist of two vegetation layers (trees and herbaceous/dwarf shrub understorey vegetation) trees contribute 90-95% of biomass, and the understorey vegetation comprises 5-10% of biomass; in forests that encompass a dense layer of shrubs, trees contribute 70% of biomass, shrubs constitute 20% of biomass and understorey herbaceous/dwarf shrub layer constitutes 10% [32,57,58]. In shrublands, we consider shrubs to account for 80-90% of biomass, and herbaceous vegetation to account

for 10-20% of biomass [32,57-59]. We considered that savannahs and forested steppes harbour 30-50% of biomass in trees and 50-70% of biomass stored in herbaceous vegetation[32,57-59].

Some of the ecoregions were not sufficiently well related to known regional patterns of mycorrhizal types (i.e. ecoregion classes 33, 35, 40, 75, 79, 82, 95, 96, and 97; Supplementary Tables 2,3). These classes were manually split into subclasses according to the known distribution of mycorrhizal types within each class. Splitting was done with ArcGIS 10.2.2 using the Raster Calculator. Because medium-sized islands (e.g. Hawaii) were missing from the ecoregions map of Bailey, we added mycorrhiza information for such islands manually based on the literature references in our dataset (Supplementary Table 2).

The resulting data used to map nowadays fractions of mycorrhizal plant biomass within each combination of continent, Bailey ecoregion and land cover type is shown in Tables S5 and S6 for continents and islands, respectively.

Our data represent relative factions of AM, EcM, ErM and NM plants within the total vegetation cover in a grid cell. In this study, we focused on the abundance of mycorrhizal plants and not on species diversity; we therefore did not map the distribution of orchid mycorrhizas. Plants species featuring orchid mycorrhizas exhibit great diversity, exceeding in species number the ErM and EcM plant species taken together[2]. However, orchid species are never abundant in ecosystems in terms of biomass, and therefore unlikely to play an essential role in biogeochemical cycles at large regional scales.

<u>Impact of crop cultivation on per grid cell biomass fractions of distinct mycorrhizal types</u>

Using the data of mycorrhizal type abundance in ecoregions by continent by land cover, we

replaced the data on AM, EcM, ErM, and non-mycorrhizal plant biomass fractions in each of the ecoregion-continent-land cover combinations that contained croplands (land-covers of types 10,11,12,20, and 30; see Supplementary Table 3) by estimates of AM, EcM, ErM and non-mycorrhizal plant fractions that were *expected* in these areas based on the natural vegetation types occurring within this ecoregion-continent combination. In ecoregions where the land cover in natural areas currently includes grasslands, shrublands and forests, we considered that the potential vegetation represents a mixture of equal proportions of these plant types; and the *expected* mycorrhizal fractions reflect mycorrhizal types associated with the respective plant types in the current vegetation (see references per ecoregion in Supplementary Table 2). In cases where forests are not expected within the ecoregion (for instance in tundra) a combination of grasslands and shrublands was assumed, and, similarly, the *expected* mycorrhizal biomass fractions were assigned following the mycorrhizal types associated with the dominant plant species in the current vegetation based on the per ecoregion references in Supplementary Table 2. This resulted in an additional dataset describing combinations of vegetation as defined by ecoregion x continent x land cover without croplands. Maps of potential mycorrhizal distribution in a cropland-free world (Extended Data Figure 4) were created based on this dataset, using the same R scripts as for the current distribution of mycorrhizas.

In this analysis we did not consider forest plantations to be croplands. Therefore, changes in land cover induced by forest restoration through, for instance pine plantations or eucalypt plantations, are not addressed as vegetation changes induced by cropland-cultivation. According to FAO and OECD reports [60,61], the total area occupied by AM tree plantations exceeds that occupied by EcM tree plantations (Extended Data Table 3), suggesting that

exclusion of tree plantations leads to conservative estimations of global reduction of EcM vegetation.

Map validation and uncertainty analysis

The maps of the current distributions of mycorrhizal biomass fractions were validated using the datasets of forest biomass structure for Eurasia[32], global analysis of impacts on mycorrhizas on carbon vs nitrogen dynamics[19], the USA-based analysis of mycorrhizal associations conducted with remote sensing techniques[33], and the map of mycorrhizal root biomass in West Australia by Brundrett [21] (see Extended Data Figure 2).

The data of forest biomass structure for Eurasia [32] provide information on per-plot tree species abundances for a large number of European sites. As the data contain all records obtained since the 19th century, we used only the data recorded after 1999. Using our database of plant species and associated mycorrhizal types we assigned every tree species with its mycorrhizal type (1344 data points, Extended Data Figure 2). This provided us with a per-site data of the relative biomass of AM and EcM trees. We used these data as proxies for AM and EcM biomass fractions to compare with the data in our maps. We used the same approach for the data of Lin and co-workers[19], which has plot-based records of vegetation structure for 100 sites across the globe accompanied with data about plant mycorrhizal associations.

The dataset of Fisher *et al* [33] provides the relative cover of AM and EcM plants from Landsat scenes centered on four sites in USA: Lilly-Dickey Woods (Indiana), long-term research site of Smithsonian Conservation Biology Institute (Virginia), Tyson Research Center Plot (Missouri), and a long-term research site of Wabikon Forest Dynamics (Wisconsin). Given that the dataset comprises forested areas only, we considered areal coverage of AM and EcM

plants provides a good estimate of AM and EcM plant biomass. Using this dataset, we directly compared the AM and EcM coverage per pixel to the data of our maps.

In the datasets [19,32,33], biomass and areal fractions of AM and EcM plants are always considered to sum up to 100%. As these datasets do not provide information about non-mycorrhizal and ericoid plants, we estimated these as 5-10% and 0-20%, respectively, depending on the dominant tree association and accordingly reduced the values of AM and EM biomass fractions in the validation calculations. While we considered this approach to be acceptable for the validation of AM and EcM data, the data quality is not high enough to validate the NM and ErM maps.

As the thee datasets[19,32,33] represent forest data, we evaluated whether all data points or raster cells[33] were indeed located in forest areas. This was done using the ESA land cover categories data[30]. All data points that were located out of the current areas registers by ESA [30] as forests were excluded from the analysis.

The West Australian map of mycorrhizal root abundance[21] provides information about the percentage of total biomass of plant roots featuring AM and EM root colonization and about the percentage of non-mycorrhizal root biomass. We used this data as a proxy for biomass fractions of AM, EcM and NM plants. To translate these root distribution data into biomass fractions of AM, EcM and NM plants and to account for a potential discontinuity of vegetation, we multiplied the root fraction data by the MODIS normalized difference vegetation index (NDVI) https://neo.sci.gsfc.nasa.gov/; resolution 10 arcmin).
To assess the uncertainty sources in the maps, we examined which land use classes represent the data points that deviate from the observed data by more than 25 percent units. Our

analysis showed that the large proportion of those deviations (63% for EcM and 40% for AM) falls into those land use classes that represent a poorly described mixture of evergreen or mixed forests and grasslands, i.e. ESA classes described as various forms of "closed to open (>15%) forest" (Supplementary Table 3). Further improvement of the ESA classification data will provide a possibility to improve precision of our maps.

Estimations of carbon stocks in the aboveground biomass of AM, EcM, ErM and NM plants.

In order to estimate the amount of carbon stored globally in the biomass of individual mycorrhizal types we multiplied mycorrhizal biomass fractions by the data of the global distribution of carbon stored in aboveground plant biomass[34] from passive microwave-based satellite observations. Given that the data of [34] has resolution of 15 arcmin, we converted our data of mycorrhizal biomass fractions to this resolution. The outcomes of these calculations are illustrated in Figure 3. To calculate the total amount of carbon stored in AM, EcM, ErM and NM plants (illustrated in Figure 2, and reported per biome in the Extended Table 1), we summed the data on carbon stocks per unit area per biome and across the globe[41].

Statistical analysis of the relationship between soil carbon content and biomass distribution of mycorrhizal types

We examined whether the soil carbon content was related to the biomass fractions of AM and EcM plants, using generalized linear model (glm) regressions of the Gaussian family with topsoil (0-20 cm) or subsoil (20-60 cm and 60-100 cm) C content per m^2 as a response variable, and biome and ecosystem biomass fraction of AM or EcM plants as predictors. The data for soil carbon content in the top 20 cm of soil was taken from the ISRIC WISE Soil Property Databases, at a resolution of 30 arcsec [42]. As we were interested in relationships between AM or EcM coverage and soil carbon in natural vegetated environments, we

excluded urban and agricultural areas, lakes and “Rock and Ice” areas according to the ESA land cover categories[30], from the analysis. We also excluded wetlands, inundated areas, and extremely dry regions (deserts and Mediterranean areas) because we considered that harsh abiotic conditions instead of biotic interactions are likely to shape biogeochemical cycles in these areas; and we excluded five land cover categories for which our maps showed higher uncertainties, i.e. those where the extent of forest vs grassland cover was unclear. Those land cover categories included “Tree cover, broadleaved, evergreen, closed to open (>15%)”, “Tree cover, broadleaved, deciduous, closed to open (>15%)”, “Tree cover, needleleaved, evergreen, closed to open (>15%)”, “Tree cover, needleleaved, deciduous, closed to open (>15%)” and “Sparse vegetation (tree, shrub, herbaceous cover)”.

Data for biome types were taken from the map of terrestrial biomes[41]. To create a more balanced dataset, we combined all natural grasslands into one single category and all coniferous forests into another single category. To minimize the impacts of unprecise estimations of biome borders we excluded from forest biomes areas that we recognized as grasslands according to the ESA land cover data[30]. Similarly we excluded from grassland biome areas that were fully covered by forests and shrubs according to[30]. However, given that AM-EcM-NM interactions are likely to relate to C stocks in the areas featuring forest-grassland and forest-tundra mosaics we kept such areas in the dataset. As soil carbon content data is known to feature high uncertainties[42] we opted to run the analyses at a resolution of 1 arcdegree, which allows grasping large scale tendencies, while reducing the problem of P-value fallacy[62].

The models, comprising top- and subsoil carbon content as a response variable, and (i) biome, biomass fraction of EcM plants, and their interactions, (ii) biome, biomass fraction of AM

plants, and their interactions, (iii) biome, amount of carbon stored in the aboveground biomass of EcM plants (product of our EcM map and[34]), and their interactions, and (iv) biome, amount of carbon stored in the aboveground biomass of AM plants (product of our AM map and [34]), and their interactions, were examined independently and evaluated based on the Akaike Information Criterion.

In all models, we assessed the total variance explained by the model by Cragg and Uhler's pseudo R-squared metric and the relative importance of each predictor using the Lindemann, Merenda and Gold (LMG) metric, which allows decomposing the total variance explained by the model, into contributions of individual model terms.

Given significant interactions between biome factor and biomass fractions of mycorrhizal plants (Table 1), we fitted glms with EcM or AM biomass fractions as predictors and topsoil and subsoil C stocks as response variables to the data within individual biomes. The outcome of this analysis is reported in the Extended Data Table 2.

Additionally, we examined whether the amount of carbon stored in AM and EcM plants per unit area is a better predictor of soil C stocks than the fractions of AM or EcM biomass per unit area. This analysis was done in exactly the same manner as the analysis of the impacts of AM and EcM biomass. The resulting models were assessed using the Akaike Information Criterion.

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Author contributions

NAS and CT generated the idea. NAS, PMvB, LT and CT designed the study, and analyzed the data. NAS wrote the manuscript. NAS and IMC have prepared the figures, with the leading role of IMC. LT provided mycorrhizal type assignments to vegetation. CT, IMC, NCdS and MvhZ performed geoinformatics data processing. MLM, JBF, and MB provided data for map validation. PMvB, CT, LT and IMC have equally contributed to this work. All authors have contributed to preparation of manuscript drafts.

Competing Financial Interests statement

There are no competing financial interests associated with this work.

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Tables.

Table 1. Summary of statistical models predicting soil carbon stocks at 0-20, 20-60, and 60-100 cm depth based on biome and fraction of EcM or AM plants in vegetation biomass. R^2 - Cragg and Uhler's pseudo R^2, LMG - relative importance of individual predictors in a model examined through the Lindemann-Merenda-Gold metric

Predicted Variable	Model	R^2	Predictor	P value	LMG (%)
Topsoil C 0-20cm	**EcM + Biome + EcM x Biome**	**0.53**	**EcM**	**<0.001**	**43**
			Biome	<0.001	56
			EcM x Biome	<0.001	1
Subsoil C 20-60cm	**EcM + Biome + EcM x Biome**	**0.34**	**EcM**	**<0.001**	**39**
			Biome	<0.001	59
			EcM x Biome	<0.001	2
Subsoil C 60-100cm	**EcM + Biome + EcM x Biome**	**0.33**	**EcM**	**<0.001**	**37**
			Biome	<0.001	61
			EcM x Biome	<0.001	2
Topsoil C 0-20cm	**AM + Biome + AM x Biome**	**0.54**	**AM**	**<0.001**	**40**
			Biome	<0.001	55
			AM x Biome	<0.001	7
Subsoil C 20-60cm	**AM + Biome + AM x Biome**	**0.33**	**AM**	**<0.001**	**39**
			Biome	<0.001	59
			AM x Biome	<0.001	2
Subsoil C 60-100cm	**AM + Biome + AM x Biome**	**0.32**	**AM**	**<0.001**	**31**
			Biome	<0.001	67
			AM x Biome	<0.001	2

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