Human-induced decrease of ectomycorrhizal vegetation led to loss in global soil carbon content

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Abstract

Vegetation impacts on ecosystem functioning are strongly controlled by mycorrhiza, a plant-fungal association formed by almost all terrestrial plants. Using global high-resolution maps of mycorrhizal associations, we quantitatively examined contributions of distinct mycorrhizal types to the processes of soil carbon sequestration in the context of land-use change. We show that shifts between mycorrhizal types within biomes modify global soil carbon content. Conversion of natural ecosystems into croplands reduced the global coverage of ectomycorrhizal plants by 19%. This global reduction in activities of ectomycorrhizas has led to 23.5 GT loss of soil carbon, contributing substantially to the total human-induced soil carbon debt. Our work provides a benchmark for global, spatially explicit and quantitative assessments of mycorrhizal impacts on ecosystem functioning and biogeochemical cycles.

Short title: Global decline of ectomycorrhizal vegetation

One Sentence Summary: Conversion of natural habitats to croplands has globally reduced ectomycorrhizal vegetation and associated ecosystem services.

Main Text

Mycorrhizas are mutualistic relationships between plants and fungi, where 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 (*1-3*). Due to the enhancement of plant nutrient acquisition (*1*) and the large biomass of fungal networks in soil (*4*), the presence and type of mycorrhiza is among the key determinants of ecosystem functioning (*5, 6*) and biogeochemical cycling (*7-10*). There is growing evidence that ecosystems dominated by EcM and ErM vegetation exhibit higher soil carbon sequestration rates compared to those dominated by AM plants (*8, 11, 12*).

Human activities such as forest logging, urbanization, and agricultural practices have altered 50-75% of the Earth's terrestrial ecosystems (*13*). These land-use changes have an enormous potential impact on biogeochemical cycles in areas where natural EcM and ErM vegetation

has been transformed to AM and non-mycorrhizal (NM) vegetation. However, the question of how such human-induced ecosystem changes have affected global distribution patterns of mycorrhizal types and hence their role in ecosystem functioning remains unanswered.

Quantitative information about the global distribution of mycorrhizas is required to understand connections between mycorrhizal distributions and shifts in ecosystem function. Despite existence of regional maps of current (*14, 15*) and past (*16*) mycorrhizal vegetation, we still lack global data on mycorrhizal vegetation patterns.

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 AM, EcM, ErM, and NM plants (Fig.1). Using these maps, we examined (i) how conversion of natural ecosystems to croplands has affected the distribution of mycorrhizal types globally, (ii) the relationship between soil carbon content and the relative abundance of AM, EcM and ErM plants in ecosystems, and (iii) to what extent conversion of natural areas to croplands has impacted soil carbon content via differential activities of mycorrhizal types.

To assemble global maps of mycorrhizal type distribution, we compiled available information about mycorrhizal status of plants and vegetation in relation to habitat type and ecoregion. Based on data accumulated over the past three decades, we established the largest data set 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 sources including published reviews, data compilations and previously neglected or recent case studies (Table S1). Based on information on locality and vegetation composition

provided by vegetation surveys obtained from 2,169 sources (Table S2), abundance estimates of mycorrhizal types were assigned to all combinations of continents and 98 ecological regions, as defined by Bailey (*17*) (Table S3), and to land cover types. The latter was obtained from the most recent high-resolution (300 m) map comprising 38 land cover types (*18*), Table S4.

Our maps provide the first quantitative estimations of current global cover of AM, EcM and ErM plants, which occupy 45, 22, and 2.4 million km^2, respectively. Non-mycorrhizal vegetation occupies 12 million km^2. Use of a detailed map of ecoregions (*17*) 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 (*18*) enabled us to provide accurate spatial positioning of ecosystem boundaries based on satellite 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 (*19*), (ii) global analysis of mycorrhizal impacts on carbon *vs* nitrogen dynamics (*20*), (iii) USA-based analysis of mycorrhizal associations using remote sensing (*21*), and (iv) West Australian map of mycorrhizal root abundance (*14*) (Fig. S1). This validation revealed that the great majority of the data (87% of the AM data points and 89% of the EcM data points) deviate by <25% from the measurements (*19-21*) (Fig. S2) when excluding ESA land use classes (*18*) that are poorly resolved and hence difficult to couple to our classification scheme.

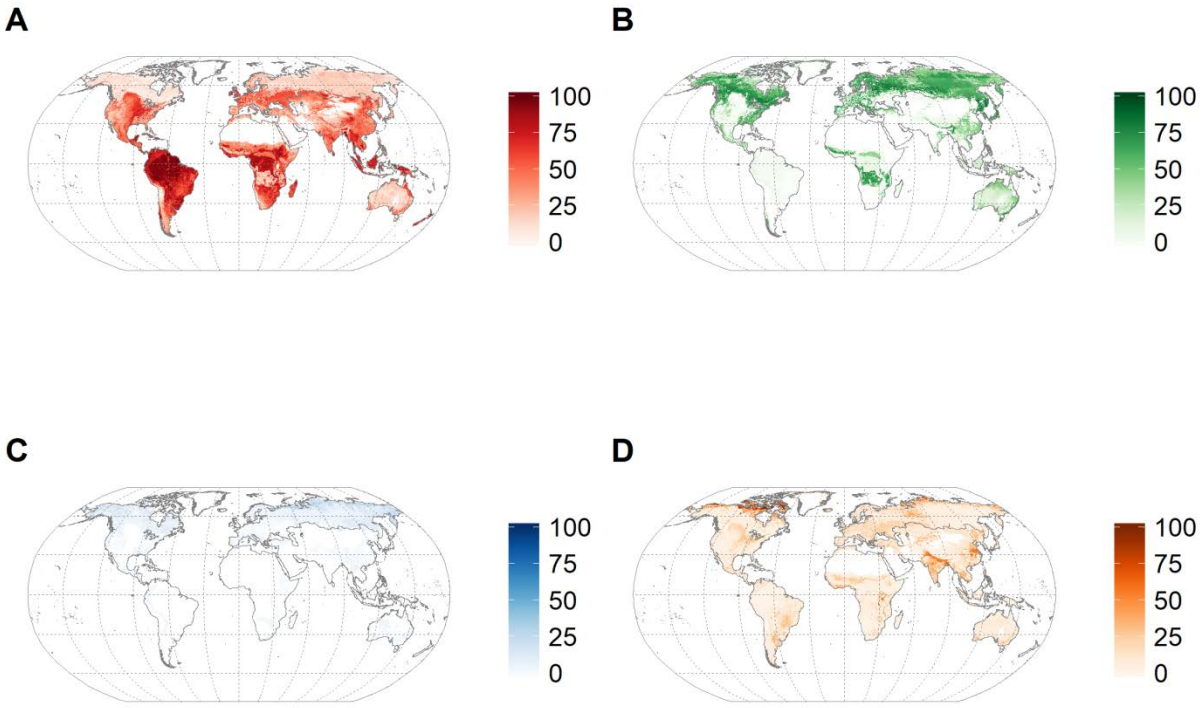

Fig. 1. Mycorrhizal vegetation cover A - arbuscular mycorrhizal plants, B - ectomycorrhizal plants, C - ericoid mycorrhizal plants and D - non-mycorrhizal plants. Color intensity reflects the percentage of area covered by plants of a given mycorrhizal type in a grid cell of 10 arcmin.

Agricultural practices drive the replacement of natural vegetation by mostly non-mycorrhizal and AM crops (*1*, *22*). Using past vegetation estimates, Swaty and co-workers (*16*) 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. The current land use data underlying our maps (Table S4) enabled us to assess mycorrhizal distributions on Earth in the absence of croplands. We replaced the data on AM, EcM, ErM, and non-mycorrhizal plant abundances in each of the ecoregion-continent-land cover

combinations that contained croplands by estimates of AM, EcM, ErM and non-mycorrhizal plant fractions that were *expected* at these locations based on natural vegetation types (see Methods for details, and Tables S7-8 for data). Based on these data, we generated additional maps presenting *potential natural* distributions of AM, EcM, ErM, and non-mycorrhizal plants in a cropland-free world (Fig. S3).

Comparison of the current and cropland-free distributions of mycorrhizal types revealed that crop cultivation has led to a 50% (5.8 million km^2) increase in non-mycorrhizal vegetation, 19% reduction (5.5 million km^2) in EcM plant cover, 5.8% reduction (0.15 million km^2) in ErM plant cover and 0.6% reduction (0.3 million km^2) in AM plant cover (Fig. 2). Current coverage of AM plants is the result of an extensive re-distribution pattern, with large increases in Europe, Asia and North America (45, 27 and 12% of total AM gain, respectively), but also large declines in Africa, Asia (mostly India) and South America (25, 40 and 24% of total AM loss, respectively), where it was mostly replaced by non-mycorrhizal crops (Fig. 2 A,C). Fig. 3 shows relative changes of each mycorrhizal type per continent. Table S5 shows the total change in mycorrhizal vegetation per continent. Coverage by EcM plants decreased over all continents with the strongest losses in Eurasia (72% of total ErM loss, Fig. 3, Table S5).

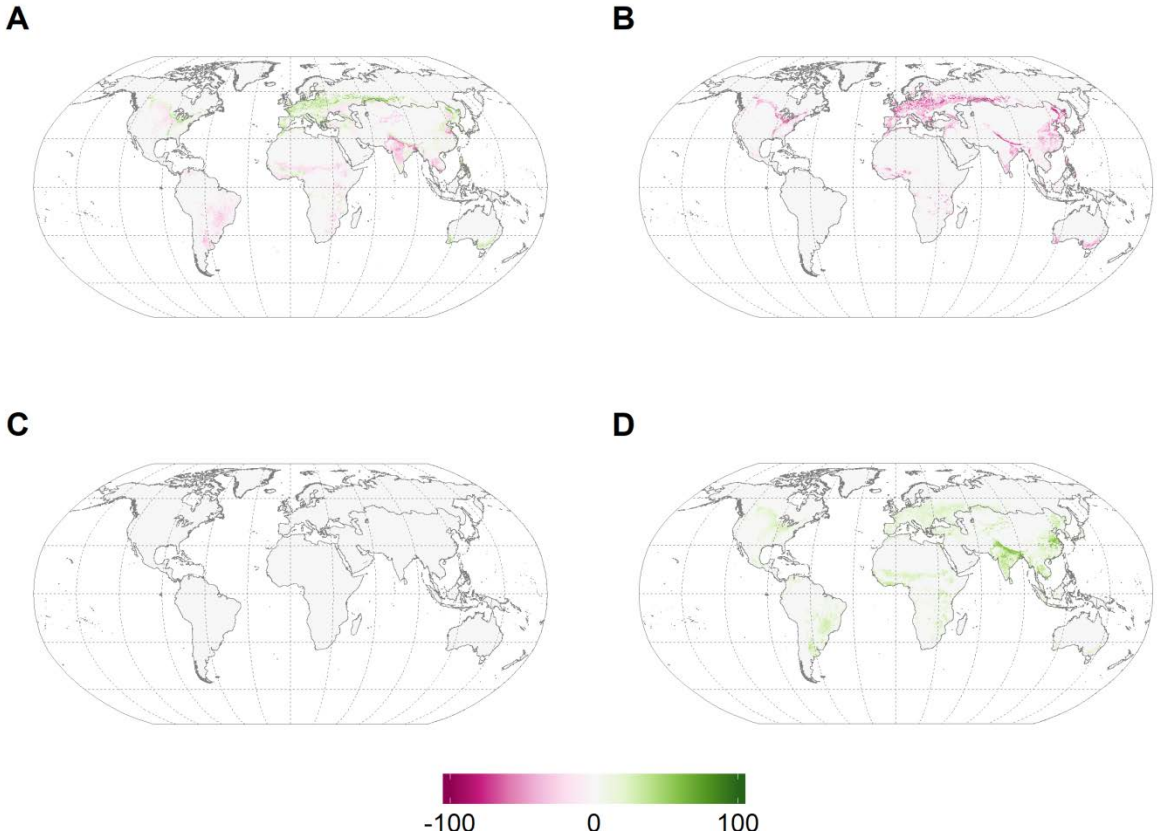

Fig. 2. Changes in areal cover of mycorrhizal vegetation induced by crop cultivation A - arbuscular mycorrhizal plants, B - ectomycorrhizal plants, C - ericoid mycorrhizal plants, and D - non-mycorrhizal plants. Red colors indicate losses in cover of plants possessing a given mycorrhizal type; green colors indicate gains.

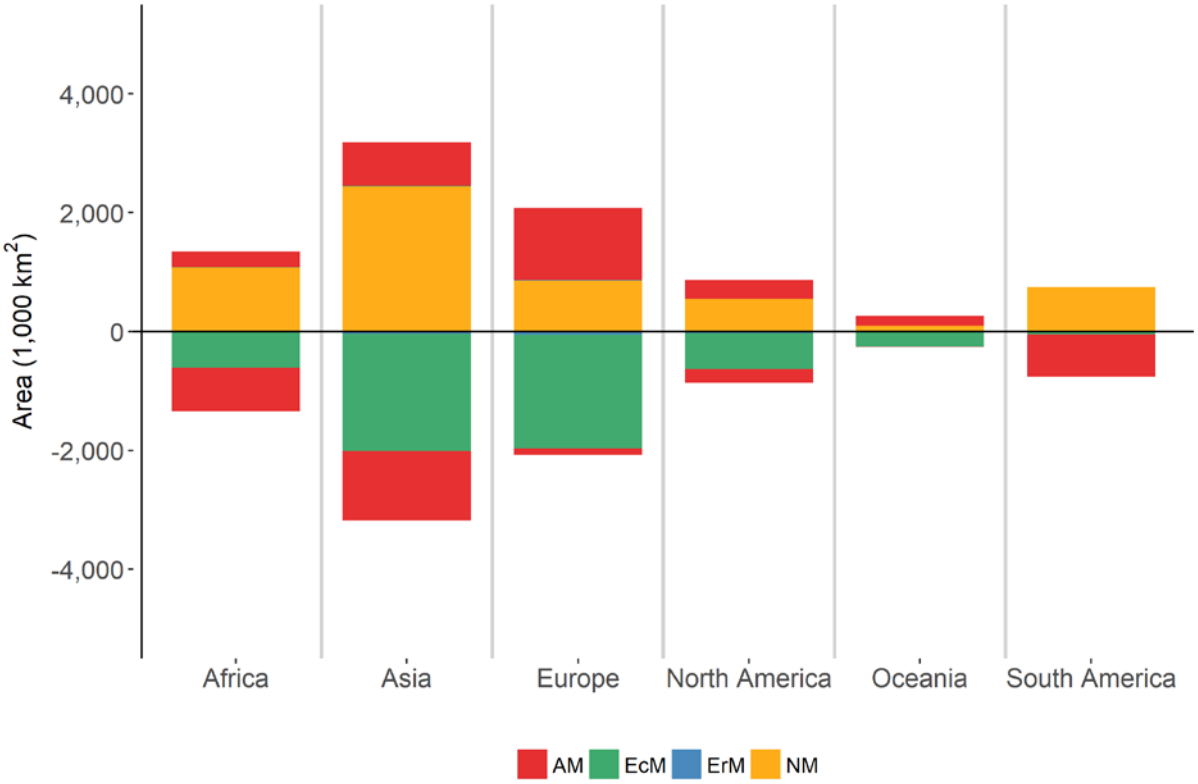

Fig. 3. Changes in areal cover of mycorrhizal vegetation induced by crop cultivation per continent. Bars below and above x-axis show decrease and increase in mycorrhizal vegetation cover, respectively. AM - arbuscular mycorrhizal plants, EcM - ectomycorrhizal plants, ErM - ericoid mycorrhizal plants, and NM - non-mycorrhizal plants.

There is growing empirical evidence that soil biogeochemical cycling processes qualitatively differ between ecosystems dominated by plants hosting distinct types of mycorrhizas, especially between ecosystems dominated by AM and EcM plants (*7-9*). For instance, EcM-dominated ecosystems often exhibit higher soil carbon-to-nitrogen ratios (proxy for recalcitrance of carbon compounds and low nitrogen availability in soils) (*8, 12*). However, it is not known how decreasing abundances of EcM plants in ecosystems are quantitatively associated with soil carbon content. The relative contribution of mycorrhizas to soil carbon sequestration processes compared to that of biome characteristics, previously suggested to be the central driver of soil carbon stocks (*23*), is also unknown. To address this question, we

examined the global relationships between soil carbon content in the topsoil (uppermost 30 cm soil layer) (*24*), biome type (*25*), and abundances of AM and EcM plants. These analyses are justified, because the data sources are independent: the ecoregion classification and hence mycorrhizal type distribution does not account for edaphic parameters, whereas our soil C data (*24*) is unrelated to that of vegetation. Model comparison was based on the Akaike information criterion (AIC). The relative importance of each predictor was examined using the Lindemann-Merenda-Gold (LMG) metric. As ErM plants contribute to a small proportion of the biomass in the majority of ecosystems, the reliability of their cover estimation is lower than for AM and EcM plants. Therefore, we did not analyze the relationship between ErM plant cover and topsoil C content.

The model comprising biome and areal cover of EcM plants explained 46% of the variance in topsoil carbon (Cragg and Uhler's pseudo R^2). Despite the large data spread, the areal cover of EcM plants was an important driver of soil carbon content across biomes ($P<0.001$), accounting for one third of the explained variation in topsoil carbon (LMG=30%) in addition to that explained by biome ($P<0.001$, LMG=65%). The interaction between biome and EcM plant cover was only marginally important (LMG=5%, while $P=0.043$), indicating that the increase in topsoil carbon along with an increase in EcM plant cover is mostly a biome-independent process. Fig. 4 shows the relationships between topsoil carbon content, biome and EcM plant cover. In contrast, AM plant cover showed a weak and idiosyncratic relationship to soil C, varying across biomes (Fig. S3). In the model comprising biome and AM plant cover as predictors of soil C content, biome was the main driver of soil C (LMG = 94%), while the explanatory power of AM cover was marginal (LMG=3%). This model performed worse than the model based on predicting topsoil C with biome and areal cover of

EcM plants (ΔAIC= 1382). These contrasting patterns provide strong evidence for a global relationship between EcM plant cover and soil carbon accumulation.

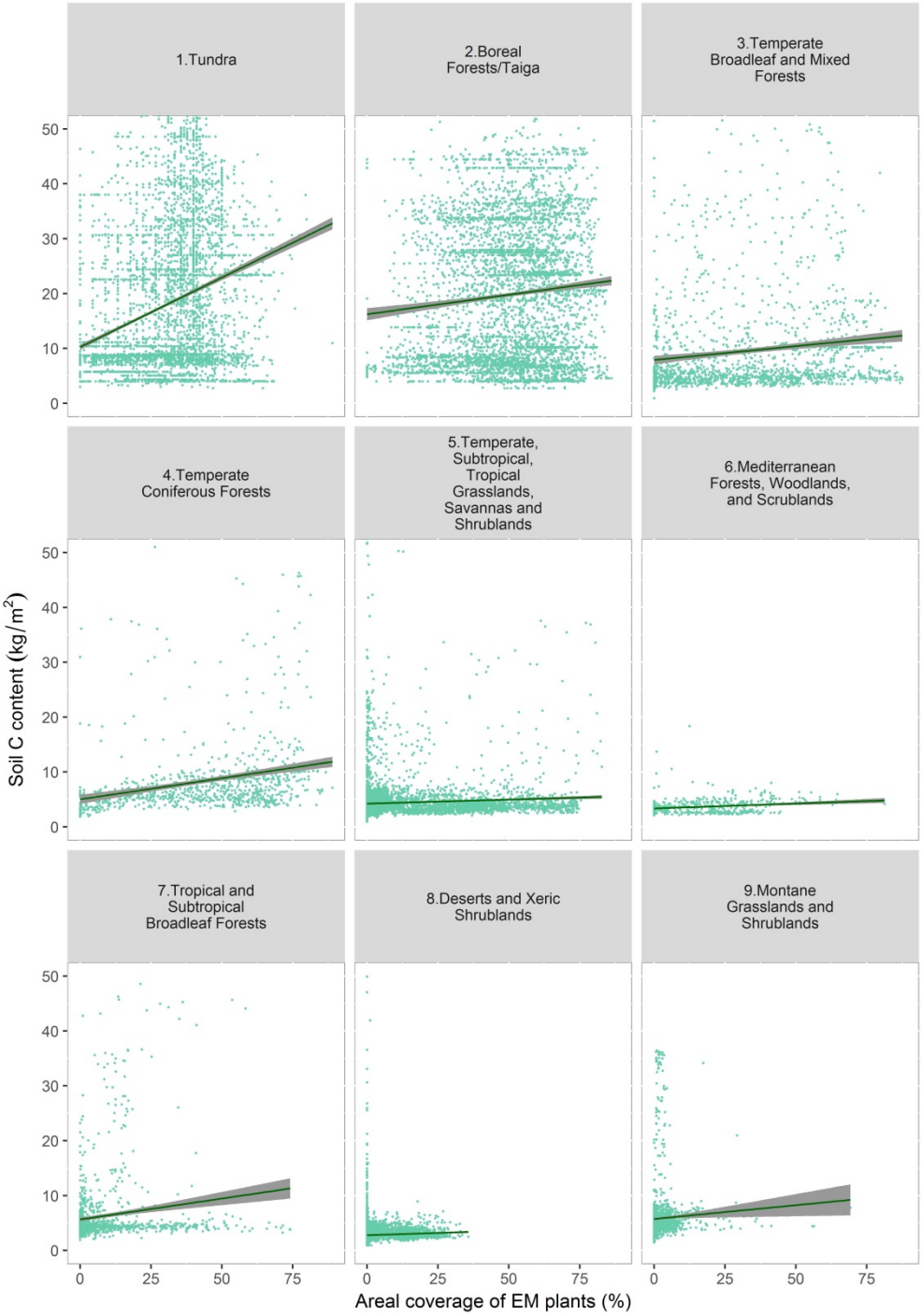

Fig. 4. Quantitative relationships between soil C and areal cover of ectomycorrhizal plants in natural ecosystems. Croplands were excluded from the analysis. Per biome predictions (n= 33,257) are shown. All predictions are based on general linear models between biome, EcM plant cover and soil C content (P<0.001).

Although it can be argued that high abundance of EcM and ErM plants is a consequence rather than a driver of soil C accumulation, a large body of recent findings provides evidence that EcM are likely to be the drivers of soil carbon accumulation through two interacting mechanisms. First, EcM and ErM fungi produce greater biomass of more recalcitrant mycelium compared to AM fungi (*4*). Second, while EcM and ErM fungi are more efficient in taking up N in N-poor soils than AM fungi or roots (*7*), the former guilds immobilize most of the N taken up in their own biomass. This suppresses saprotrophic decomposition (*26*) and may further aggravate the soil N limitation and reinforce the competitive advantage of the EcM and ErM plants, although the extent to which EcM fungi affect activities of saprotrophic organisms has been suggested to be context-dependent (*26*). In agreement with these findings, recent paper of Averill and co-workers (*27*) suggest that at a local scale, decreases in abundance of EcM plants in ecosystems negatively affects carbon accumulation in topsoil.

Building on this hypothesis, we estimated the impact of declining EcM vegetation cover and EcM-mediated processes on global carbon content in topsoil. We based this estimation on the quantitative relationship between the within-biome cover of EcM plants and topsoil carbon content, provided by our glm (Fig. 2). Using the model, we calculated the difference in the amount of total soil carbon associated with mycorrhizal activities for the current distribution of ectomycorrhizal plants and their distribution in a cropland-free world. See Methods for the assumptions of these calculations.

Cultivation of non-mycorrhizal and AM crops in areas previously dominated by ectomycorrhizal plants coincides with 23.5 GT±7.3 GT reduction in global soil carbon stocks.

The relationship between EcM cover and topsoil C is significant and clearly shows the same trend across biomes, even though it is associated with a high uncertainty (Fig. 4).

Recent estimations (*28*) 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 (*28*). Our results suggest that soil C losses associated with reduction of ectomycorrhizal impacts due to agricultural practices account for 20% of total lost carbon. The magnitude of soil C losses associated with the reduction of activities of EcM due to loss of ectomycorrhizal vegetation is roughly 28% of the values of aboveground carbon losses due to deforestation in the period between 1700 and 2000 (86 GT C (*28*)). These estimates collectively suggest that changes in mycorrhizal vegetation types, associated with the conversion of natural habitats to croplands, constitute an important driver in the development of agriculture-induced soil carbon debt.

Our findings provide quantitative estimates for the importance of plant-soil interactions in human-driven alterations of the global carbon balance. Previous research has revealed that ecosystems dominated by EcM plants are typically associated with soils featuring higher carbon content (*7, 11*). However, recent analyses conducted at regional scales suggest that while increased EcM dominance is associated with higher soil carbon-to-nitrogen ratio, it may be that decline in nitrogen rather than increase in carbon is the main factor underpinning the relationship(*12, 20, 27*). In contrast to these regional scale studies, our analysis indicates that across large geographical scales, higher cover of EcM vegetation is broadly associated with higher soil C content in topsoil.

In this study, we aim to provide a benchmark for global assessments relating ecosystem processes to the functioning of distinct types of mycorrhizas. Considering the virtual absence

of quantitative global data about mycorrhizal distribution while there is a major demand for such data (*9, 10, 29*), our mycorrhizal distribution maps provide an essential basis for detailed and systematic analyses of mycorrhizal biogeography and the environmental drivers thereof. Inclusion of these data into vegetation models will allow accounting for impacts of mycorrhizas on ecosystem processes from landscape to global scale as well as for spatially explicit and quantitative assessments on the role of mycorrhizas in the functioning of terrestrial ecosystems and in the provisioning of associated ecosystem services.The quantitative nature of the observed relationships between abundances of mycorrhizal types and carbon cycling for the first time allows inclusion of the relationship between mycorrhizal abundances in ecosystems and soil carbon content into global scale analyses of biogeochemical cycles as well as into policies aiming to improve soil carbon sequestration via land management practices.

References

1. S. E. Smith, D. J. Read, *Mycorrhizal Symbiosis*. (Academic Press, London, 2008).
2. M. C. Brundrett, Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* **320**, 37-77 (2009).
3. D. J. Read, Mycorrhizas in ecosystems. *Experientia* **47**, 376-391 (1991).
4. J. R. Leake *et al.*, Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Canadian Journal of Botany-Revue Canadienne De Botanique* **82**, 1016-1045 (2004).
5. J. A. Bennett *et al.*, Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**, 181-184 (2017).
6. F. P. Teste *et al.*, Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* **355**, 173-176 (2017).
7. D. J. Read, J. Perez-Moreno, Mycorrhizas and nutrient cycling in ecosystems - a journey towards relevance? *New Phytologist* **157**, 475-492 (2003).
8. C. Averill, B. L. Turner, A. C. Finzi, Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**, 543–545 (2014).
9. R. P. Phillips, E. Brzostek, M. G. Midgley, The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytologist* **199**, 41-51 (2013).
10. C. Terrer, S. Vicca, B. A. Hungate, R. P. Phillips, I. C. Prentice, Mycorrhizal association as a primary control of the CO2 fertilization effect. *Science* **353**, 72-74 (2016).

11. D. J. Read, J. R. Leake, J. Perez-Moreno, Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany-Revue Canadienne De Botanique* **82**, 1243-1263 (2004).
12. K. Zhu, M. L. McCormack, R. A. Lankau, J. F. Egan, N. Wurzburger, Association of ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. *Journal of Ecology* **106**, 524-535 (2018).
13. E. C. Ellis, K. K. Goldewijk, S. Siebert, D. Lightman, N. Ramankutty, Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* **19**, 589-606 (2010).
14. M. C. Brundrett, in *Biogeography of Mycorrhizal Symbiosis*, L. Tedersoo, Ed. (2017), chap. 17, pp. 361-394.
15. S. Hempel *et al.*, Mycorrhizas in the Central European flora - relationship with plant life history traits and ecology. *Ecology* **94**, 1389-1399 (2013).
16. R. Swaty, H. M. Michael, R. Deckert, C. A. Gehring, Mapping the potential mycorrhizal associations of the conterminous United States of America. *Fungal Ecology*, (2016).
17. R. G. Bailey, *Ecoregions. The Ecosystem Geography of the Oceans and Continents*. (Springer New York, 2014), pp. 180.
18. European Space Agency CCI Land cover map 2015 (https://www.esa-landcover-cci.org/) (2017).
19. D. Schepaschenko *et al.*, A dataset of forest biomass structure for Eurasia. *Scientific data* **4**, 170070 (2017).
20. G. Lin, M. L. McCormack, C. Ma, D. Guo, Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytologist* **213**, 1440-1451 (2017).
21. J. B. Fisher *et al.*, Tree–mycorrhizal associations detected remotely from canopy spectral properties. *Global Change Biology*, (2016).
22. B. Wang, Y. L. Qiu, Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* **16**, 299-363 (2006).
23. E. G. Jobbágy, R. B. Jackson, The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* **10**, 423-436 (2000).
24. ISRIC WISE Soil Property Databases. http://isric.org/explore/wise-databases
25. D. M. Olson *et al.*, Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933-938 (2001).
26. C. W. Fernandez, P. G. Kennedy, Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? *New phytologist* **209**, 1382-1394 (2016).
27. C. Averill, C. V. Hawkes, Ectomycorrhizal fungi slow soil carbon cycling. *Ecology Letters* **19**, 937-947 (2016).
28. J. Sanderman, T. Hengl, G. J. Fiske, Soil carbon debt of 12,000 years of human land use. *Proceedings of the National Academy of Sciences*, 201706103 (2017).
29. N. A. Soudzilovskaia *et al.*, Quantitative assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon cycling. *New Phytologist* **208**, 280-293 (2015).
30. J. L. Harley, E. Harley, A check-list of mycorrhiza in the British flora. *New Phytologist* **105**, 1-102 (1987).
31. C. G. Bueno *et al.*, Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecology and Biogeography*, (2017).

32. L. Tedersoo, M. C. Brundrett, in *Biogeography of mycorrhizal symbiosis*, L. Tedersoo, Ed. (Springer, 2017), pp. 409-468.
33. M. C. Brundrett, in *Biogeography of mycorrhizal symbiosis*, L. Tedersoo, Ed. (Springer, 2017), pp. 533-557.
34. P. Kohout, in *Biogeography of mycorrhizal symbiosis*, L. Tedersoo, Ed. (Springer, 2017), pp. 179-193.
35. ORNL DAAC Spatial Data Access Tool (SDAT), Bailey Ecoregions of the Continents (Province) http://webmap.ornl.gov/ogcdown/wcsdown.jsp?dg_id=10010_3.
36. L. Tedersoo, in *Biogeography of mycorrhizal symbiosis*, L. Tedersoo, Ed. (Springer, in press, 2017).
37. K. A. Kron, J. L. Luteyn, Origins and biogeographic patterns in Ericaceae: new insights from recent phylogenetic analyses. *Biol Skr* **55**, 479-500 (2005).
38. N. Batjes, Harmonized soil property values for broad-scale modelling (WISE30sec) with estimates of global soil carbon stocks. *Geoderma* **269**, 61-68 (2016).
39. FAO, Global forest resource assessement., (2000).
40. OECD FAO, *Oilseeds and oilseed products. 2013. OECD-FAO Agricultural Outlook.*, OECD Publishing, Paris.

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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 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 interests: Authors declare no competing interests;

Data and materials availability: All data is available in the main text or the supplementary materials.

Supplementary Materials:

Materials and Methods

Figures S1-S4

Tables S1-S6

References (26-40)

Supplementary Materials

Materials and Methods

Global data sets of mycorrhizal types and mycorrhizal vegetation

We integrated information about the plant mycorrhizal types and registered occurrences 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, 15, 22, 29-32*). 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 'colonisation' 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*). Table S1 provides a list of the literature sources included in the data set.

Information about non-mycorrhizal plant species was derived from the work of Brundrett (*2, 33*). All Diapensiaceae and Ericaceae were considered ericoid mycorrhizal (*34*), except for *Enkianthus* (AM), *Arbuteae*, *Pyroleae*, *Monotropeae* and *Pterosporeae* (all subtypes of EcM). We critically re-evaluated the literature (*15, 22*) 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%.

Areal coverage of mycorrhizal plants within ecoregions per land cover type

We selected the global ecoregion map of Bailey (2014) (*17*) that features 98 ecoregions (Table S3), provided by the Oak Ridge National Laboratory Distributed Active Archive Center (*35*) (spatial resolution 10 arcmin), as a basis for mapping global-scale distribution of mycorrhiza types. This map was preferred over that of biomes provided by Olson and co-workers (*25*) because of higher level of detail for ecoregions and because the boundaries of ecoregions were more strongly related to the distribution of mycorrhiza types. We examined the vegetation descriptions of ecoregions-by-continents as provided by Bailey (*17*), and assessed the available literature about geographical distributions of AM, EcM, and ErM plants based on 1,568 data sources (Table S2). Additionally, we examined biogeographic and phylogeographic studies of EcM plants. For the latter two groups, we made use of the fact that these types of mycorrhiza are featured by a relatively small number of plant species (i.e. EcM and ErM plants account for ca 2% and 1.4% of overall plant species richness (*2, 32*)). Thus, we additionally examined GBIF (www.gbif.org) records for each known EcM (*36*) and ErM (*37*) plant species.

Combining these data, we estimated the relative areal coverage of EcM, AM, ErM and non-mycorrhizal plants in each ecoregion. We assessed vegetation composition of each of the 98 ecoregions for each continent separately, using the continent division based upon the FAO Global Administrative Unit Layers (http://www.fao.org/geonetwork/srv/en/). 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; Tables S2, S3). 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 were missing from the ecoregions map of Bailey, we added mycorrhiza information for such islands manually based on the literature references in our dataset (Table S2).

To correct for impacts of anthropogenic activities, water regime and edaphic factors on the areal distribution of mycorrhiza types within each ecoregion, we overlaid the distribution of mycorrhizal types obtained using the ecoregion approach with an up-to-date satellite observation-based land cover map for the year 2015 (38 land cover categories, spatial resolution of 300 m), generated by the European Space Agency (*18*) (see Table S4 for the list of land cover categories). Using this overlay and the vegetation by ecoregion data (Table S2), we determined the distribution of mycorrhizal types for each of the 38 land cover types and ecoregion-by-continent combinations. In mosaics of vegetation types, the average mycorrhizal fraction for each land cover category was used and multiplied by the proportion of AM, EcM, ErM and non-mycorrhizal plants in each category. In case of a mix of natural vegetation types (e.g. a mix of grasslands, forests, shrublands), we assumed that each vegetation type is present in equal proportion. This conservative assumption was chosen to minimize overestimating cropland-induced changes on mycorrhizal distribution. For urban habitats, we considered that 50% of the land is covered by plants and took into account the practices of ornamental and fruit tree planting and proliferation of weeds..

Our data represent relative cover of AM, EcM, ErM and NM plants within the total vegetation cover in a grid cell. We accounted for potential discontinuity of vegetation multiplying our data with the MODIS normalized difference vegetation index (NDVI; https://neo.sci.gsfc.nasa.gov/; resolution 10 arcmin). This resulted in the absolute vegetation percentage cover for AM, EcM ErM and NM plants.

To calculate the total area covered by plants of distinct mycorrhizal types, we summed up products of cell area and percentage cover of mycorrhizal types. Map assembly and area calculations were done using R software for statistical computing, version 3.4.4. The maps are shown in Fig. 1.

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 ErM and EcM plant species together (*2*). However, orchid species are never abundant in ecosystems in terms of biomass, and therefore are unlikely to play an essential role in biogeochemical cycles.

Impact of crop cultivation on areal coverage of distinct mycorrhizal types

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 fractions in each of the ecoregion-continent-land cover combinations that contained croplands (land-covers of types 10,11,12,20, and 30; see Table S4) 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 Table S2). 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 fractions were assigned following the mycorrhizal types associated with the respective plant types in the current vegetation based on the per ecoregion references in Table S2. This resulted in an extra dataset describing combinations of vegetation as defined by ecoregion-continent-land cover without croplands (Table S7 for continent data and Table S8 for island data). Maps of potential mycorrhizal distribution in a cropland-free world (Fig. S4) were created based on this dataset, using the same R scripts as for the current distribution of mycorrhizas. We calculated the changes in area covered by particular mycorrhizal types for the current situation and the cropland-free world based on the sum of projected areas of grid cells for which land cover differed, multiplied by the fraction of each type of mycorrhizal vegetation in the grid cell.

Map validation and uncertainty analysis

The maps of the current mycorrhizal distributions were validated using the datasets of forest biomass structure for Eurasia (*19*), global analysis of impacts on mycorrhizas on carbon vs nitrogen dynamics (*20*), the USA-based analysis of mycorrhizal associations conducted with remote sensing techniques (*21*), and the map of mycorrhizal root biomass in West Australia by Brundrett (*14*), see Fig. S1.

The data of forest biomass structure for Eurasia (*19*) 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, Fig. S1). This provided us with a per-site data on the relative biomass of AM and EcM trees. We used these data as proxies for AM and EcM cover to compare with the data in our maps. We used the same approach for the data of Lin and co-workers (*20*), 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* (*21*) 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). Using this dataset, we directly compared the AM and EcM coverage per pixel to the data of our maps, taking the precautions described in Supplementary Text 'Data processing for map validation'.

The West Australian data of mycorrhizal root abundance (*14*) is based on a combination of Australian vegetation data and data about the relative dominance of plants with AM, EcM and NM root colonization. We used these data as proxies for cover of the AM, EcM and NM plants. In order to account for discontinuity of vegetation, we multiplied the data with the MODIS-normalized difference vegetation index (NDVI) https://neo.sci.gsfc.nasa.gov/; following the same procedure as for construction of our maps.

All datasets used for map validation contain data on proxies of relative plant mycorrhizal cover of AM, EcM, ErM and NM plants. Supplementary text 'Data processing for map validation' describes the steps applied to each of the datasets to enable its direct comparison

to our maps. 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 >25% (Supplementary Text ‘Map uncertainty analysis’').

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

We examined whether the soil carbon content was related to the abundance of AM and EcM plants, using generalized linear model (glm) regressions of the Gaussian family with top 30 cm soil C content per m^2 as a response variable, and biome and percentage areal cover of AM or EcM plants as predictors. The data for soil carbon content in the top 30 cm of soil was taken from the ISRIC-WISE global soil properties database (*24*). As we were interested in relationships between AM or EcM coverage and soil carbon in natural environments, we excluded urban and agricultural areas, according to the ESA land cover categories (*18*), from the analysis. We also excluded the four 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%)” and “Tree cover, needleleaved, deciduous, closed to open (>15%)”.

Data for biome types were taken from the map of terrestrial biomes (*25*). To create a more balanced dataset, we excluded the biomes “Flooded Grasslands and Savannas” and “Mangroves” (that contained few data points only) and merged the biomes “Tropical and Subtropical Moist Broadleaf Forests” and “Tropical and Subtropical Dry Broadleaf Forests” into one biome and the biomes “Tropical and Subtropical Grasslands, Savannas, and

Shrublands” and “Temperate Grasslands, Savannas and Shrublands” into another biome. Preliminary checks showed that the relationships between cover of mycorrhizal types and soil carbon content did not differ considerably among the groups of merged biomes.

Two models, comprising soil carbon content as a response variable, and (i) biome, EcM coverage and their interactions, or (ii) biome, AM coverage and their interactions, were examined independently and evaluated based on the Akaike Information Criterion. In both 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.

Assessment of the impact of reduced EcM vegetation cover on global soil carbon content

We calculated the amount of soil carbon associated with the presence and activities of ectomycorrhizas based on predictions provided by the glm model between biome, areal coverage of ectomycorrhizal plants and soil carbon content (Fig. 4). For each grid cell of the EcM vegetation map, which had different values of current EcM cover compared to the EcM cover expected in the cropland-free world, we calculated the values of carbon stocks associated with the presence and activity of EcM within a given biome, and the standard errors of these values at confidence interval of 95%. We performed these calculations for the current distribution of EcM plants (Fig. 1) and the for distribution of EcM plants in a cropland-free world (Fig. S3). Subsequently, we calculated the differences between the two outcomes. We estimated the uncertainty in our calculations of the total topsoil carbon loss, taking square root of the sum of squared standard errors calculated for the topsoil carbon content based on current EcM distributions and distributions in a cropland-free world.

This calculation is warranted under the assumption that within the natural ecosystems, for which our glm model was built, (i) EcM plants are to some extent present in every biome, and (ii) the total tree cover is decoupled from the cover of EcM trees (i.e. each biome features AM trees and some pre-dominant non-tree EcM plants, such as shrubs, dwarf shrubs and herbaceous plant species such as *Kobresia* spp.). The data in our maps provide evidence for the correctness of the first assumption (i.e. Fig. 4 suggests that all examined biomes possess EcM vegetation). We considered the second assumption to be valid for all biomes except for boreal forest (i.e. taiga), which are heavily dominated by coniferous EcM plants. However, boreal forests are only marginally affected by conversion of natural ecosystems to croplands (*13*) (see also Table S7). We verified our calculations by comparing the results by either including or excluding the boreal forest biome, and found that the inclusion of this biome only marginally affected the calculation outcomes (adding the boreal forest biome yielded an extra 1 GT loss).

Recent research conducted at regional level suggests that the patterns of EcM – soil carbon relationship change with soil depth (*12*), weakening at the deeper soil layers. However the carbon content is up to four-fold lower in the soil layers deeper than 30 cm (*38*). Thus we focused this study on the assessment of mycorrhizal impacts on topsoil carbon.

Our analysis 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 (*39*, *40*), the total area occupied by AM tree plantations exceeds that occupied by EcM tree plantations (Table S6), suggesting that exclusion of tree

plantations leads to conservative estimations of topsoil carbon loss associated with global reduction of EcM vegetation.

Supplementary Text

Data processing for map validation

In the datasets (*19-21*), AM and EcM plant coverage is always considered to sum up to 100%. As these datasets do not provide information about the cover of 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 AM of and EM cover 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 (*19-21*) represent forest data, we evaluated whether all data points or raster cells (*21*) were indeed located in forest areas. This was done using the ESA land cover categories data (*18*). All data points that were located out of the current areas registers by ESA (*18*) as forests were excluded from the analysis.

The West Australian map of mycorrhizal root abundance (*14*) 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 plant coverage of AM, EcM and NM plants. To translate these root distribution data into percentage cover for 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).

Map uncertainty analysis.

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” (Table S4). Further improvement of the ESA classification data will provide a possibility to improve precision of our maps.

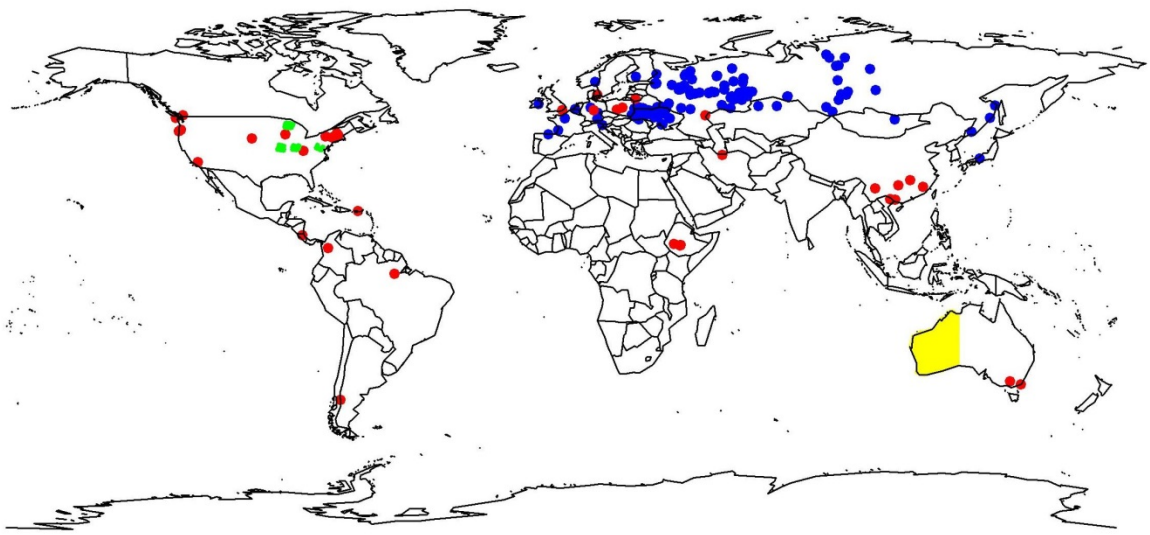

Fig. S1. Data used for map validation with the data of Schepachenko and co-workers (*19*) (blue points), Lin and co-workers (*20*) (red points), Fisher an co-workers (*21*) (four areas in USA, green) and Brundrett (*14*) (West Australia, yellow).

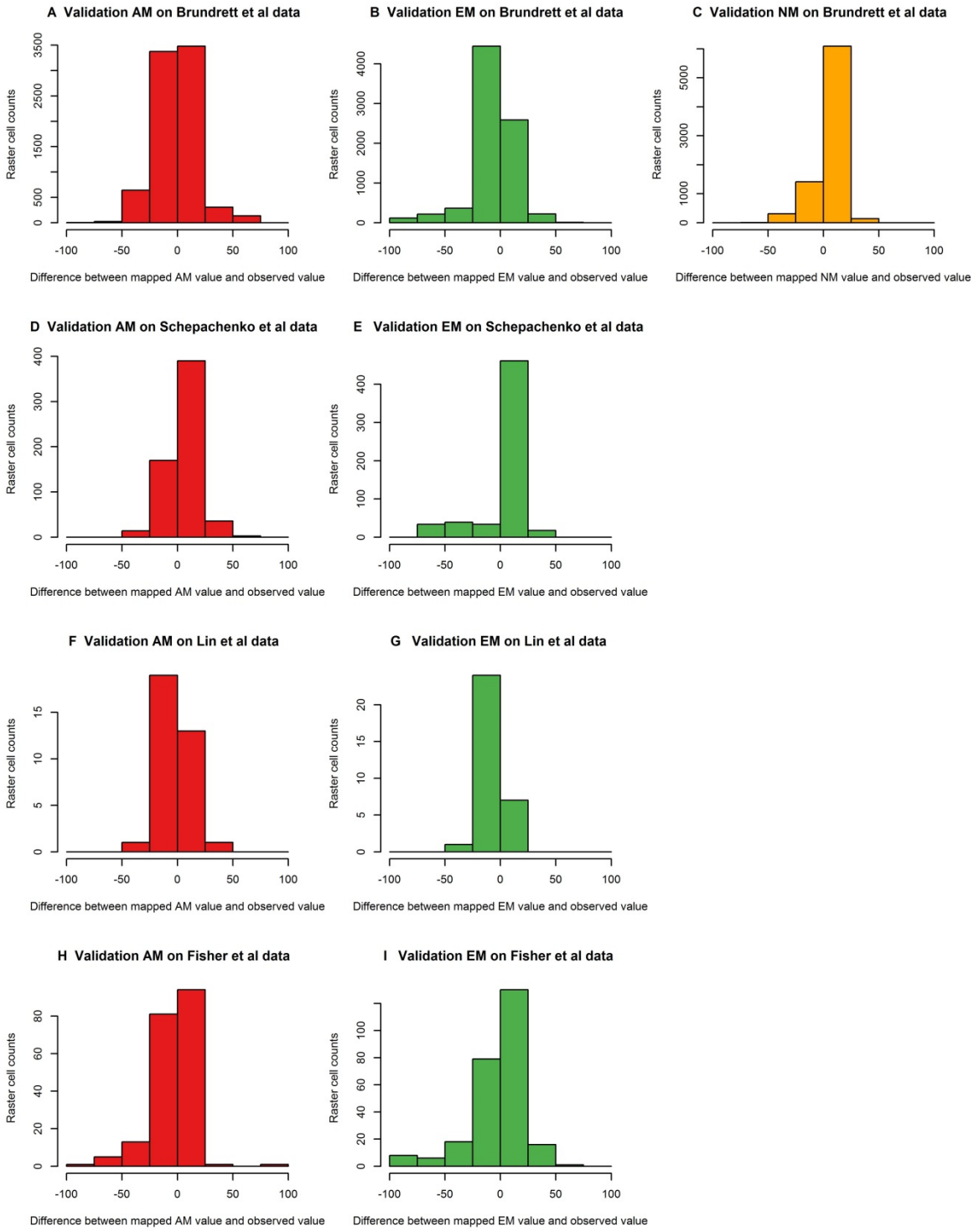

Fig. S2. Map validation results for the current distribution of mycorrhizal plants. The data was validated separately for AM (A,D,F,H), EM (B,E,G,I) and NM (C) plant cover using four individual datasets (*14, 19-21*).

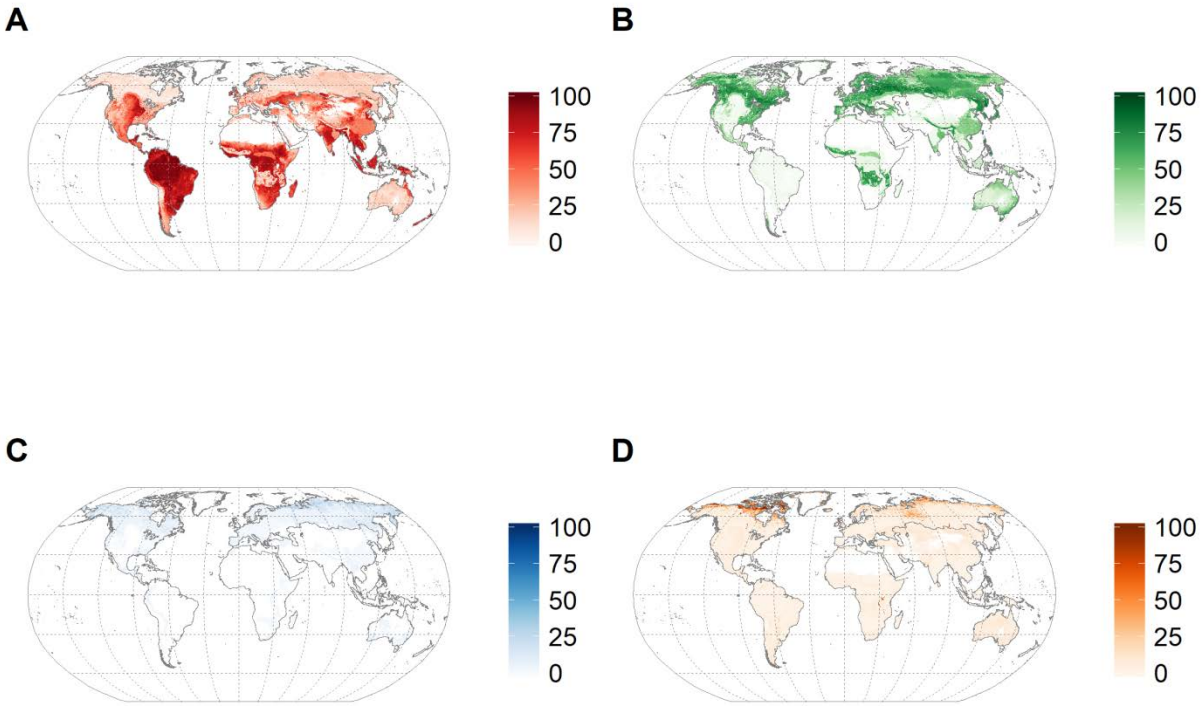

Fig. S3. Potential distribution of mycorrhizal vegetation in a cropland-free world. A - arbuscular mycorrhizal plants, B - ectomycorrhizal plants, C - ericoid mycorrhizal plants, and D - non-mycorrhizal plants. Color intensity reflects percentage of area covered by mycorrhizal plants of a given type in a grid cell of 10 arcmin.

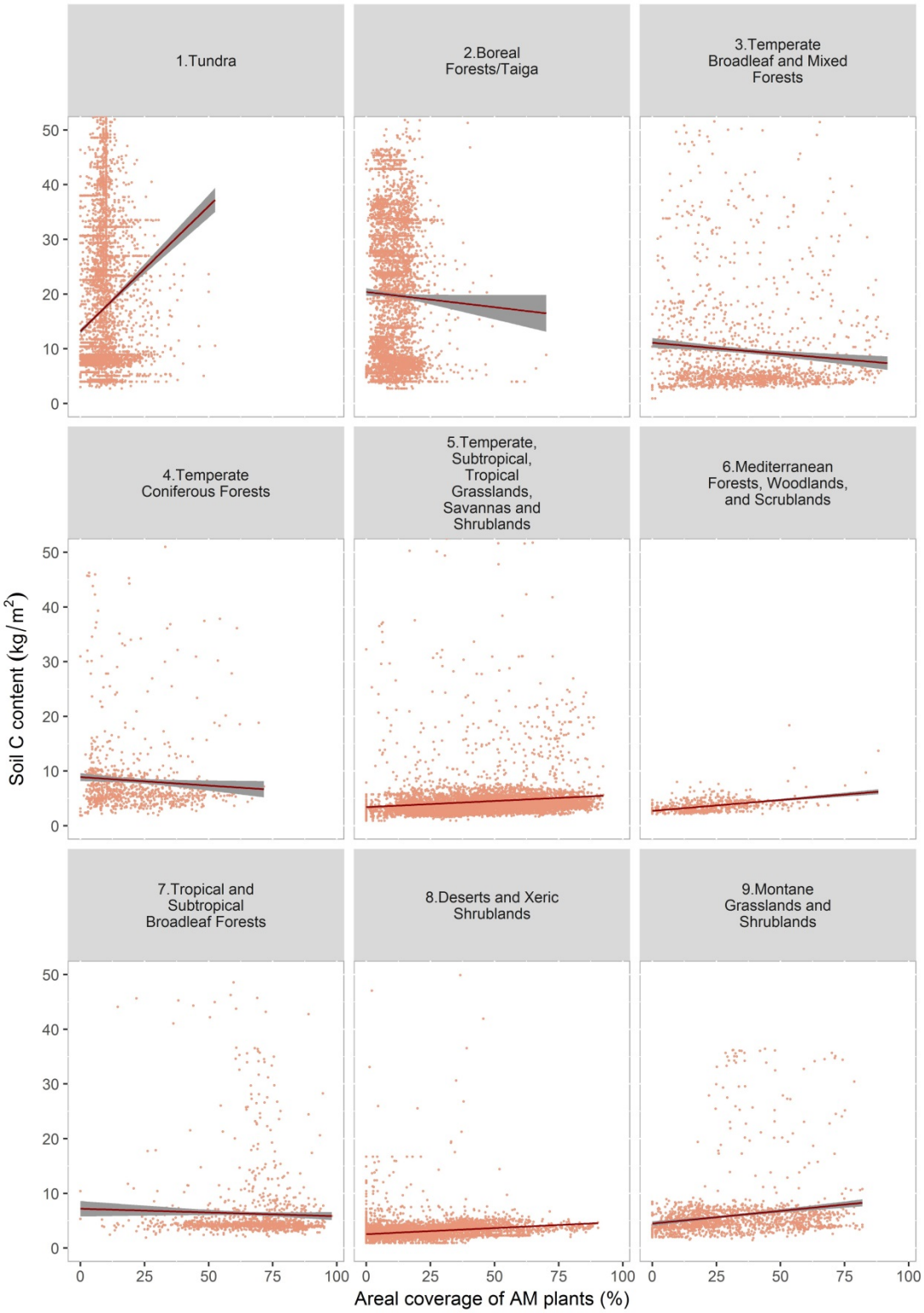

Fig. S4. Quantitative relationships between soil C and areal coverage by AM plants in an ecosystem. Per biome predictions are shown. N= 33,257. All predictions are based on general linear models between biome, AM plant cover and soil C content.

Table S1 (separate file)

Literature sources used in assessment of mycorrhizal association types of plant species

Table S2 (separate file)

Literature sources used in assessment of distribution of mycorrhizal types across continents and ecoregions.

Table S3 (separate file)

List of Ecoregions used to assemble maps of mycorrhizal plants distribution.

Table S4 (separate file)

List of land cover categories within the ESA CCI Land Cover dataset, used to assemble maps of mycorrhizal plants distribution

Table S5. Per continent gain and loss in coverage of distinct mycorrhizal vegetation types

Total gain and loss of vegetation coverage per mycorrhizal type, area 1,000 km^2								
Continent	**AM gain**	**EcM gain**	**ErM gain**	**NM gain**	**AM loss**	**EcM loss**	**ErM loss**	**NM loss**
Africa	265.3	4.6	0.1	1075.0	741.1	594.2	9.6	0.0
Asia	734.8	1.7	0.2	2442.9	1173.5	1961.8	44.3	0.0
Europe	1219.2	0.0	0.4	860.1	118.1	1902.1	59.4	0.0
North America	316.1	0.0	1.1	549.1	234.9	606.7	24.3	0.3
Oceania	168.0	0.4	0.4	91.6	6.7	244.2	9.4	0.0
South America	3.3	0.0	0.0	750.7	707.2	43.1	3.6	0.0
% of total gained and lost area								
Africa	9.8	68.3	3.0	18.6	24.9	11.1	6.4	0.0
Asia	27.1	25.8	7.3	42.3	39.4	36.7	29.4	0.0
Europe	45.0	0.0	18.8	14.9	4.0	35.5	39.5	0.0
North America	11.7	0.0	52.8	9.5	7.9	11.3	16.1	100.0
Oceania	6.2	5.9	18.0	1.6	0.2	4.6	6.3	0.0
South America	0.1	0.0	0.0	13.0	23.7	0.8	2.4	0.0

Table S6 Areas occupied by tree plantations of distinct mycorrhizal types. For the entire cover of unspecified tree species the OECD FAO report (*39*) provides an estimate 0.536 mln km^2 . In this analysis we have split this area between EcM tree plantations and AM tree plantations.

	Area mln km^2	Data source
Global area plantations EcM trees		
Pinus spp. (pines)	0.400	*(39)*
Other coniferous trees (mostly EcM)	0.274	*(39)*
Unspecified tree species	0.268	*(39)*
Total	**0.742**	
Global area plantations AM/EcM trees		
Eucalyptus spp. (eucalypts)	0.200	*(39)*
Acacia spp. (wattles)	0.083	*(39)*
Total	**0.283**	
Global area plantations AM trees		
Elaeis guineensis (oil palm)	0.170	*(40)*
Hevea brasilensis (rubber tree)	0.098	*(39)*
Tectona grandis (teak)	0.057	*(39)*
Other broadleaf tree species (mostly AM)	0.335	*(39)*
Unspecified tree species	0.268	*(39)*
Total	**0.928**	