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Review

Mycorrhizal mycelium as a global carbon pool

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SUMMARY

For more than 400 million years, mycorrhizal fungi and plants have formed partnerships that are crucial to the emergence and functioning of global ecosystems. The importance of these symbiotic fungi for plant nutrition is well established. However, the role of mycorrhizal fungi in transporting carbon into soil systems on a global scale remains under-explored. This is surprising given that ~75% of terrestrial carbon is stored belowground and mycorrhizal fungi are stationed at a key entry point of carbon into soil food webs. Here, we analyze nearly 200 datasets to provide the first global quantitative estimates of carbon allocation from plants to the mycelium of mycorrhizal fungi. We estimate that global plant communities allocate 3.93 Gt CO_2e per year to arbuscular mycorrhizal fungi, 9.07 Gt CO_2e per year to ectomycorrhizal fungi, and 0.12 Gt CO_2e per year to ericoid mycorrhizal fungi. Based on this estimate, 13.12 Gt of CO_2e fixed by terrestrial plants is, at least temporarily, allocated to the underground mycelium of mycorrhizal fungi per year, equating to ~36% of current annual CO_2 emissions from fossil fuels. We explore the mechanisms by which mycorrhizal fungi affect soil carbon pools and identify approaches to increase our understanding of global carbon fluxes via plant–fungal pathways. Our estimates, although based on the best available evidence, are imperfect and should be interpreted with caution. Nonetheless, our estimations are conservative, and we argue that this work confirms the significant contribution made by mycorrhizal associations to global carbon dynamics. Our findings should motivate their inclusion both within global climate and carbon cycling models, and within conservation policy and practice.

Introduction

Partnerships formed between land plants and mycorrhizal fungi are among the most widespread and important symbioses on Earth. Mycorrhizal fungi have played a key role in the formation and functioning of global ecosystems by enhancing plant access to mineral nutrients and facilitating the movement of plants onto land >400 Ma[1–4]. Symbiotic associations with fungi are the ancestral state of terrestrial plants — by the time roots evolved from simple thalli and rhizoids, plants had already been associating with mycorrhiza-forming fungi for some 50 million years[4]. Today, mycorrhizal fungi lie at the base of terrestrial food webs supporting life on Earth. By helping move nutrients across ecosystems, mycorrhizal fungi are among the most ecologically important soil organisms in both natural and managed environments.

Mycorrhizal fungi are a broad class of soil fungi defined by their ability to associate with roots and engage in nutrient exchange with plants[5,6]. Nearly all land plants form symbioses with mycorrhizal fungi of one type or another[5]. The fungi form intricate networks of extraradical (external) mycelium that can extend beyond plant root systems, where they forage in the soil for phosphorus, nitrogen, sulfur, and trace elements[5]. Together with water[7], these nutrients are delivered to roots in exchange for photosynthetically derived carbohydrates and fats from the plant partner. The symbiosis is a fundamental part of plant nutrition: as much as 80% of phosphorus[8–10] and up to 20% of nitrogen[11–14] can be transferred to plants via mycorrhizal pathways. Nutrient allocation strategies between fungi and plants are highly context dependent[15–20]. In some cases, the exchange of resources is reciprocal, whereby the release of carbon from roots stimulates transfer of nutrients from fungi, and *vice versa*[21–24]. In other cases, one or other of the partners can receive more than they provide[4,25].

The earliest plants to colonize terrestrial landmasses >400 Ma faced harsh challenges. Chief among these was limited access to essential mineral nutrients, particularly given the skeletal mineral soils[26], the dense biological soil crusts[27], and lack of roots and vasculature of the earliest land plants[28,29]. Thanks to the remarkable ability of symbiotic fungi to extract nutrients from minerals[30] and transfer these nutrients to their plant partners, symbioses with mycorrhiza-like fungi were likely critical to the success and diversification of early land plants[5,31].

The Rhynie chert, a remarkably well-preserved fossilized Lower Devonian (411 ± 1.3 Ma) ecosystem in Aberdeenshire, Scotland, provides strong fossil evidence that early land plants formed symbioses with mycorrhiza-like fungi[1–3] (Figure 1).

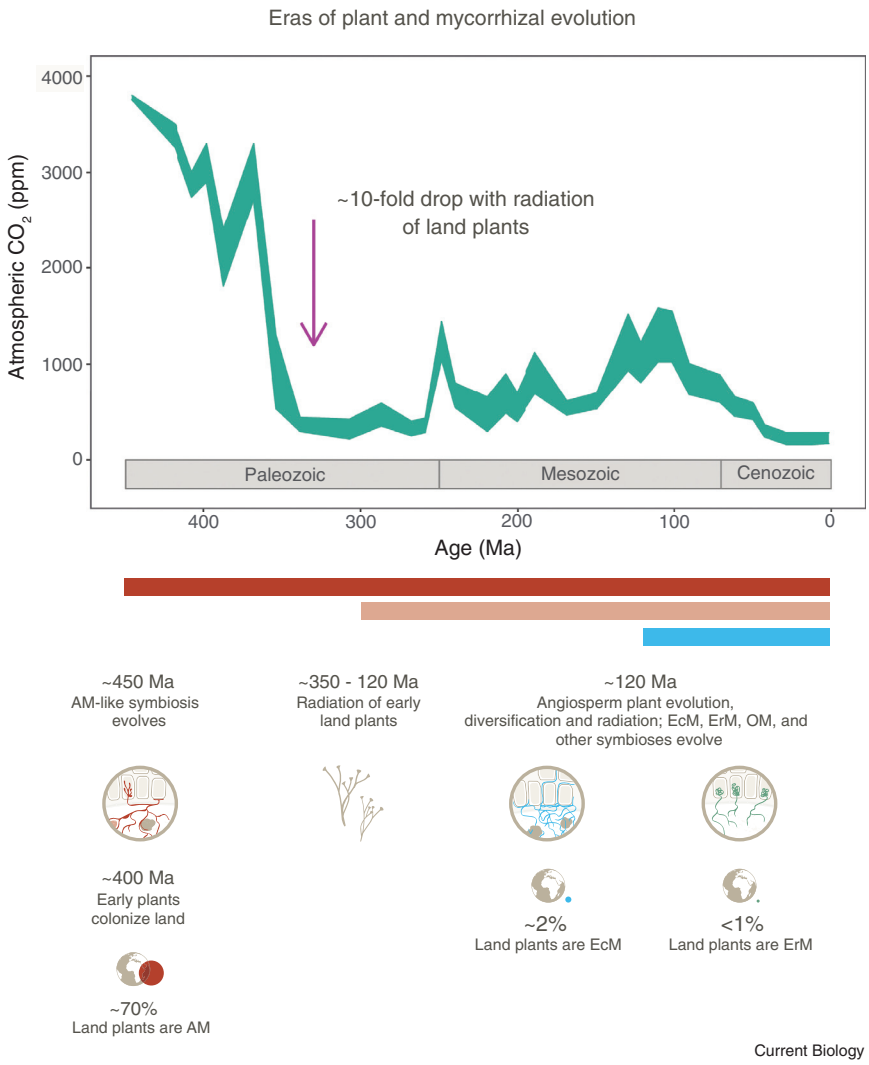

Figure 1. Illustration of how the evolution of the plant–fungal symbiosis coincided with plant radiation and a ~10-fold reduction in atmospheric CO_2 levels during the Paleozoic Era and beyond.
Circular, microscopic views of plant roots (light brown) and fungi (coloured lines) indicate the colonization of early land plant roots by different types of mycorrhizal or mycorrhizal-like fungi over time. Below this, the present-day percentage (%) of land plant species thought to be colonized by mycorrhizal fungi globally is indicated. Carbon dioxide data were reconstructed from Mora *et al.*[38] and Breecker *et al.*[39] . Timelines of plant and mycorrhizal evolution are based on Mills *et al.*[37], Martin *et al.*[41], and Tedersoo and Smith[40]. Abbreviations: AM (arbuscular mycorrhizal fungi); EcM (ectomycorrhizal fungi); ErM (ericoid mycorrhizal fungi); OM (orchid mycorrhizal fungi).

Physiological[32,33] and genetic evidence[34–36] supports the hypothesis that early plant–fungal associations were mutualistic, and that mycorrhiza played a key role in land colonization by early plants. In supplying land flora with otherwise poorly available nutrients, alongside other non-nutritional benefits, early mycorrhiza-like fungi helped drive proliferation and diversification of ever more complex land plants, increasing the net global photosynthetic drawdown of atmospheric CO_2 and burial of organic carbon[30,37]. Climate models suggest that these processes, together with other biological and tectonic factors[38], helped to drive a 10-fold reduction in atmospheric CO_2 levels during the Paleozoic Era, with concentrations falling from ~3000 to 300 ppm (Figure 1). The reduction of atmospheric CO_2 levels corresponded with a decline in global temperatures, and oxygenation of the atmosphere[37]. Atmospheric CO_2 remained relatively low during the Mesozoic and Cenozoic[39] when other types of mycorrhizal fungi are thought to have evolved[37,40,41] (Figure 1).

Given the persistence of mycorrhizal fungi across the vast majority of modern land plants[5], mycorrhizal associations likely continue to play an important, yet largely unrecognized, role in modulating global climate through their influence on terrestrial biogeochemical cycling of nutrients and carbon. Globally, soils contain ~1500 Gt C — more carbon than in the atmosphere and plant biomass combined — meaning that some 75% of all terrestrial carbon is stored belowground at any one time[42]. Despite mycorrhizal fungi being stationed at a key entry point of carbon into soil food webs, we lack a robust quantitative and mechanistic understanding of the contribution of mycorrhizal associations to the global carbon cycle. Mycorrhizal fungi are frequently cited as receiving anywhere from 4 to 20% of total plant-fixed carbon[43–45]. Scaled to a global level, these figures imply that — even after accounting for fungal respiration — millions of tons of carbon may be allocated to mycorrhizal biomass every year. If this is the case, accounting for carbon fluxes mediated by mycorrhizal fungi should improve models of climate and carbon cycling in past, present, and future scenarios.

Here, we provide the first quantitative analysis of the contribution of mycorrhizal fungi to global soil carbon pools across different mycorrhizal functional types. Using 194 datasets, we estimate the amount of carbon (photosynthate) that terrestrial plants allocate to different mycorrhizal functional types, expressing it as a fraction of annual Net Primary Productivity (NPP) of global vegetation. First, we describe the main functional types of mycorrhizal fungi and — where data were available — quantify their absolute and relative contributions to global soil carbon pools. We then explore the mechanisms by which mycorrhizal fungi contribute to or deplete soil carbon pools, and whether they may represent a significant carbon stock or store. Finally, we identify research that would further develop our understanding of global carbon dynamics via plant–fungal pathways.

Functional types of mycorrhizal associations

Mycorrhizal fungi can be divided into five functional types based on their morphology and physiology. Fungi that form arbuscular

Box 1. Definitions of abbreviations and units used in the text.

Mycorrhizal fungal types	
AM	Arbuscular mycorrhizas are symbiotic associations between fungi from the Glomeromycota phylum and the roots of ~70% of land plant species (both herbaceous and woody), distributed widely across the globe, but most densely in the (sub-)tropics. The fungus forms inter- and intracellular aseptate hyphae in roots as well as intracellular structures called 'arbuscules', which are the main sites of carbon-for-nutrients exchange.
EcM	Ectomycorrhizas are symbiotic associations between fungi from several phyla (Basidiomycota, Ascomycota, Mucoromycota) and the roots of ~2% of land plant species (e.g., pine, oak, dipterocarp), distributed in tropical, temperate, and taiga/boreal regions, but most densely in the latter. Septate fungal hyphae form an extracellular mycelial mantle around plant root tips (including a 'Hartig net'), where carbon-for-nutrients exchange takes place.
ErM	Ericoid mycorrhizas are symbiotic associations between fungi from two phyla (Ascomycota and Basidiomycota) and the roots of fewer than 1% of plant species (ericaceous plants mainly in the Ericaceae family). Distribution includes heathlands and forest understories in boreal/taiga regions, and heathlands in Mediterranean ecosystems. The fungus forms inter- and intracellular septate hyphae as well as coiled intracellular structures in the fine hair roots, where carbon-for-nutrients exchange takes place. Much less is known about these fungi than AM or EcM.
DSE	Dark septate endophytes are endophytic associations between certain fungal taxa and roots of many plant species across a wide geographic distribution. The fungus forms inter- and intracellular, melanized and septate hyphal structures in roots of these plants, but it is not certain whether this association is a functional mutualism.
MFRE	Mucoromycotina 'fine root endophytes' are endophytic, usually symbiotic associations between fungi from Mucoromycota fungal phylum and the rhizoids and roots of a wide variety of vascular and nonvascular plants (liver- and hornworts). The fungus forms inter- and intracellular, hyphal structures in roots of these plants, usually as part of an AM-like, functional mutualism.
OM	Orchid mycorrhizas are symbiotic associations between fungi, largely within the Basidiomycota, and most orchid plant species. Characteristic of this association is the dependance on the endophytic fungus by the plant in the early phase of its lifecycle, for both nutrients and carbon substrates (mycoheterotrophy or mycotrophy), while the fungus may subsequently acquire carbon from (photosynthetic) adult plants.
Other abbreviations and units	
C:N	Carbon to nitrogen ratio
C	1 unit C is equal to 3.67 units of CO_2
CO_2	Carbon dioxide
CO_2e	Carbon dioxide equivalents; the CO2e is a unit used to express all greenhouse gases as carbon dioxide equivalents in terms of global warming potential.
FAIR	Findable, accessible, interoperable, reusable (data)
GRSP	Glomalin related soil proteins
Gt	Gigatons
Ma	Million years ago
MAOM	Mineral associated organic matter
NPP	Net Primary Productivity

mycorrhiza (AM; see Box 1 for glossary of terms and definitions of units) fall entirely within the phylum Glomeromycota and form associations with ~70% of all land plant species (Figure 1), covering over 55% of global vegetation[46] (Table 1). This includes herbaceous plants like grasses, forbs, and most crop species, but also woody angiosperm trees such as ash and maples, many tropical tree species, and some gymnosperms like cedars, redwoods and *Araucaria* sp.[47]. Arbuscular mycorrhizal fungi, which predominately scavenge for inorganic but also simple organic soil nutrients[10,11], form intracellular structures in roots called 'arbuscules'. Arbuscule means 'a branched tree-like organ' and they are the main sites of carbon-for-nutrient exchange between plants and their fungal partners. Based on colonized fine-root biomass, the highest AM abundances are estimated to occur in the (sub-)tropics[48].

Unlike AM fungi, those forming ectomycorrhiza (EcM) do not grow into plant cells ('ecto' means outside). Instead, these fungi form a mycelial mantle around plant root tips, including a 'Hartig net', where exchange of nutrients and carbon takes place. This structure provides a large surface area between the partners for nutrient exchange. Some EcM fungi produce exoenzymes, which allows them to break down complex organic molecules[49]. The EcM association evolved after AM (Figure 1) from lineages of saprotrophic fungi[41]. Since the first colonization of land by plants, the EcM association has evolved more than seventy times into more than 6000 species within the phyla Basidiomycota, Ascomycota, and more rarely, Mucoromycota (specifically zygomycetes, part of the now abandoned phylum Zygomycota)[40,50]. Only two percent of plant species depend on ectomycorrhizal associations (Figure 1), but these species cover over 25% of global vegetation (Table 1). These include gymnosperms (e.g., pine and spruce) in boreal and taiga forests, many angiosperm trees common in both boreal and temperate forests (birch, beech, oak, and willow), and some tropical forest trees (dipterocarp)[41]. The highest EcM abundances are estimated to occur in the taiga regions[48].

Table 1. Estimates of global carbon fluxes to the main mycorrhizal fungus types and what proportion this comprises of fossil fuel emissions of 2021.

Mycorrhizal fungus	Land cover (%)	Vegetation NPP (Gt C yr^{-1})	Average NPP allocation (%)	Carbon flux to mycelium (Gt C yr^{-1})	(Gt CO_2e yr^{-1})	Proportion of fossil fuel emissions (2021) (%)
AM	**57.4**	**33.87**	**6.20**	**1.07 (0.95–1.14)**	**3.93**	**10.83**
Herbaceous	19.4	6.94	6.52	0.45 (0.39–0.48)	1.66	4.57
Woody	38.0	26.93	2.30	0.62 (0.56–0.66)	2.27	6.25
EcM	**25.7**	**13.01**	**13.10**	**2.47 (2.29–2.56)**	**9.07**	**24.99**
Broadleaf	12.4	7.51	26.10	1.96 (1.8–2.0)	7.19	19.81
Needleleaf	13.3	5.50	9.36	0.52 (0.48–0.54)	1.89	5.21
ErM	**2.6**	**0.93**	**3.50**	**0.03 (0.03–0.04)**	**0.12**	**0.33**
NM	**14.3**	**5.76**	**n/a**	**n/a**	**n/a**	**n/a**
Total	**100.0**	**53.58**	–	**3.58**	**13.12**	**36.14**

The NPP units of the annual MODIS Terra data product (MOD17A3HGF[100]) were converted from kg C m^{-2} to Gt per pixel (matching the pixel resolution of 500 m). Mycorrhizal vegetation data from Soudzilovskaia *et al.*[46] were used to mask NPP data proportional to the different mycorrhizal types, which were further refined by plant functional groups (herbaceous *versus* woody for AM; broad- *versus* needleleaf for EcM) using land cover data (Copernicus Dynamic Land Cover map, CGLS-LC100[101]). All unmasked pixels were then summed to estimate the total annual NPP in vegetation per mycorrhizal type for the years 2001 through 2021. These NPP values were multiplied with our average NPP allocation to external hyphae to provide a non-spatial estimate of global NPP that is allocated to each of the three main mycorrhizal fungus types, i.e., carbon flux to mycorrhizal mycelium (values are 20-year averages including upper and lower 96th percentiles). Abbreviations: AM (arbuscular mycorrhizal fungi); EcM (ectomycorrhizal fungi); ErM (ericoid mycorrhizal fungi); NM (non-mycorrhizal); CO_2e (carbon dioxide equivalents); NPP (net primary productivity).

Fungi forming ericoid mycorrhiza (ErM) belong to both Ascomycota and Basidiomycota phyla and form coils mainly inside the roots of Ericaceae (e.g., heather, blueberries, cranberries)[51], but also non-Ericaceae and -Ericales taxa[52]. Less than one percent of plants have ErM associations and they cover less than three percent of global vegetation (Figure 1 and Table 1) including the understory of boreal forest and subarctic taiga, although this areal value is less certain than AM and EcM ones[46]. Ericoid mycorrhizal fungi associate with the fine hair roots of ericaceous plants found in acidic and infertile soils of bogs and heathlands, and like EcM, can produce exoenzymes[53,54]. Hair roots of ericaceous plants are often co-colonized by diverse, as yet poorly defined communities of fungi including ErM, dark septate endophytes (DSE), and saprobe fungi[55,56], with research on the ecophysiology of the ErM lagging far behind that of the AM and EcM fungi[51,56].

Orchid mycorrhiza (OM) are formed between most orchids and saprophytic or EcM fungi, largely within the Basidiomycota. While OM fungi may receive carbohydrates from adult orchids, orchid seeds lack reserves and require OM fungi to supply carbon substrates during germination (mycoheterotrophy or mycotrophy)[4]. The EcM, ErM and OM, as well as non-mycorrhizal roots, are thought to have evolved around 120 Ma during the period of rapid radiation of the angiosperms (Figure 1). Mucoromycotina 'fine root endophytes' (MFRE) form distinctive structures and functional nutritional mutualisms inside roots[57], but it remains unclear whether other fungi such as the DSE form functional mutualisms or are simply endophytes[58]. While the contribution to carbon fluxes by these groups has not been well documented, recent research has started to confirm their significance for plant carbon and nutrient relations[57]. Lastly, certain plants can associate with more than one type of mycorrhizal fungus[59,60], but there are very few quantitative datasets on carbon allocation under these mixed colonization conditions.

Carbon allocation to mycorrhizal fungi averages between 1% and 13% depending on fungal type

To quantify estimates of carbon allocation from plants to the mycelium of mycorrhizal fungi, we searched the peer-reviewed literature using the following search string on Scopus: *(TITLE-ABS-KEY (mycorrhiza* AND "carbon sequestration") OR (mycorrhiza* AND "13C fatty acids") OR (mycorrhiza* AND 14C) OR (mycorrhiza* AND 13C) OR (mycorrhiza* AND npp) OR (mycorrhiza* AND "carbon stor*"))*. *Searches on other platforms* yielded no additional results, but several studies were found within reference lists of literature. We extracted study details and data directly from articles, from figures using WebPlotDigitizer (version 4.5), or received data from the authors. We harmonized all NPP allocation data as percent of total NPP.

This approach yielded 194 datasets from 61 peer-reviewed papers and four from unpublished studies (AM bryophytes and grasses) on NPP-derived carbon allocation to the external mycelium of different mycorrhiza fungal functional types. Most measurements of NPP allocation were based on isotope tracing (radioactive $^{14}CO_2$ or stable $^{13}CO_2$), where the proportion of carbon label transferred from the plant to hyphal biomass within a root-free, mycelial compartment or ingrowth core was measured. Generally, the allocation of NPP to the fungus was calculated as $\%NPP = \frac{Label\ in\ mycelium}{Total\ label\ assimilated\ by\ plant} \times 100$. Most studies reported soil respiration, but where they did not, this proportion of label was never included with the labelled fungal biomass. The ^{14}C-labelling studies were short-term (hours to days) experiments in pots or *in vitro*. These experiments represented an instantaneous snapshot of labelled carbon allocation (primarily as plant hexoses) to mycorrhizal fungal mycelium, and could account for all the label within a sealed chamber (e.g., Cameron *et al.*[61] and Thirkell *et al.*[62]). Experiments using ^{13}C were relatively longer-term (months to years) occurring mostly in the field, but also in pots. This technique labelled *inter*

alia fungal storage (lipids) and structural (chitin) material, but could not account for all the label (being in open air, unsealed containers). However, these experiments were more representative of natural conditions (e.g., Albarracin *et al.*[25] and Birgander *et al.*[63]). In a few studies, other techniques such as mass balance[64,65], free-air CO_2 enrichment[66], biomass estimation[67], and biogeochemical modelling[65] were used. The collected studies covered a wide range of habitat types including forests, shrublands, heathlands, grasslands, and croplands across locations in Central Europe, United States, South America, and Asia. We could not locate any data from Southeast Asia, Oceania, or Africa. For more study details, see Data availability.

Plant NPP allocated to mycorrhizal fungi can be used to form internal and external hyphae, sporocarps, exudates, and dead fungal litter[67]. To effectively compare studies, we focused on a single common structural feature: external mycelium — tubular hyphae that make up the underground portion of mycorrhizal fungi. External mycelium is a good, albeit incomplete, proxy for measuring NPP allocation because it can be harvested separately to the root when hyphal compartments are used (as is common in labelling studies), has high activity, and high biomass[68–71].

In studies where labelled hyphal biomass of AM, EcM or DSE could not be collected (N = 7, 8, and 1, respectively), NPP allocation was based on total labelling in a root-free, soil- or substrate-containing hyphal compartment. Because these compartments contained not only hyphae but likely also fungal exudates, we reduced the reported NPP values by 7%, a factor previously used to account for mycorrhizal exudates[72]. For ErM, one study (N = 3 datasets) used mass balance to calculate NPP allocation to the external mycelium[73], another (N = 3 datasets) used axenic culture with a hyphal compartment[74], but two (N = 22 datasets) were field-based[75,76], and here we based NPP allocation on carbon in hair roots. This is because of the difficulty in isolating external ericoid hyphae and distinguishing them from other fungal hyphae in the field. While colonization rates of hair roots by ErM fungi vary widely (10–90%)[55,77–79] and there are no reliable estimates of the proportion of ErM fungal biomass in hair roots or extending from them, both field studies reported heavy colonization. Therefore, we assumed much of the carbon label was from the fungus.

The diversity of experimental approaches, labelling duration, plant growth conditions, symbiont species, and habitats creates uncertainty across studies. For this reason, we explored not only mycorrhizal type but also study type (*in vitro*, pot, field), experimental approach, and plant woodiness plus other traits as potential drivers of carbon allocation to the fungus. Analyses of variance (ANOVAs) were performed using R version 4.2.2[80], with additional functionalities from the *lmer*[81] package for linear mixed-effects models. See Data availability for a full list of studies, data, methods, and code.

Allocation of plant-fixed carbon to mycorrhizal fungi based on extraradical hyphae varied significantly across fungal functional types (Figure 2A; $P < 0.0001$, $Df = 5$, $F = 6.39$). We found that 6.2% ± 0.11 of a host plant's NPP was allocated to mycelium when associated with AM fungi (N = 89); 13.1% ± 0.22 when associated with EcM fungi (N = 63); 3.5% ± 0.14 to ErM fungi (N = 28); 1.0% ± 0.47 to OM fungi (N = 3), and 4.6% ± 0.29 to DSE fungi (N = 7). Mycorrhizal fungus type, study type, and

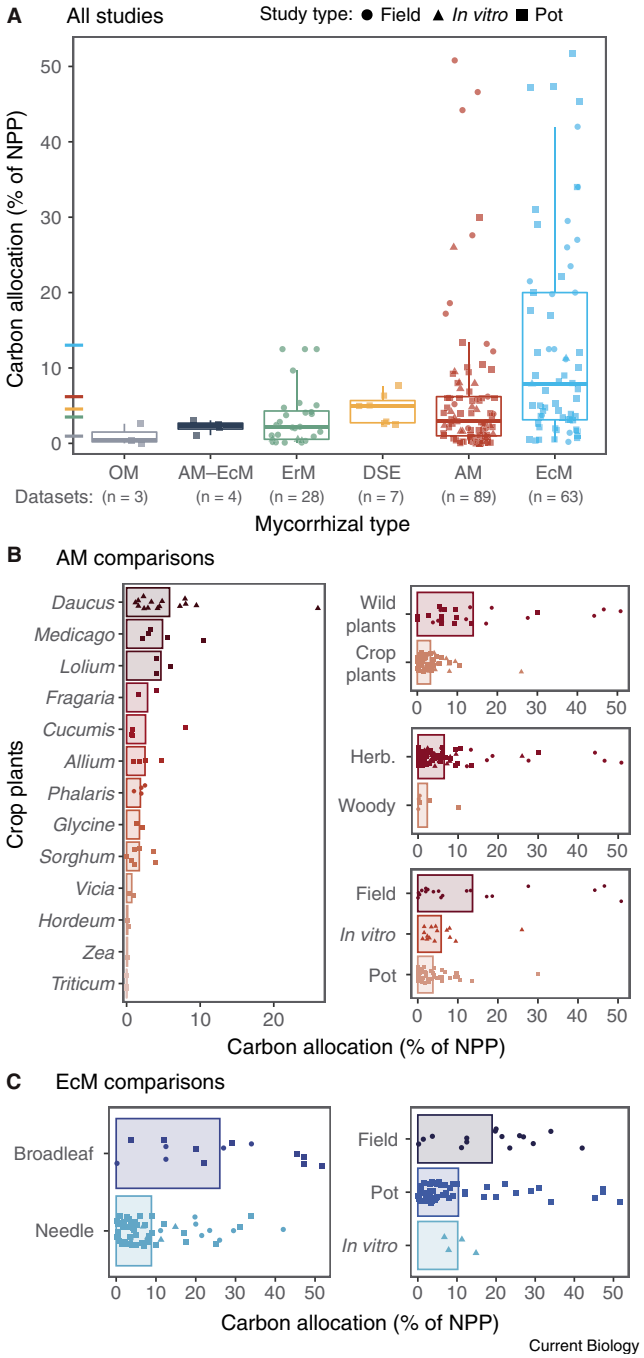

Figure 2. Carbon allocation patterns vary with mycorrhizal functional type.

(A) Percentage of net primary productivity (NPP) allocated to mycorrhizal external hyphae, based on studies (N = 194) from Central Europe, United States, South America, and Asia. Boxes indicate where half of the data is distributed, and whiskers indicate 25th and 75th percentiles. Number of datasets are noted beneath the x-axis groups, and coloured y-axis ticks are positioned at each mean allocation level per mycorrhizal type. Shapes indicate the distribution of data points per study type (triangle: axenic; circle: field; and square: pot). Comparisons of NPP allocation between plant and study types show key differences for both arbuscular (B) and ectomycorrhizal fungi (C), with bars indicating mean values for each group. Data on NPP allocation to external hyphae were extracted from the literature and harmonized to be expressed in percent. Abbreviations: AM (arbuscular mycorrhizal fungi); EcM (ectomycorrhizal fungi); ErM (ericoid mycorrhizal fungi); DSE (dark septate endophytes); OM (orchid mycorrhizal fungi).

woodiness were all drivers of %NPP allocation according to linear mixed effects models (for details see Data availability).

The %NPP allocated to EcM was higher than that allocated to AM or ErM fungi, but allocation to OM and DSE were not different to any of the other fungal symbionts at the P = 0.05 level. Although EcM fungi had a higher average %NPP allocation, values in some experiments for both AM and EcM fungi reached as high as ~50% of a host plant's NPP (Figure 2A). The number of studies on ErM, OM, DSE and MFRE fungi were low, and more data are required to provide robust estimates of plant to mycorrhizal transfer in these functional types. Only ~30% of the datasets (55 datasets from nine studies[45,63,76,82–87]) measured NPP allocation across seasons or plant age, meaning that these estimates mostly reflect mycorrhizal carbon dynamics at a single time point. Application of our estimates to global NPP measurements (see following section) accounts for seasonal and spatial variation in plant photosynthesis, but still assumes that a constant proportion of that NPP is allocated to the fungus, which may not be the case.

Overall, these data represent studies from a diversity of habitats and growth types. The AM associations included mostly herbaceous plants (grasses, forbs and many crop plants), but also woody plants (shrubs, trees). Crops are of particular interest because they are estimated to cover ~12.5 million km^2 or 8% of terrestrial surface area[88]. The extent of crop land has increased by ~9% since 2003, with a near doubling of the annual expansion rate largely due to growth in the global south[88,89]. We found crops allocated an average of 3.3% ± 0.55 (N = 55) of NPP to AM fungi. When considering pot or field studies, the cover crop medic (*Medicago truncatula*) and ryegrass (*Lolium perenne*) allocated the most with an average of ~5%, while wheat, barley and maize allocated the least at less than 0.1% (Figure 2B). Carrot (*Daucus carota*) values were also high, but all derived *in vitro,* which we discuss below. Importantly, carbon allocations to AM fungi of legumes (*M. truncatula*, *Glycine max*, *Vicia faba*) were not inflated by allocations to N_2-fixing bacteria in root nodules because values were based on hyphae from root-free compartments. Relatively low carbon allocations to Poaceae crops (wheat, barley) may be due to fine-rootedness, and selective breeding for responsiveness to fertilizers, fungal resistance, and intensive cultivation techniques that generally do not favour the formation of diverse mycorrhizal fungal communities[90]. Compared with wild grasses and forbs, crops (including barley, cucumber, onion, maize, soya bean, wheat) allocated ~4 times less NPP to AM fungi (Figure 2B).

We next compared the allocation to AM fungi from herbaceous plants with that from woody plants and found %NPP to be nearly 3 times higher in herbaceous (6.5% ± 0.12; N = 83) than in woody (2.3% ± 0.66; N = 6) plants, but there were a low number of woody plant replicates (N = 6), so this finding should be interpreted with caution (Figure 2B and Table 1). Likewise, we found average allocation of NPP to AM fungi was ~3 times higher in field (N = 19) *versus* greenhouse (N = 55) studies, and field measurements were more than 2 times higher than *in vitro* root organ culture studies (all *D. carota*; N = 15; Figure 2B). For *in vitro* studies that rely on root organ cultures, it is possible to harvest the entire hyphal network, and this might result in comparatively high values compared to pots (Figure 2B). However, these studies are difficult to compare meaningfully to those using whole plants with leaves. Similarly, pot studies are difficult to compare to field studies. For instance, pots may restrict hyphal and root growth, whereas it is difficult to systematically control for environmental differences in field studies.

Data for ectomycorrhizal plants included temperate, tropical, and boreal forest trees such as spruce, pine, beech, and various shrubs. The NPP allocation to EcM fungi was relatively high at 13.1%, a finding consistent with previous estimates (e.g., 9% [91,92] to 14%[87]), with some authors suggesting that the extraradical hyphae of EcM can account for more than half of the carbon added to soil[70,93,94]. Within EcM trees, we found that broadleaf trees (26.1% ± 1.22; N = 14) allocated ~2.8 times more NPP than needleleaf trees (9.4% ± 0.2; N = 49; Fig. 2C; Table 1). We speculate that this might be due to the lower N levels and photosynthetic rates of needles[95], albeit over longer life-spans[96]. Allocation to EcM fungi in field experiments (N = 15) was ~2 times higher compared with pot (N = 46) and *in vitro* studies (N = 2), a trend similar to the one observed for AM fungi (Figure 2C). Overall, it appears that faster growing plants (herbaceous *versus* woody; broad- *versus* needleleaf trees) allocate more NPP to mycorrhizal mycelium (Figure 2B,C).

There were few studies on ErM, OM, and DSE fungi, and these were limited to forest ecosystems except for six datasets on ErM plants (crow-, blueberry and rhododendron) in heathland shrublands, which means that these patterns should be interpreted cautiously. Our dataset shows that ericoid plants allocated about 3.5% of their NPP to ErM fungi. Likewise, due to low replicate numbers of OM fungi (N = 3), we cannot be confident about our estimate of 1.0% of NPP, nor our estimate of 4.6% to DSE fungi (N = 7). Data for bryophytes (liverworts and hornworts in this database) and pteridophytes (ferns in this database) had allocations of NPP ≤1%. Such low NPP allocation in these groups may reflect their limited photosynthetic rates[97], or the root traits of the species in question: mycorrhizal colonization of bryophytes was limited to specific areas within the thallus [98,99] and the root systems of the pteridophytes were relatively coarse.

Global carbon flux to mycorrhizal mycelia forms a substantial fraction of anthropogenic CO_2 emissions

We next calculated the fraction of global NPP directed to the mycelium of the three main mycorrhizal types (AM, EcM, ErM; Table 1), excluding OM and DSE because of low replicate number. Mycorrhizal vegetation data from Soudzilovskaia *et al.*[46] were used to mask global NPP data[100] proportional to the different mycorrhizal types, which we further refined by plant functional groups[101] (for more detail, see Table 1). Using our estimates for allocation to each of the mycorrhizal types (Figure 2), we found that per year, plant communities direct 1.07 Gt C (3.93 Gt CO_2e; see Box 1 for an explanation of these units) to arbuscular mycorrhizal fungi, 2.47 Gt C (9.07 Gt CO_2e) to ectomycorrhizal fungi, and 0.03 Gt C (0.12 Gt CO_2e) to ericoid mycorrhizal fungi (Table 1). The additional use of CO_2 equivalents (CO_2e) to express flux is useful here, as it is the standard unit of measure to convey climate effects of various greenhouse gases.

In total, we estimate that every year 3.58 Gt C or 13.12 Gt CO_2e taken up by terrestrial plants is allocated underground to the mycelium of mycorrhizal fungi (Table 1). Our quantitative flux

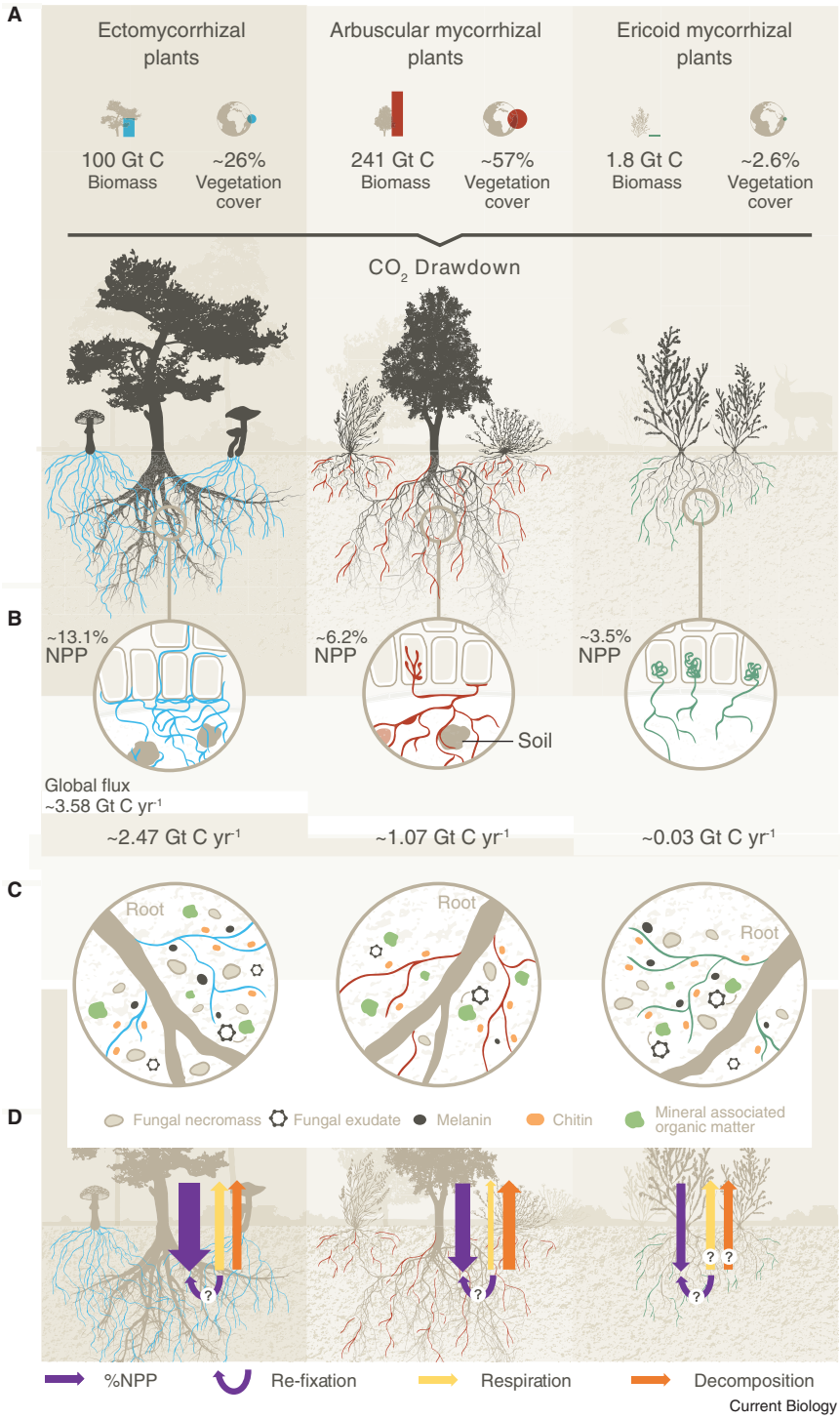

Figure 3. Illustration of the mechanisms by which mycorrhizal fungi help gain and lose carbon in soil.

(A) Drawdown of atmospheric CO_2 into plant biomass during photosynthesis (net primary productivity (NPP)) varies for the different types of plants categorized according to their mycorrhizal associations (data from Soudvilovskaia *et al.*[46]). (B) Plant-derived carbon is used to build and support an active mycelial network. Globally, it appears that faster growing plants (herbaceous *versus* woody; broad- *versus* needleleaf trees) allocate more photosynthate to their mycorrhizal partners. Also, while vegetation with AM covers more land and has higher biomass, EcM fungi contribute relatively more to the soil carbon pool (%NPP and carbon flux values from this study). (C) Carbon remains in the form of fungal necromass, acting as a scaffold for soils. Also, mycorrhizal fungi produce compounds that help retain carbon in the soil including exudates, and chitin or melanin in hyphae, where especially small organic compounds become bound and stabilized on mineral surfaces. (D) Carbon is lost during soil respiration and decomposition of organic matter, and may also be re-fixated anapleurotically, remain in the soil, or be released into the atmosphere. While more data are required, the relative width of arrows is based on values from this study (%NPP) or the available literature (respiration/re-fixation[68,137,138,148–151,153]; decomposition[155,156]). Question marks indicate a lack of data. Abbreviations: AM (arbuscular mycorrhizal fungi); EcM (ectomycorrhizal fungi); ErM (ericoid mycorrhizal fungi).

estimate is surprisingly similar to the approximation (based on only a few studies) of 5 Gt C yr^{-1} (~18 Gt CO_2e per year) made by Bago *et al.* in 2000[102]. Our 13.12 Gt CO_2e per year estimate equates to ~36% of anthropogenic CO_2 emissions from fossil fuels in 2021 (Table 1), which includes global combustion- and industry-related emissions such as for electricity and heat, industry, transport and building[103].

Mechanisms by which mycorrhizal fungi affect carbon storage in soils

To better understand how soil carbon sequestration is influenced by mycorrhizal pathways (reviewed by Frey *et al.*[104]), we explore three main mechanisms by which these fungi increase carbon in soils. We follow this with a discussion of the ways in which carbon is lost through mycorrhizal turnover, decomposition, and respiration.

Carbon is used to build and support an active mycelial network

Vegetation with different mycorrhizal types store different amounts of carbon[46]. Specifically, AM-associated vegetation covers more land and has greater aboveground biomass (241 Gt C) than that of EcM- (100 Gt C) or ErM-associated (1.8 Gt C) vegetation (Figure 3A)[46]. Non-mycorrhizal associated plant biomass stores 8-fold less global carbon (29 Gt C) than AM-associated vegetation[46]. As our data synthesis has shown, some of the plant's non-biomass carbon is used by mycorrhizal fungi to build hyphae and support their active mycelial networks[105], which draw plant-fixed carbon down into the soil matrix (Figure 3A,B). While AM are more ubiquitous, NPP allocation to the EcM mycelium is higher than that of AM. This

means that, overall, EcM fungi contribute relatively more to the global soil carbon flux, according to our estimates (Figure 3B).

As obligate biotrophs, AM are dependent on host plants for their carbon requirements[102]. This means that all carbon used to grow their networks is directly supplied by their host plants. Arbuscular mycorrhizal fungi can grow extensive hyphal networks — for example, AM hyphae found in prairie soils reached total lengths greater than 100 meters per cubic centimeter of fresh soil, and a hyphal dry weight of ~ 0.5 mg per gram of soil[69]. Drawdown of plant-fixed carbon can be proportional to hyphal density[106]. The AM networks are aseptate, meaning they are essentially open pipe systems, with no septa breaking the cells into individual compartments. In one laboratory study of root organ cultures, carbon was observed to flow away from roots within AM hyphae at velocities up to 80 μm per second[107].

As mycorrhizal networks grow, they move carbon away from the rhizosphere soil to areas of lower respiratory activity[108]. Simultaneously, the fine filamentous hyphae foraging for nutrients become attached to soil particles, which helps create and stabilize soil aggregates that protect soil organic matter from decomposition[108] (Figure 3B). Arbuscular mycorrhizal hyphae may have relatively short life spans[71], but a healthy network can make up anywhere from 20–50% of the total living microbial biomass in temperate grasslands[109].

Ectomycorrhizal hyphal biomass can comprise over 30% of total soil microbial biomass[110], with even more extensive mycelial networks than AM fungi, reaching up to 2000 m per cubic centimeter of fresh soil[59], with colonized root tips that can persist in the soil for months[93]. Ectomycorrhizal fungi can be classified as obligate biotrophs because their capacity to decompose lignocellulose is downregulated compared to saprotrophs, and they are likely 'coincidental decomposers', releasing carbon from soil organic matter only as a by-product of acquiring nitrogen[41,111]. Therefore, we can expect that, under some conditions, their hyphal masses are almost entirely comprised of plant-fixed carbon. While exact estimates of extraradical hyphal lengths vary widely and have been shown to be affected by fungal taxa, plant host, and soil conditions, these fungal structures are a key contributor to soil carbon inputs[108,112]. Measuring the physical extent of fungal hyphae belowground remains a challenging but important step for understanding mycorrhizal impacts on soil carbon fluxes.

Carbon remains in the form of fungal necromass, acting as a scaffold for soils

When mycelium dies, it becomes fungal litter or 'necromass' (Figure 3C). This dead tissue leaves a complex scaffold of organic material. Although the network no longer draws down carbon from a plant partner, the enmeshed necromass helps to form and stabilise soil aggregates. As soil particles attach to these scaffolds, soil aggregate size increases and organic matter becomes increasingly protected from decomposition, stabilizing soil organic carbon[113]. Some have argued that fungal necromass could contribute considerably more to pools of soil organic carbon than living fungal biomass[104,114] and can exceed that from plant litter[70]. Recent research has demonstrated that AM and EcM fungi differ markedly in chemical composition, and thus likely in decomposability[115–117]. Some hyphal components like chitin are relatively labile[118], while large nonhydrolyzable components like melanin[119] impede decomposition of fungal residues and enhance mycorrhizal necromass accumulation[120,121] (Figure 3C). The fast turnover rate of AM hyphae leaves large amounts of chitin in the soil[122]. While less recalcitrant than previously thought[118], chitin may help slow decomposition. Early successional EcM fungal species have been associated with rapid turnover of mycelial biomass, whereas later successional EcM and ErM fungi have been linked to long-term humus build-up through production of melanized hyphae[123]. Thus, changes in fungal communities could shift belowground carbon storage patterns. Mycorrhizal necromass turnover is yet another important and poorly understood variable affecting mycorrhizal fungal contributions to the global carbon budget.

Mycorrhizal fungi exude compounds that help retain soil carbon

Mycorrhizal hyphae growing through soil environments release exudates (Figure 3C), including low-molecular weight sugars and organic acids[124]. These carbon and nitrogen containing exudates are used and immobilized by other soil microbes, and this carbon can subsequently form the most stable soil carbon pool — mineral-associated organic matter[125] (Figure 3C). The attachment of this carbon to mineral surfaces protects it from microbial degradation within soil aggregates[104]. For example, aromatic metabolites secreted by a common ectomycorrhizal symbiont, *Paxillus involutus*, have been shown to enhance the formation of mineral-associated organic matter[126]. There is increasing evidence that fungal residues play an important role in forming stable soil organic matter[127], and may contribute more to mineral-associated organic matter than plants[128,129].

Glomalin-related soil proteins are thought to be sticky glycoproteins associated with increased soil aggregate size and stability, soil water holding capacity, and rhizosheath formation, and are a direct means of increasing soil carbon[122,130,131]. However, there is criticism that glomalin-related soil protein isolation methods result in a variety of compounds that may be indistinguishable from fungal necromass[113], questioning whether glomalin-related soil proteins are even a direct metabolic product of AM[132].

Plant exudates of energy-rich organic compounds, which were thought to be primarily released from root tips into the rhizosphere, are also rerouted through AM hyphae before entering the soil[133]. This means mycorrhizal hyphae are a conduit for a substantial amount of plant-derived exudates that need to be considered in carbon cycle dynamics, especially because plants allocate up to 17% of NPP, and 20–40% of recently fixed photosynthates to root exudates[134,135]. Large amounts of these exudates are released into the rhizosphere, where they can stimulate bacterial growth, activities that increase mineralization and nutrient availability[133,136].

Mycorrhizal fungi respire and play a role in decomposition resulting in soil carbon loss

Mycorrhizal fungi are an important route for plant carbon to enter the soil, but losses will occur via fungal respiration and decomposition. (Figure 3D). Field studies show that fungal respiration makes up a variable portion of soil respiration (e.g., 6–14% for AM[137–139]; 6–25% for EcM[140–142]), and comprises a substantial fraction of autotrophic (roots plus fungus) respiration (e.g., ~25% for AM[137,139]; 35–40% for EcM[140,143]). In the growing season, arctic trees and their associated EcM fungi contributed more (43–53%[144,145]) to soil respiration compared with ericoid shrubs and their associated ErM (11%[145]). However, EcM also

seem to suppress soil respiration by competing with free-living decomposers for nitrogen[146,147]. Fungi return small to large amounts of plant-derived carbon back to the atmosphere (<1%[137]; 4–6%[138,148] for AM; 1–8%[68,149,150] up to 14–19% for EcM[151]). Annual AM hyphal respiration rates can vary widely — 1–32 mg C per square metre per hour in a tropical forest[139]; 25 mg C per square metre per hour in mesocosms[152]; and 11 mg C per square metre per hour in pot culture (recalculated from[137]). In the AM forest example, substantial amounts of carbon (0.14 kg C m^{-2} yr^{-1}) were returned to the atmosphere[139]. Fungal respiration is highly dependent on species, the environmental conditions, and the availability of photosynthate[137,138,140,141]. Besides efflux to the atmosphere, soil respired carbon can also remain in the soil, or even be re-fixed anapleurotically by roots or microbes[153] (Figure 3D).

The decomposition of old soil carbon by the addition of new soil carbon is called 'priming'[154], where this new carbon may include fungal exudates and necromass. Priming occurs consistently across ecosystems and is increased or decreased by carbon and nitrogen addition, respectively[154]. Mycorrhizal fungi may increase[155] or decrease[156] priming, but generally increase it to a lesser extent than roots, for example, by one-tenth (AM) to one-fifth (EcM)[155]. Some studies have found that AM marginally increased priming compared with EcM, which has been linked to the relatively larger amounts of AM-derived extracellular, carbon-degrading enzymes that break down root exudates[155]. However, soil type, soil C:N, and season seem to be more important in driving priming than commonly proposed mechanisms (changes in microbial biomass/turnover, extracellular enzyme activity or microbial C-to-N ratio)[154]. No single unifying mechanisms for priming has yet emerged, possibly due to the diverse substrates for decomposition[154]. Finally, relatively high leaf litter and fine root turnover[157] have been linked to both relatively high soil carbon accumulation and soil respiration[157]. This hints at a trade-off between soil carbon storage and loss and may well apply to hyphal turnover. We found no studies that account for all carbon fluxes (inputs and outputs) and pools (and their turnover) associated with mycorrhizal fungi and their colonized roots, so this remains a major research challenge.

A global understanding of mycorrhiza as a carbon sink requires a more complete and nuanced quantification of pools and fluxes

Our %NPP measures are imperfect initial estimates based on the best available evidence and should be interpreted cautiously. We hope that our caveats reveal the urgent need for further empirical study of carbon and nutrient fluxes in mycorrhizal systems. These estimates are, for the most part, based on single time point measurements, and may not reflect the carbon dynamics of the symbiosis over the plant's life cycle. For instance, carbon allocation in grain crops switches from investment belowground to aboveground (inflorescence and grain filling) over time, and some plants even go so far as to seasonally oscillate between mutualism and mycoheterotrophy (e.g., *Ophioglossum vulgatum*[158]). Also, needleleaf trees may have relatively low instantaneous photosynthetic rates, but have longer growing seasons than many broadleaf trees[159]. Thus, our estimates could represent peaks or troughs of carbon allocation to fungi, depending on plant habit and/or which stage of the plant's life cycle the experiment was conducted. Therefore, a key overall question remaining is whether mycorrhizal fungi constitute a considerable carbon sink once all carbon stocks and flows have been accounted for.

All measures were based on extraradical hyphae alone, which means that actual carbon fluxes to symbiotic mycorrhizal fungi may be far higher (again at certain plant growth stages). This is because methodological constraints meant that we did not include sporocarps, fungal exudates, and hyphae inside the roots. While taxonomic differences occur[160], the biomass of intraradical mycelium, at least for AM, can be four times the biomass of hyphae in soil[161]. Improved quantification of the carbon stocks and flows from plant-fixed carbon to all structures of the mycorrhizal symbiont, through to respiration, decomposition, mineralization, and eventual association with the soil fraction will help form a more complete understanding of mycorrhizal fungi and carbon cycling (Figure 3). This includes improved estimations of fungal biomass (including intraradical biomass), necromass, and exudates. Identifying these carbon stocks remains a technical challenge for tracer studies, especially under field conditions.

We found high variability of %NPP allocation estimates, even within mycorrhizal functional types. The sources of variation for these estimates likely include different experimental approaches, plant age, plant growing conditions, and symbiont physiology. In addition, the estimates for the mycorrhizal functional types of OM, DSE, and ErM fungi were based on too few studies to be interpretable. Importantly, our dataset suffered from a lack of representation across different landcovers per mycorrhizal functional type — specifically those from tropical and temperate forests, savannas, grasslands, and Mediterranean areas, particularly of the global south. The EcM diversity in tropical and southern temperate ecosystems is particularly understudied[40].

Even if we were able to include all fungal tissue types and could assemble a representative dataset, our estimates would still underestimate the full impact of mycorrhizal fungi on global carbon cycling because of their significant indirect influence. For instance, mycorrhizal fungi are conduits for the release of plant root exudates into the soil, which play an important part in soil carbon cycling[162]. In addition, mycorrhizal fungi indirectly increase carbon drawdown into inorganic carbon via weathering — a process that plays an important part in regulating the composition of the Earth's atmosphere[38]. Acidic exudates and protons released by plant roots and mycorrhizal fungal hyphae weather soils and the resulting carbonates and cations draw atmospheric CO_2 down into soil as calcium or sodium carbonate[37,163].

Further, most studies on mycorrhizal fungi quantify carbon allocation patterns to single mycorrhizal types and even single fungal species, or strains. These results are unlikely to be representative of ecosystems such as temperate forests, which consist of trees that associate with mixed communities of mycorrhizal types[78]. Here, the relative abundance of mycorrhizal type may affect root exudates[128] and shift patterns of soil carbon storage[23,78]. Another key future challenge is therefore to explore the effects of mixed mycorrhizal communities on ecosystem level carbon storage.

Finally, our estimations present fluxes of carbon into the compartment of mycorrhizal fungi, but we did not assess the

losses of carbon from fungal necromass through soil respiration processes. Large parts of the carbon allocated into fungi is probably lost through this efflux. Thus, our calculations provide an estimation an influx of CO_2 into the soil fungal biomass, while the duration of stay of this carbon in soil, and the intensity of efflux remain to be estimated in future research efforts.

Conclusion

Mycorrhizal fungi are a major global carbon pool, drawing an average of ~3–13% but up to ~50% of a plant partner's NPP belowground when hosts are associated with the main mycorrhizal types. We estimate a flux of ~13 Gt of CO_2e moves through plants into carbon that is allocated to mycorrhizal mycelium every year. Methodological limitations mean that this figure may over- or underestimate the total sum of carbon that moves from plants into soils via mycorrhizal pathways. Nonetheless, our study confirms the significant contribution made by mycorrhizal associations to global carbon fluxes and should motivate an inclusion of mycorrhizal fungi both within global climate and carbon cycling models, and within conservation policy and practice[164].

DATA AVAILABILITY

This review adheres to FAIR data. Associated data and code are available at https://doi.org/10.5281/zenodo.7286515. Further information and requests for resources should be directed to and will be fulfilled by the lead contact, H.-J.H. (heidi.hawkins@uct.ac.za).

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AUTHOR CONTRIBUTIONS

E.T.K. and R.I.M.C. conceived the ideas in discussion with all authors, R.I.M.C. and H.-J.H. collected the data, N.A.S. assisted in conceptualization of the data collection, H.-J.H. analyzed the carbon allocation data, K.J.F. contributed data, M.E.V.N. and S.H. collected and analyzed spatial data, H.-J.H., K.J.F., M.E.V.N., R.I.M.C., and E.T.K. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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