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Will fungi solve the carbon dilemma?

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ABSTRACT

Soils are hotspots of diversity and sustain many globally important functions. Here we focus on the most burning issue: how to keep soils as carbon sinks while maintaining their productivity. Evidence shows that life in soils plays a crucial role in improving soil health yet soil ecological processes are often ignored in soil sciences. In this review, we highlight the potential of fungi to increase soil carbon sequestration while maintaining crop yield, functions needed to sustain human population on Earth and at same time keep the Earth livable. We propose management strategies that steer towards more fungal activity but also high functional diversity of fungi which will lead to more stable carbon sources in soil but also affects the structure of the soil food web up to ecosystem level. We list knowledge gaps that limit our ability to steer soil fungal communities such that stabilising carbon in top soils becomes more effective. Using the natural capacity of a biodiverse soil community to sequester carbon delivers double benefit: reduction of atmospheric carbon dioxide by storing photosynthesized carbon in soil and increasing agricultural yields by restoring organic matter content of degraded soils.

1. Introduction

"*A nation that destroys its soils, destroys itself*", the legendary quote of Franklin D. Roosevelt in 1937 just after the Dust Bowl, the great depression in the United States of America. Severe droughts at America's great plains combined with overexploitation by agricultural practice at times when artificial fertilizer were not yet on the market created wind erosion (dust storms) of the top soil and desertification of large areas of agricultural land. For the first time, people experienced that intensive management of the land and resulting loss of the valuable organic layers of soils can lead to famine. Once desertification starts to happen it is hard to reverse (Allington and Valone, 2010). The wide application of artificial fertilizer just after the Second World War increasing the productivity of crops across the world made us forget this quote (Stewart et al., 2005). However, after years of population growth and prosperity, we face yet another great challenge: global climate change Climate change leads to global temperature rise, seawater rise, increased and prolonged drought periods followed by other extreme weather events such as heavy snow or rainfall leading to floods in delta areas (IPCC, 2019). To make things worse, we have overexploited our croplands and grasslands to feed the growing world population (Montanarella, 2015; Panagos et al., 2019). Ultimately, artificial fertilizer diminished nitrogen and phosphorous shortages in crops, but did not replenish organic material harvested as crop biomass (Sanderman et al., 2017). Due to resulting carbon loss, trace minerals and nutrients can leach out more readily because of a lack of charged binding sites in the top soil offered by soil organic matter (Blume et al., 2016).

Soils are full of life and this life in soil provides many ecosystem services, which can be coined with the term soil multifunctionality (Maestre et al., 2012; Wagg et al., 2014). These functions modulated by soil life include nutrient cycling, carbon storage and turnover, water maintenance, soil structure arrangement, regulation of aboveground diversity and productivity, biotic regulation, buffering, and the transformation of potentially harmful elements and compounds (Blume et al., 2016). Soil diversity is also a reason to protect soils: it is a much unexplored resource of genetic potential, for example a source of novel antibiotics produced by soil bacteria (Tyc et al., 2014).

In this perspective we focus on one of the most burning issue facing the soils: namely how to keep the organic material in soils while maintaining their productivity. Soils have an enormous potential to store soil organic carbon (SOC) for long time periods (Lal, 2004; Keesstra et al., 2016; Minasny et al., 2017) and soil carbon can be several

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hundred years old (von Lützow et al., 2006). Furthermore, soils are the largest organic terrestrial carbon pool (Scharlemann et al., 2014). Fossil fuel and rocks form the long carbon cycle, while photosynthesis by green plants and algae, respiration and litter decomposition along with wild fires form the short carbon cycle (Archer, 2010) Besides soils, also oceans, sediments, and plants are large sinks of carbon (Avelar et al., 2017; Bastin et al., 2019). The carbon stocks in oceans and sediments are considered difficult to control (Avelar et al., 2017). However, through proper management, we can control the soil carbon stock and significantly increase the amount of carbon in soils (Hungate et al., 1997; White et al., 2000). Unfortunately, we are hampered by our limited understanding of the mechanisms that control stabilisation of soil carbon to determine proper management.

Our natural ecosystems are deteriorating at a faster rate than ever before (Díaz et al., 2019). In terrestrial systems we can see the decline in iconic large species, mainly top-predators and species with a narrow niche. Belowground we are only recently uncovering the massive diversity of micro-organisms and the network of interactions in which they function (Bahram et al., 2018). It is estimated that only 0.01% of the microbial world is described (Locey and Lennon 2016) and we know little about their ecology (Baldrian, 2019). Most organisms in soils play crucial roles in storing carbon, recycling carbon and retaining/mineralising nutrients for plant growth, which provides humans with the food necessary to sustain our ever growing world population (Bardgett and van der Putten, 2014; Delgado-Baquerizo et al., 2020; Kopittke et al., 2022). Yet, in human-induced agricultural systems soil life is often considered as something we want to limit and measures like biocides and soil steaming are applied to kill most of the soil life (Zaller et al., 2014)

2. Importance of soil life for crop growth and carbon stocks

Intensive agriculture has contributed substantially to the increase in crop production needed to feed the growing world population (Tilman et al., 2011) and currently, agricultural and pasture land represent over 40% of the Earth's land surface (Foley et al 2005). Agricultural intensification has led to major problems such as the loss of soil organic carbon (SOC), resulting in decline in soil fertility (Tilman 1998). Many current agricultural practices have negative impacts on the environment. The raw fertilizer resource in the case of P-mining is being rapidly depleted or requires a large energy input in the case of N-fixation. At the same time using inorganic fertilizer results in loss of soil organic matter as it is used up by crop growth but not restocked, and as a result also ultimately results in nutrient loss due to leakage to groundwater because of a lack of nutrient binding sites in the top soil (Food and Agricultural Organization (FAO) of the United Nations, 2012; Blume et al., 2016). Consequently, soil organic pools that took thousands of years to form can be lost in decades (DeLong et al., 2015). Furthermore, agricultural soil management practices such as tillage and use of inorganic fertilizers bypass beneficial soil biota and results in increased pest and pathogen outbreaks (Fisher et al., 2012) at the same time decreasing the biomass and the diversity of mutualistic and saprotrophic (i.e. decomposer) fungi found commonly in natural soils (Hannula et al., 2010). This all leads ultimately to reduced soil biodiversity (Tsiafouli et al., 2015), resulting in a decline of multiple ecosystem functions related to C and N cycling (de Vries et al., 2013; Wagg et al., 2014), and is clearly not a sustainable strategy (Foley et al., 2005). In order to reach the climate mitigation goals set by COP21 (Global Climate Change Agreements), we need to investigate how we can use our soils and the organisms residing in them in the most sustainable way possible.

To keep carbon and nutrients in the soil, it is suggested to reduce tillage, use complex crop rotation schemes, apply cover crops during crop-free periods, and leave crop residues on the surface of the soil (Freibauer et al., 2004; Janzen, 2015; Bowles et al., 2017). All these management strategies potentially act through changes in the soil fungal community composition and steer the structure of the whole soil food web (Jansson et al 2021). For example, soil tillage breaks down connections in fungal hyphal network thus reducing the capacity of soil fungi to store carbon (Conant et al., 2007; Wang et al., 2010; Anderson et al., 2017) while at the same time changing the soil food -web and affecting other organisms directly or indirectly (Morriën et al., 2017). Furthermore, inversion tillage also disturbs natural community physical zonation of microbes by homogenising microhabitats in the top 30 cm soil. On the positive side, a diversified crop rotation restores the diversity of fungal communities (Ellouze et al., 2014; Mariotte et al., 2018) cover crops further diversify and increase the quantity of organic inputs (Detheridge et al., 2016), and organic amendments increase fungal biomass and soil organic matter (SOM) stabilisation due to more microbial growth and activity in the top soil by improving soil structure (Lucas et al., 2014; Rahman et al., 2017; Clocchiatti et al., 2020). Using the capacity of a healthy and biodiverse soil fungal community to sequester carbon in the soil can deliver double benefit: reduction of the rate of climate change by storing photosynthesized carbon in soil as SOC from plant litter or -exudates and as fungal necromass, -exudates and -residues, and increasing agricultural yields by restoring the organic matter content of degraded soils (Minasny et al., 2017; Chenu et al., 2019). However, little is known about how agricultural management influences the soil fungal community in a way that results in both enhanced carbon sequestration and, simultaneously, ensures high crop yields and other soil functions.

In previous research, it is shown that the management of grassland systems affects fungal community composition (i.e. species assemblage of fungi actively using plant derived carbon) and function (Hannula et al., 2017; Hannula et al., 2020). These impacts on fungal communities in turn impact fungal-feeding organisms and cascade through the soil food web, leading to a more efficient cycling of nutrients and storage of carbon (Morriën et al., 2017). Here, we propose that for soils used for agriculture, very similarly to grass-based systems, the shifts in fungal community composition and following shifts in fungal food-web channel leads to improved soil 'health'. Soil health is a term that can be interpreted in many ways (see for example Fierer et al., 2021), but is traditionally related to crop growth (Lehmann et al., 2020a). Here we use the term for increase in soil organic carbon (SOC) as this is in our opinion the fuel for microbial activity, one of the best measures of actual soil health (Schjønning et al., 2018). In the grassland systems, and potentially also in arable soils, stimulation of the fungal food web channel leads to an increase in fungal feeders such as collembola (springtails), mites and fungal feeding nematodes, and their predators (Neher and Barbercheck, 2019). Increases in mesofauna (and macrofauna) increase the spatial distribution of (plant beneficial) microbes and improve soil structure through bioturbation (Lavelle et al., 2006) (Fig. 1). An increase in the abundance and relative dominance of beneficial fungi in agricultural systems will have positive implications for net ecosystem carbon exchange, mineralization and sequestration as well as plant productivity and eventually yield (Fig. 1) constituting to the main ecosystem services of arable soils (de Vries et al., 2013; Wagg et al., 2014).

3. Soil carbon stabilisation

Organic carbon enters the soil via three pathways: in recent photosynthetic products of plants secreted as root exudates, dead shoot- and root plant material, and via added organic amendments (Fig. 2, number 1). Root exudates form the largest pool of carbon entering the soil (Nguyen, 2009) and up to 20% of carbon in root exudates enters rhizosphere via mycorrhizal fungi Canarini et al., 2019). There are three highly variable components that are essential for carbon stabilisation: 1) the nature of the molecules in which the carbon occurs, 2) the vegetation, microbial activity and necromass, and 3) the soil structure (Blume et al., 2016). Besides the more inert properties like soil type (sand-, silt-, clay- percentage and soil forming processes and environmental properties (i.e. pH, moisture, temperature, parent material (mineralogy)

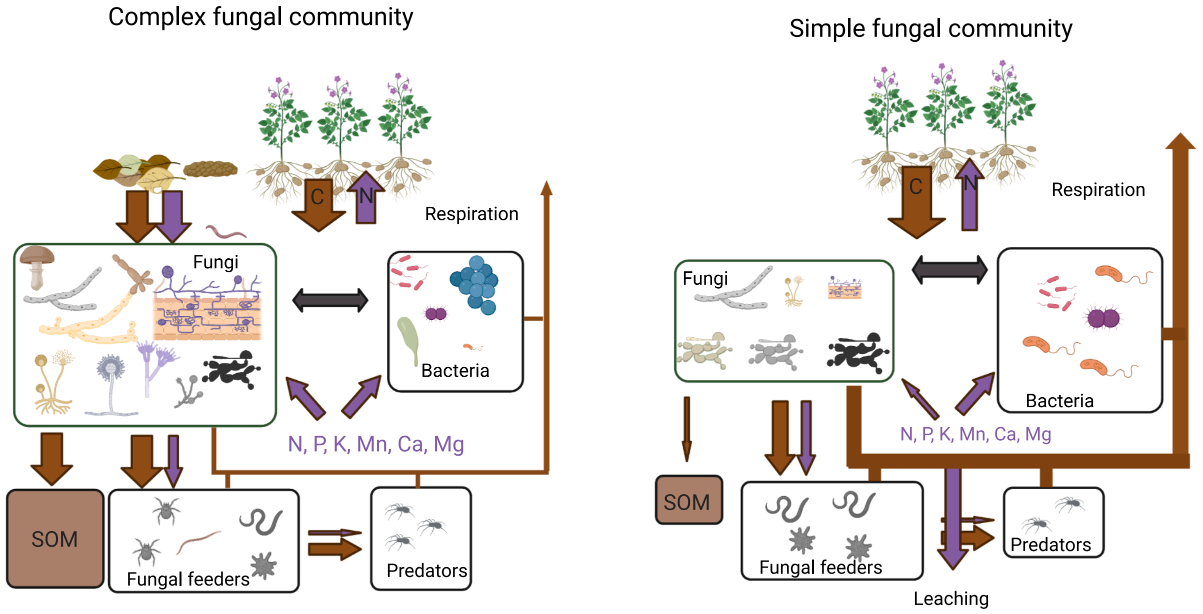

Fig. 1. Schematic diagram of carbon (black) and nutrient (purple) flow between the plant, soil organic matter and soil food web in complex fungal communities (high trait diversity) in croplands (fungal channel stimulated) and simple fungal communities in cropland soils (fungal channel not stimulated, poor trait diversity). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

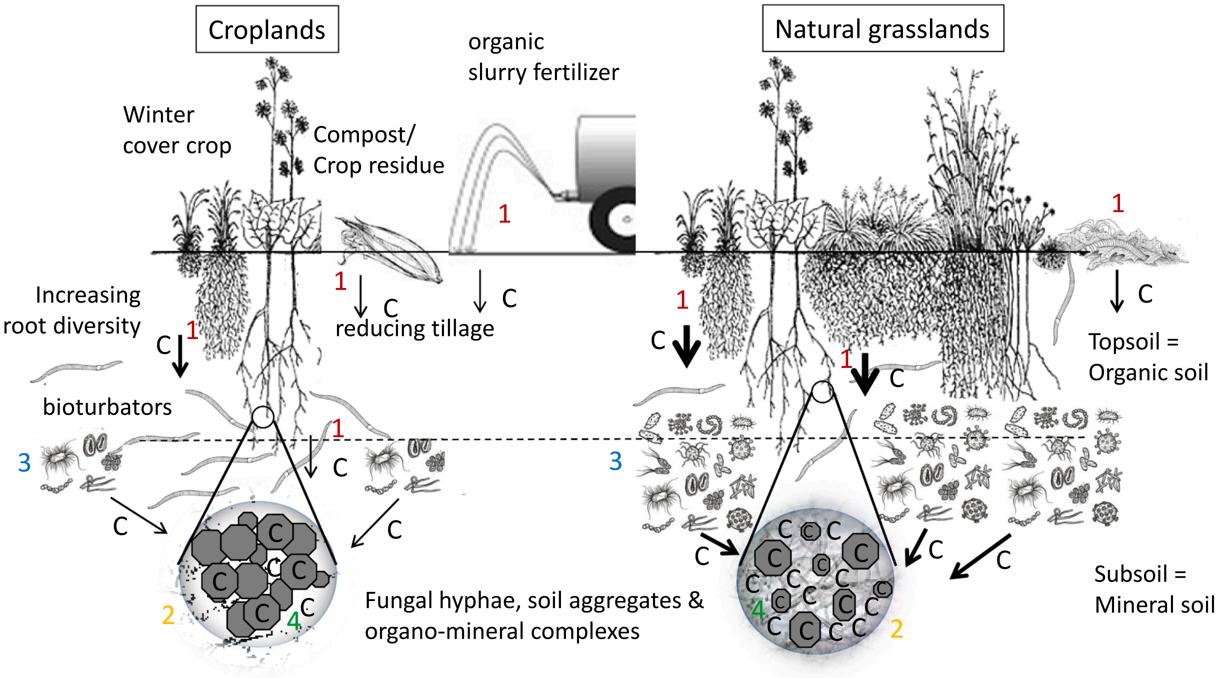

Fig. 2. Conceptual figure of carbon flows towards stable pools in croplands versus natural grasslands. Number 1 represents carbon input. Number 2 represents carbon in, on and around soil aggregates whereby aggregate size variation and pore space as well as hyphal density is larger in natural grasslands then in croplands. Number 3 represents the involvement of soil biota in carbon stabilisation where there is a more diverse microbial community in natural grasslands than in croplands. Number 4 represents the fungal hyphal density in the enlargement circle, which is larger and more dense in natural grasslands then in croplands.

determine the degradability of the carbon (Wiesmeier et al., 2019). Carbon can be stabilised in soils due to physical protection against further degradation by microbes in soil aggregate (Fig. 2, number 2) (Six et al., 2000) or due to binding to the organo-mineral fraction (Fig. 2, number 2) (Sokol et al., 2019), mainly by clay particles or by complexation into FeOH/AlOH-complexes in calcium-poor soils (Singh et al., 2017). However, we lack understanding how occlusion of organic matter in aggregates may be increased, or how organic matter is being deposited at microhabitats in the soil where complexation is maximized.

In the last 10 years a paradigm shift has occurred in our understanding of the carbon stabilisation processes. Until a decade ago it was thought that molecular structure determined the rate of microbial degradation. The chemical complexity of molecules is likely less important for soil carbon storage than previously thought (Lehmann and

Kleber 2015). Experiments performed outside the laboratory show that supposedly stable carbon structures can sometimes be easily broken down into bioavailable substrates while carbon in simple molecules might persist (Schmidt et al., 2011; Dungait et al., 2012). This sheds new light on how carbon is being stored in soils. Substances such as lignin, conventionally regarded as one of the most complex molecules from plant materials, can be degraded by specialised (i.e. lignolytic) fungi already in early decomposition stages (Klotzbücher et al., 2011). This means that the molecular structure of complex carbon molecules might be less resistant to chemical breakdown *in situ* in soils than previously thought. Therefore, microbial transformation of C inputs into microbial products and necromass may be as important as the effect of soil mineral structure on soil carbon stabilisation and much more important than the molecular complexity of the substrate (Kleber et al., 2015; Kaiser et al 2016a; Woolf and Lehmann 2019).

Soil structure is the last but equally crucial component that determines soil carbon stabilisation. Soils are formed as a complicated 3D structure, with aggregates of varying sizes, of which the surface is colonised by fungi and bacteria (Woolf and Lehmann, 2019), and with pores in between. Plants stimulate soil pore formation. Diverse plant communities root more and deeper compared to monocultures and therefore favour the development of 30–150 um pores (Fig. 2, Natural grasslands; Kravchenko et al., 2019). At the same time such pores are micro-environments associated with higher enzyme activities and a greater spatial footprint of micro-organisms (Kravchenko et al., 2019). Therefore, pore formation by plant roots and fungal activity are hitherto, unrecognized determinants of whether new carbon inputs are stored or lost to the atmosphere (Keiluweit et al., 2017; Yang et al., 2019). This labyrinth of pores and aggregates determine whether inputs of organic carbon material from the plants can be degraded by microbes because they are in direct contact with the organic source or their enzymes can reach the organic material. The surface of these aggregates thus forms a hotspot of microbial interactions and decomposition (Kuzyakov and Blagodatskaya 2015). Currently, our knowledge on the effects of roots, soil fauna and microbes on soil pore formation and the effects of the pores on the biota is limited. Similarly limited is our knowledge about the dynamic role of soil fungi in soil aggregate formation and vice versa (yet see Lehmann et al., 2020b).

4. Increasing soil carbon stocks

We have earlier presented ways to stimulate soil fungal biomass in agricultural systems by changing the soil management levels: the consensus is that extensive or regenerative farming usually favours the fungal channel and enhances the carbon accumulation (de Vries et al., 2013; Clocchiatti et al., 2020). Another way to enhance fungi is through selection of plant species promoting associations with fungi and especially plant species diversity which has a double benefit: it increases both above-ground and below-ground diversity (Mommer et al., 2018). If we want to stimulate fungal biomass and necromass, we need to increase plant diversity both in spatial and temporal scales. At the same time, growing higher plant diversity results in more root biomass due to overyielding effects and root differentiation (Hendriks et al., 2013). This results in more root exudate input which leads to more microbial biomass (Fig. 2, number 3) and consequently more microbial necromass (Prommer et al., 2020; Kallenbach et al., 2019) (Fig. 3). If microbial Carbon Use Efficiency (CUE, i.e. amount of carbon that is used for microbial growth compared to the carbon uptake) is high, more carbon is incorporated into microbial tissue, relative to the amount of carbon respired (Woolf and Lehmann 2019). Fungi generally have a higher CUE than bacteria (Allison et al., 2005; Keiblinger et al., 2010). However, the argument that fungi grow more efficiently than bacteria has been challenged quite extensively over the years (e.g. Thiet et al., 2006; Rousk and Frey 2015; Anthony et al., 2020). Yet we know that greater fungal biomass increases CUE and in turn SOC formation (Kallenbach et al., 2016). Moreover, fungi contribute approximately 20% more to C storage in agricultural soils compared to bacteria (Liang et al., 2019). In short, more fungal biomass leads to more fungal necromass (Figs. 1 and 2 (number 4)) which favours more stable carbon storage (Fig. 3) (Anderson and Domsch, 2010).

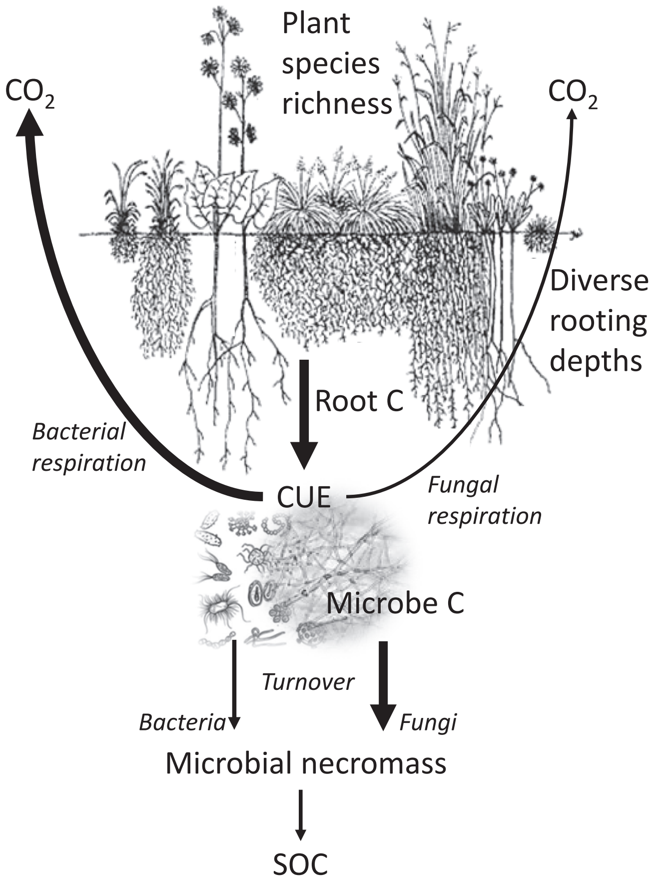

Fig. 3. Schematic figure showing the relation between plant species richness, root C exuded by plants which fuels microbial growth and respiration. The microbial carbon use efficiency (CUE) determines how much root C ends up in the microbes (mostly fungi). Unknown is how fungi can actively sequester C in stable organic carbon (SOC) pools. Also not entirely clear is yet how and at which rate fungal necromass with root C ends up in the SOC pool.

CUE does not only depend on microbial identity, but also on the nature of the substrate. Microbes have a higher CUE when they use input from root exudates, consisting mostly of simple sugar molecules (Strickland et al., 2015) compared to more complicated organic molecules from litter input. So counterintuitively, simple carbon compounds can thus lead to stabilized carbon in the soil if the CUE is high (Fig. 3) (Kallenbach et al., 2016; Liang et al., 2019). Therefore, using mixed crops, or deep-rooting crops in combination with amendments that stimulate growth of mainly saprotrophic fungi, will enhance carbon stock in agricultural systems.

Grasslands store more soil carbon in the mineral-associated organic matter (MAOM) fraction (<53 μm) than in the particulate organic matter (POM) fraction (53–2000 μm). The MAOM is generally more persistent and has a higher nitrogen content (Jilling et al., 2018). This is a consequence of microbial pre-processing, which results in a mix of plant-derived material and microbial residues (microbial tissue has a higher nitrogen content than plant derived material). Because of the high N demand of microbes the MAOM fraction probably consists of organic matter residues of high quality (relatively high N to C than litter-derived material only) (Lavallee et al., 2020). The MAOM fraction cannot store more once saturated (Fig. 2, fractions bound to particles (number 4)). The carbon saturation theory (Castellano et al., 2012) suggests that the proportion of new C inputs that can be stabilised in the MAOM fraction decreases in proportion to the amount of C already present in that fraction, following a saturation curve (Castellano et al., 2012).

Ectomycorrhizal forests store more carbon as POM on and in soil aggregates (occluded POM (oPOM)), which is more vulnerable to microbial degradation, but these residues are less processed by microbes due to the lower nitrogen content. Any remaining straw-containing residue from crops can end up as POM (Cotrufo et al., 2019). Moreover, this fraction of oPOM inside aggregates can potentially accumulate indefinitely as it is not dependent on surface charge, but is dependent on factors involved in aggregate stabilisation (Cotrufo et al., 2019; Witzgall et al., 2021). The division of carbon between MAOM and oPOM together with microbial activity, which is temperature and fresh carbon input dependent, determines soil carbon stocks (Cotrufo et al 2019).

Understanding the physical distribution of organic matter in pools of MAOM versus POM can inform land management for optimal carbon sequestration, which is also dependent on stoichiometry of available nitrogen : phosphorous : sulphur, which can vary and depend on soil type, land use and inputs (Buchkowski et al., 2019). Therefore, binding to the MAOM fraction could be optimised by setting the right abiotic conditions due to optimisation of the surface charge of these minerals such that organic matter can bind to these mineral particles onto which also other organic parts could sorb even better than on ‘empty’ sites, also called the onion-layering model (Sollins et al., 2006). The part where most leverage is possible is the POM. Although litter derived POM increases microbial priming effects, it also heavily increases microbial biomass and necromass in hotspots on the POM surface (Wang et al., 2021). Due to this high activity it stimulates aggregate formation due to the production of extracellular polymeric substances (EPS) and hyphal enmeshment. These form POM with a higher necromass component and are more stable (Witzgall et al., 2021) but also leads to more aggregate formation which then leads to more oPOM from litter-derived origin. In this way increasing POM could still lead to more stable SOC. However due to the low carbon stocks in some agricultural fields this also leaves room for MAOM improvement in order to promote agricultural C sequestration and manage towards increasing stable carbon in soils. Focusing on POM is most suited for soils with already high soil C levels whereas focusing on POM and MAOM together is important in soils with low C availability (Witzgall et al., 2021). Increasing soil carbon in agricultural systems would in our opinion not lead to nutrient shortages for crops, because nutrients are often provided in these systems, but rather to a better sorption of nutrients which protects the soil from nutrient loss through leaching. More evidence on the origin and stabilisation of MAOM and POM and the interaction with microbial activity is rapidly accumulating.

5. Manipulating organic matter flows

Microorganisms are critical in terrestrial carbon cycling because their growth, activity, and interactions with the environment largely control the fate of recent plant carbon inputs as well as protected soil organic carbon (Schimel and Schaeffer 2012). Soil carbon stocks reflect a balance between microbial decomposition of organic carbon and stabilisation of microbial assimilated carbon. The balance can shift under altered environmental conditions (Davidson and Janssens 2006).

Selective pressures from suboptimal environmental conditions (very low pH, drought, lack of fresh carbon input) to optimal environmental conditions for most microbes (near to neutral pH, moist soil, fresh carbon input) could lead to greater allocation from maintenance driven energy transfer in microbes to growth driven energy transfer in microbes (Kaiser et al., 2016b; Větrovský et al., 2019). The first creates potential carbon loss due to respiration by microbes while the latter may lead to carbon stabilisation due to investment in microbial biomass (Prommer et al., 2020). Microbial characteristics influence these processes, thereby impacting soil carbon cycling (Fig. 1). Identifying microbial life history strategies based on an organism’s phenotypic characteristics, or traits, and representing these strategies in ecosystem models can be a valuable tool in optimising global carbon models (Malik et al., 2020). Organisms appear to respond to specific environmental variables. For example, oxygen (van Bodegom et al., 2001), moisture (Lennon et al., 2012), pH (Fierer and Jackson 2006) and even varying levels of these parameters (DeAngelis et al., 2010) can select for specific organisms. In some cases, this selection operates at high phylogenetic levels – e.g., pH controls the relative growth of fungi vs. bacteria (Rousk et al., 2009). In other cases, selection operates at phylum, family, genus, or trait level (Fig. 1).

In abandoned agricultural fields carbon- and nitrogen mineralisation increases. Nitrogen and other nutrients, especially phosphorous, become more scarce over a timespan of several decades (Holtkamp et al., 2011). This forces soil microbes, meso- and macrofauna to compete for resources, but also to become more efficient, leading to a tightening in soil networks (Morriën et al., 2017). Next to this tightening, which is defined as an increase in interactions strength between food web components, this also has consequences for soil carbon cycling. Opposite to what might be expected in a shift from agricultural land to natural grassland, fungal to bacterial ratios did not change, neither did the composition and diversity of the soil community (Morriën et al., 2017). But when we traced carbon flows with stable isotope tracing, more carbon entered the fungal energy channel during the transition from agricultural field to species-rich grassland. This also fed the fungal consumers and their predators (Morriën et al., 2017). Agriculturally degraded and abandoned lands can remove atmospheric CO_2 and sequester it as soil organic matter during secondary succession (Yang et al., 2019). However, this process may be slow, requiring at least some decades or longer to reattain pre-agricultural soil carbon levels (Powlson et al., 2013). Restoration of late-successional grassland plant diversity leads to accelerating annual carbon storage rates (Yang et al., 2019). Restoration of high plant diversity may greatly increase carbon capture and storage rates on degraded and abandoned agricultural lands (Yang et al., 2019; Prommer et al., 2020). Although, we obviously need agricultural land for food production, grasslands are better carbon sinks than croplands. Yet, we should learn from the mechanisms we see in natural soils to inform decisions made in arable soil management.

When the fungal energy channel was studied in more detail during restoration of ex-arable soil towards species-rich grasslands, there was a shift in composition of active soil fungal communities from unicellular yeasts and potential plant pathogens (Zanne et al., 2020) dominating soils used recently for agriculture towards fungi that are more specialised saprotrophs and plant symbionts including arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) in later stages of restoration (Fig. 4; Hannula et al., 2017). This was measured using stable isotopes to follow active derived carbon from exudates from labelled plants in a chronosequence of 45 years. This indicates, that a functional shift of the fungal community follows the land use changes that has taken place.

6. Opportunities to steer soil life

The transitions of functional changes from croplands to species-rich grasslands, raise the question whether there are opportunities to steer transitions from a degraded form to a natural situation, or a cropland that may function as effectively as a natural system in less than decades. Opportunities to steer soil life can be obtained via influencing the root exudation pattern, thereby influencing soil microbial communities. It has already been proven that soil communities are influenced by changing exudation patterns under drought (Williams and Vries, 2020). During secondary succession the exudates of the plant community steered the active fungal communities towards plant symbionts and well defended and slower growing saprotrophic taxa (Hannula et al., 2017). Steering soil microbial communities leads to altered community structures also higher in the soil food web. This can be studied by tracing the carbon flows through trophic levels using gut content analyses of fungal

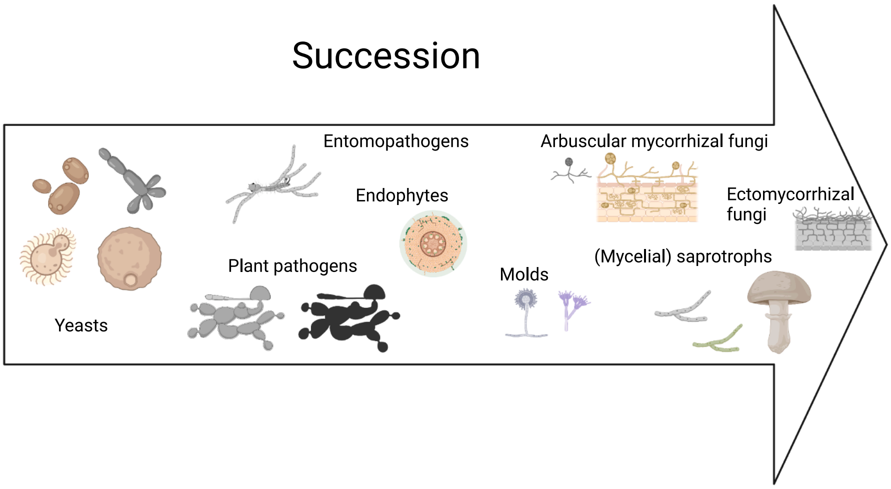

Fig. 4. The sequence of fungal guilds during secondary succession of ex-arable fields.

consumers and their predators (Morriën, 2016). With these methods actual feeding preferences within the soil food web can be revealed and indicate which groups of microbes need to be stimulated to increase diversity and biomass of certain higher trophic level organisms. This can not only steer soil communities to become more efficient in their carbon and nutrient flows but also enhance natural pathogen suppression, increase bioturbation, exchange of microbes via body lifting on mesofauna cuticles, increase soil structure by stimulating aggregation (Maaß et al., 2015) and increase the degradability and the microbial CUE of substrates (Yang et al., 2012). To steer the soil communities it is not only applying beneficial substrates to soils that enhances the fungal energy channel (Clocchiatti et al., 2020), but also to reduce disturbances (such as inorganic fertilizers and tillage) and use more ‘natural’, extensive agricultural practises targeting protection of soil biota and its multiple functions (Frąc et al., 2018) without increasing the production of other greenhouse gases (e.g. NO_x). See Table 1 for an overview of agricultural management practices and their potential effects on fungal communities.

Hence, an increase in the abundance and relative dominance of beneficial (i.e. saprotrophic and mycorrhizal) fungi in agricultural systems will potentially have positive implications for net ecosystem carbon exchange as well as plant productivity and eventually yield. Yet, more data on arable systems is still needed to link the relative dominance of fungi and ecosystem processes such as carbon cycling and plant productivity. Both in operating and abandoned agricultural systems, fungi take up approx. 50–70% of root exudate carbon (Hannula et al., 2012; Hannula et al., 2017; Morriën et. al 2017) while they only represent a small amount of the total microbial biomass. How can fungi be so effective in carbon uptake? Most probably because fungi have a very intimate and ancient relation with plants as endosymbionts (Humphreys et al., 2010; Sarkar et al., 2021), which provide them pole position for the uptake of plant-exudates. Fungal taxa have a high variation in turnover rates (de Vries et al., 2009; Anthony et al., 2020). Whereas AMF have a turnover rate similar to bacteria, EMF and saprotrophic fungi have slower turnover rate compared to bacteria (Anthony et al., 2020; Hannula et al., 2019a). As hyphal growing fungi can produce prolific amounts of mycelium while scavenging for nutrients (Boddy, 1999), they usually produce large amounts of biomass which is in absence of fungal feeding organisms turned into necromass when the fungus dies (Buckeridge et al., 2020). In agricultural soils, fungal necromass contributes to approximately 40% to the SOC stock whereas bacterial necromass contributes to approximately 20% (Liang et al., 2019). In general, microbial necromass is an important component in the carbon stabilisation route (Fig. 3) (Kallenbach et al., 2016; Prommer et al., 2020). The extensive hyphal system of fungi also enmeshes soil particles, POM and microaggregates, thereby increasing aggregate stability and provide an opportunity for POM to get stabilised (Rillig and Mummey, 2006). When ex-arable fields transform to natural systems, the soil food web components become more tightly connected and carbon- and nutrient cycling becomes more efficient (Morriën et al., 2017; Holtkamp et al., 2011). This leads to a more efficient use of carbon and nutrients in the root zone, and less leakage of nutrients to deeper soil layers. Similar differences can be found between conventional farms and organic farms (Banerjee et al., 2019). Agricultural intensification reduces microbial network complexity leading to a loosely connected network, loss of AM fungi especially due to tillage and more nutrient leakage towards the groundwater. In natural- and organic farming systems (regenerative sustainable management practices with reduced tilling) a larger percentage of carbon potentially ends up in stable carbon pools. These systems also have a higher fungal activity while their fungal to bacterial ratio does not increase (Morriën et al., 2017). We therefore propose that fungi due their extensive mycelial network and necromass accumulation are the key players in mediating carbon stabilisation in natural but also in agricultural soils. Furthermore, by increasing the proportion of beneficial fungi, such as AMF and some groups of saprotrophic fungi, has been recently shown to reduce the pathogen pressure which should lead to a better crop yield in the system (Clocchiatti et al., 2020). Yet, more research on this topic is needed.

Table 1
Common agricultural management practices and their potential effects on fungi.

Common agricultural management practices	Potential effects on fungi
(Inversion) tillage	Negative through destroying hyphae
Inorganic fertilizer	Neutral-negative; does not provide substrate for saprotrophic fungi; makes AMF redundant
Organic fertilizer (manure with/ without crop residues)	Positive; stimulates fungal growth, especially if crop residue is mixed in. As this stimulates fungi with diverse enzyme portfolia
Increase bioturbators (e.g. earthworms)/reduce soil compaction	Positive as reduced soil compaction stimulates the soil food web including fungi
Amendments (e.g. compost, bokashi, crop residue)	Mostly positive; some substrates especially boost fungi in combination with N addition, although not all amendments have long-term effects on fungal biomass increase
Increase plant diversity	Positive; diverse plant communities have diverse root architectures and root traits that will increase fungal biomass as well as biodiversity.

7. Optimisation the soil multifunctionality with fungi

Fungal hyphae form large mycelial networks in soil that provide transportation highways for bacteria (Rudnick et al., 2015) and for organic carbon. Also mycelial necromass can form non-degraded organic matter in deeper soil layers (Anthony et al., 2020). AMF have a symbiotic relation with 80% of all plants in grasslands (van der Heijden 2002). After chemical communication with the plant, the plant allows the AM fungus in its root cells, where it grows arbuscules in which plants trade fatty acids and lipids in return for soil phosphorous and nitrogen acquired by the fungus (Hodge et al., 2001; Keymer et al., 2017; Choi et al., 2018). AMF can work as an elongated root system under circumstances that benefit the fungus as well as the plant (Kiers et al., 2011). This extended root zone is coined as 'mycorrhizosphere' (Rudnick et al., 2015)' and the microbiome and functions under the influence of the hyphae 'hyphosphere' (See et al., 2022). Due to their large hyphal network, AMF are key players in transporting carbon in the soil (Rillig and Mummey 2006) they can even move phosphorous from rich to poor places in the plant network (Whiteside et al., 2019). Saprotrophic fungi that scavenge on all other carbon sources in the root zone also grow hyphae and can therefore perform a similar function as AMF in terms of carbon stabilisation due to translocation of carbohydrate components in the soil matrix as well as through the enmeshment effect, which captures organic material with soil particles and occludes OM in aggregates (Frąc et al., 2018; Lehmann and Rillig 2015). Thus carbon sequestration depends on fungal activity (i.e. anabolism, production of chemical substances and turnover yet see above for discussion on necromass), as active fungi sequester and transport a myriad of organic substances from the root zone into deeper soil layers, as well as transport these organic substances into zones where aggregates are formed and organic matter is bound to minerals (Guhra et al., 2022; See et al., 2022). This indicates that fungal-friendly agro-ecosystems have a huge potential to store more soil carbon if we have a better understanding of the underlying mechanisms.

Higher fungal activity leads to more aggregate formation via fungal enmeshment, which leads to carbon that ends up inside aggregates, thereby becoming physically protected against further degradation (Witzgall et al., 2021). The rhizosphere around the roots forms the perfect place for microbes to occur due to fresh carbon inputs (Sokol and Bradford 2019). The deeper cropland species root, the deeper microbes occur and the deeper gluing agents, like Extracellular Polymeric Substances (EPS), enter the soil (Costa et al., 2018). This stimulates aggregate formation (soil structure) in deeper soil layers (Kravchenko et al., 2019). Therefore, management practices in croplands like (winter)cover crops and composting (organic inputs) have different impacts on surface and subsurface soils depending on the diversity of the rooting depth of the plants (Tautges et al., 2019). Also, the quality (indicated by the carbon to nitrogen ratio) of the cover crop, the organic fertilizer, the root litter and the root exudates (Kallenbach et al., 2019) determines the microbial growth response and the microbial CUE (Blagodatskaya et al., 2014; Poeplau and Don 2015).

Enhanced pore space connectivity will lead to a higher functional diversity of microbes, including fungi, which are then better able to stabilise carbon by stimulating binding to the mineral fraction. Soil porosity around aggregates are influenced by the activity of bacteria and fungi present during their formation (Crawford et al., 2012; Wilpiszeski et al., 2019). The dynamic nature of aggregate turnover (4D aspects: life time, formation and degradation) is less well understood. The dynamics of aggregates also determine community interactions of soil biota, because sub-communities from the soil matrix of mainly bacteria get locked up inside aggregates (Rillig et al., 2017). Previous locked up sub-communities of microbes change if, after disintegration of the aggregate, communities on microaggregates coalesce with other sub-communities (Lehmann et al., 2017). It is generally believed that more diverse plant communities with extended root systems increase the diversity of the microbial community of both bacteria and fungi in and on the surface of soil aggregates (Upton et al., 2019).

We need to also remember that these proposed measures to increase soil biodiversity and multifunctionality need not to be evaluated in isolation but an ecosystem approach needs to be taken. Overwhelming amount of research over the past two decades has shown that plants are pivotal in mediating interactions between aboveground and belowground organisms. For instance, root-associated organisms can influence foliar feeding insects on the same plant (Koricheva et al., 2009; Pineda et al., 2010). Thus, increasing the crop diversity can affect the soil biodiversity but also directly the pollinators and above ground insects (Murdoch et al., 1972) which in turn affect the animals feeding on them (van der Putten et al., 2001; Klein et al., 2007). There is also a direct link between plant community legacy via the soils on plant feeding insects (Hannula et al., 2019b) that take up also soil particles to enrich their microbiome. We think that the mechanisms here proposed to increase carbon storage in soils are generally favourable to most of the interactions and multifunctionality.

8. Towards sustainable crop production using soil fungi

Rather than predicting global distributions of soil biota and carbon dynamics via global distribution maps, advanced algorithms, and machine learning, we think it is important to fill the knowledges gaps between soil ecology and soil sciences first (Table 2). Before we can make proper predictions about future climatic models, soil biotic parameters need to be properly incorporated in these models. Current data is not necessarily limited by how much data there is but rather how little data on relevant variables exists (e.g. aggregates, soil pores, POM, MAOM, fungal traits) to optimise these future climatic models. This knowledge gap needs to be filled urgently.

For the abiotics we need to better understand the physical distribution of organic matter in pools of organo-mineral-associated versus particulate organic matter to inform land management for nitrogen-efficient carbon sequestration, which should be driven by the inherent soil carbon capacity and nitrogen availability in ecosystems. On top of that, binding to the MAOM fraction could be optimised by setting the right abiotic conditions due to optimisation of the surface charge of these minerals. The part where leverage is possible is mostly situated in the POM, which is incorporated in or between soil aggregates. We have to find a way to investigate the role of fungi in the dynamics and turnover of soil aggregates and the life-time of occluded POM.

Management of agricultural soils could be modified to profit from beneficial soil fungi in terms of increased carbon sequestration and enhanced crop yield (Table 3). Increasing soil fungi and especially beneficial fungi in natural systems as well as in agricultural systems will enhance soil carbon contents, increases natural pathogen suppression and results in healthier crops that also sustains insect communities providing food sources higher trophic level organisms such as meadow birds. To keep carbon and nutrients in the soil, it is suggested to reduce tillage, fight soil compaction, use complex crop rotation schemes by

Table 2
Knowledge gaps that need to be filled to be better able to steer soil fungal communities.

1. Limited understanding of the mechanism by which fungi can control soil carbon stabilisation
2. Lack of understanding of how occlusion of OM in aggregates can be increased
3. Limited understanding on how microhabitats where complexation of OM takes place is optimised
4. Effects of roots, soil fauna and microbes on soil pore formation and the effects of soil pores on the soil biota is still limited
5. Limited knowledge on the dynamic role of soil fungi in soil aggregate formation and vice versa
6. More knowledge on microbial life history strategies will aid optimizing global carbon models
7. Have a better understanding of the mechanisms by which saprobic fungi in particular can stabilise POM in aggregates

Table 3
Recommendations for agriculture and policy development.

1. Decrease soil compaction
2. Restoration of high plant diversity in grasslands
3. Optimise Mineral Associated Organic Matter (MAOM) by adjusting pH to enhance complexation to the mineral fraction of the soil
4. Increase occluded Particulate Organic Matter (oPOM) in aggregates by providing organic manure and leaving crop residues on the field
5. Feed the soil fungi all year round, prevent the field to remain fallow over the winter
6. Mix crops with different rooting depths on the same field
7. Choose deep rooting crops
8. Add amendments (with additional N) that stimulate fungal growth

mixing deep and shallow rooting crops, apply cover crops during crop-free periods, and leave crop residues on the surface of the soil (also see Table 1). All these management strategies potentially act through changes in the soil fungal community composition and steer the structure of the whole soil food web (Table 3). Using the natural capacity of a biodiverse soil fungal community to sequester carbon in the soil can deliver double benefit: reduction of the rate of climate change by storing photosynthesized carbon in soil and increasing agricultural yields by restoring the organic matter content of degraded soils. Identifying microbial life history strategies based on an organism's phenotypic characteristics, or traits, and representing these strategies in ecosystem models can be a valuable tool in optimising global carbon models.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

S.E.H. and E.M. developed the proposed ideas together and both contributed equally to the writing of the manuscript.

Data statement

This study did not generate nor analyse datasets or used code.

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