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Mycorrhizas for a changing world: Sustainability, conservation, and society

Societal Impact Statement

Mycorrhizal fungi are of huge significance for plants, people, and the planet. In addition to the fruiting bodies of many mycorrhizal fungi having great culinary, medical, and sometimes religious significance, by forming partnerships with the vast majority of land plants, mycorrhizal fungi are essential in the formation and functioning of global ecosystems. As such, mycorrhizas have great potential for future exploitation and management to facilitate a variety of sustainability programs in agriculture, conservation, and restoration, considerations that are particularly relevant during this time of global change and widespread depletion of natural resources.

Summary

Mycorrhizal fungi, of all types, hold huge significance for our planet and society. By forming mutualistic symbioses with the vast majority of land plants, mycorrhizas play an essential role in the formation and maintenance of global ecosystems. They also have great potential for exploitation to facilitate a variety of sustainability programs in agriculture, conservation, and restoration, particularly relevant in the context of global climate change and depletion of natural resources. As such, in addition to the fruiting bodies of many mycorrhiza-forming fungal species being delicious, mycorrhizal symbioses are of critical and increasingly appreciated importance to human society. This editorial provides an overview of the relevance and potential roles of mycorrhizal fungi toward achieving global goals in sustainability, conservation and their significance within society, and highlights key directions for future research.

are of significant cultural importance for modern and ancient civilizations, including Mesoamerican cultures who regarded mushrooms as “flesh of the gods” (Hernández-Santiago, Martínez-Reyes, Pérez-Moreno, & Mata, 2017; Krippner & Winkelman, 1983). Today, fungi not only form the basis of many culturally important foods (Chang, 1999), medicines (Beulah, Margret, & Nelson, 2013; Wasser & Weis, 1999), and ceremonies (Arthur, 2000), but their key role in maintaining modern ecosystems by forming vast, underground networks that connect plants to one another is increasingly recognized (Leake et al., 2004) (Figure 1). Through these fungal networks, mycorrhizal fungi supply their plant hosts with nutrients from soil. In return, most host plants transfer organic carbon-based compounds (e.g., sugars and lipids) to their fungal symbionts, meaning mycorrhizal symbiosis is usually considered to be a mutualistic interaction (Smith & Read, 2008). The benefits of being mycorrhizal are not limited to nutrient assimilation—neighbouring plants interconnected by a fungal network are able to transmit and receive signals between each other in response to, for example, herbivory (Babikova et al., 2013). The mechanisms for such signal transmission that allows plants to respond to and potentially mitigate the challenge, remain unclear and represent exciting future research directions.

Mycorrhizal symbioses between plant roots and soil fungi (known as “mycorrhiza-like” in plants without roots) are ancient, having evolved with the earliest plants to colonize Earth’s land surfaces >500 Mya (Morris et al., 2018). By supplying otherwise unobtainable nutrients, extracted from Earth’s early mineral soils to the earliest rootless plants, ancient mycorrhizal fungi are likely to have played a critical role in facilitating the transition from an aquatic to a terrestrial existence (Field, Pressel, Duckett, Rimington, & Bidartondo, 2015), facilitating the development of a breathable atmosphere over hundreds of millions of years (Mills, Batterman, & Field, 2018).

The Earth is currently undergoing some of the most dramatic and rapid changes in its history. As a result of these changes, modern society collectively faces many significant and pressing challenges. Chief among these is the urgent need to balance the needs of a rapidly growing human population with depletion of natural resources and the changing climate. In order to face these challenges in a sustainable way, new methods of farming, building, and developing as

1 | INTRODUCTION

People have interacted with mycorrhiza-forming fungi, consciously or not, for millennia. The fruiting bodies of some of these fungi

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FIGURE 1 The symbiotic relationships formed between plant roots and certain groups of soil fungi which together are known as mycorrhizas, hold huge significance for our planet and society. Mycorrhizas, and the networks they form, play a critical role in global ecosystem structure and function, from tropical rainforests through to temperate grasslands and managed agricultural land. Mycorrhizal plants and their fungal fruiting bodies have great historical and, increasingly, modern societal significance in both cultural and clinical applications. There is great potential for future exploitation of mycorrhizas and their networks in our changing world. In an upcoming Special Issue of *Plants, People, Planet* we will explore the relationships and significance of mycorrhizas in human society and development, and how they might contribute toward the global goals of food security, sustainability and well-being

a global society must be found while simultaneously working to protect natural habitats, resources, and biodiversity. One way these aims could be achieved may be by harnessing the power of some of the most ancient, naturally occurring ecosystem engineers such as mycorrhizal fungi. These fungi have, in their long association with land plants, previously withstood dramatic shifts in Earth's climate, flora, and fauna but have since been impacted by modern, intensive agricultural practices.

2 | MYCORRHIZAL CONTRIBUTIONS TO SUSTAINABILITY

The world's human population has increased exponentially, putting unprecedented pressure on Earth's natural resources. Against a background of a changing climate where, if no intervention and mitigation strategies are implemented, global temperatures are set to rise $>1.5^{\circ}\text{C}$ by end of the 21st Century (IPCC, 2014) with additional impacts through increases in the frequency of severe weather events. In addition, land degradation associated with unsustainable farming practices is contributing to plateauing of crop yields in the face of increasing fertilizer and pesticide inputs (Grassini, Eskridge, & Cassman, 2013). In parallel, extraction of phosphorus from rock phosphate, which remains the only source of phosphorus for fertilizers, is expected to become more difficult and costly in the next decades (Cordell & White, 2011). Together, these factors present a perfect storm for our planet and society. Of particular and pressing

concern is the need to meet the dietary requirements of the ever-growing population, with the UN putting food and water security, together with well-being, climate action, and sustainable land management among its top Sustainable Development Goals (UN, 2015).

There is significant potential to exploit the power of soil fungi in the production of food which, if successfully applied, could help to reduce agricultural fertilizer inputs while maintaining, or even increasing, crop yields (Godfray et al., 2010). The physiological function of mycorrhizas and mycorrhiza-like symbioses is dependent upon a number of abiotic and biotic factors (Field & Pressel, 2018). For instance, plant and fungal identity play a key role in determining the precise stoichiometry of the exchange of carbon and nutrients between symbionts (Walder et al., 2012). The vast majority of staple food crops form symbioses with mycorrhizal fungi (Smith & Read, 2008), although the functional significance of these symbioses is by no means ubiquitous across species. Key exceptions include non-mycorrhizal brassicas, although mycorrhizal fungi will attempt to colonize them (Fernández et al., 2019).

Responses of plants to mycorrhizal colonization range from mutualistic, whereby both parties benefit from the association, to parasitic, where one party benefits at the expense of the other (Newton, Fitt, Atkins, Walters, & Daniell, 2010). Some, including economically and socially important species such as the vanilla orchid, are effectively parasitic upon their fungal partners for some, if not all, of their lifecycles (Leake & Cameron, 2010). Environmental factors may impact upon the diversity and function of mycorrhizal symbioses, atmospheric CO_2 concentrations (Cotton, 2018) and changing

temperatures having previously been shown to affect the rate and quantities of carbon and nutrients exchanged between mycorrhizal partners (Gavito, Schweiger, & Jakobsen, 2003). Insight into the extent, and drivers of nutrient exchange between fungi and socially important plant species is a critical future goal.

The benefits of mycorrhizal fungi within agroecosystems are of course not limited to the supply of plant nutrients. One of the most pressing concerns in agriculture is soil “health” and structure. The extraradical hyphae of mycorrhizal fungi play an important part in maintaining soil structure, holding soil particles together, increasing soil aggregation, and thus increasing soil pore size (Mardhiah, Caruso, Gurnell, & Rillig, 2016). Additionally, soils rich in mycorrhizal fungi have greater water holding capacity and reduced drought susceptibility (Jayne & Quigley, 2014; Ortiz, Armada, Duque, Roldan, & Azcon, 2015; Raviv, 2010). There are many important issues to resolve; however, before mycorrhizal fungi should be deployed as part of a sustainable management regime. There are a number of scenarios where the carbon drain imposed by mycorrhizal fungal symbionts outweighs the nutritional benefit to the host resulting in depression of biomass and reduction in crop yield (Ryan & Graham, 2018). This effect may be caused by weak plant-fungal compatibility (Klironomos, 2003), light availability (Veresoglou et al., 2019), nutrient status of the soil or any one of a number of other abiotic, and biotic interactions (Thirkell, Charters, Elliott, Sait, & Field, 2017). These effects highlight the urgent need for sustained research efforts to be made in crop-mycorrhizal interactions.

Given that agricultural practices have been shown to reduce availability and diversity of naturally occurring mycorrhizal propagules in the soil (Helgason, Daniell, Husband, Fitter, & Young, 1998), commercially available inocula are often used to encourage mycorrhization of crops. The effects of application of such mycorrhizal inoculants onto agricultural fields is largely unknown, both in terms of the efficacy of the inoculant in encouraging colonization of crop roots by fungi and then in turn, promotion of nutrient assimilation and increases in yield as a result of colonization. Research is urgently needed to assess the impact of such inoculants on these factors, to assess the quality and efficacy of the inoculants themselves and, as a community, to draw up appropriate standards and certification for such products (Schwartz et al., 2006).

It is largely unknown whether the addition of mycorrhizal fungi as an inoculant has any lasting impacts upon the native mycorrhizal fungal communities within the soil (Schwartz et al., 2006). It is possible that fungal additions encourage competition between fungi within the soil and thus facilitates proliferation of species likely to provide benefit to the plants they associate with—a desirable outcome for sustainable crop production. It is likely that inoculant additions will encourage the growth of generalist mycorrhizal fungal species, able to associate with a wide variety of host plants and to withstand a range of soil conditions. In another scenario, there could be incompatibility between crop and mycorrhizal genotypes (Hetrick, Wilson, & Todd, 1996; Klironomos, 2003), with the outcome being parasitic behavior of the fungi resulting in

increased carbon drain on host plants and a reduction in yield. It is also possible that the introduced species are unable to compete with existing fungi and are thus rapidly lost from the population (Verbruggen, Heijden, Rillig, & Kiers, 2013), in which case questions should be raised regarding the application of inoculants at all, unless, for example, they enable short-term gains in establishment. Compatibility, receptivity, and function of mycorrhizas across crop cultivars are therefore critical factors to take into account when considering the use of mycorrhizas within a sustainable agricultural management strategy.

The interaction between crops and the environment is important in agriculture, and it follows that this will also be true for the application of mycorrhizal fungi in agricultural systems. The stoichiometry of bidirectional resource exchange between symbionts is highly dependent on abiotic factors such as soil nutrient availability (organic and inorganic), temperature and CO₂, as well as biotic interactions with rhizospheric microbes, invertebrates and above ground biota. Research in these areas is leading to important new insights not only into the fundamental biology, ecology, and evolution of mycorrhizal associations, but also their exploitation in an agricultural context. Indeed, consideration of mycorrhizal symbioses in the context of the concept of “Darwinian Agriculture” (Denison, 2012) offers promise to enhance sustainability of agriculture (Kiers & Denison, 2014).

3 | MYCORRHIZAL APPROACHES TO CONSERVATION AND RESTORATION

The environment plays a large role in the benefits derived from mycorrhizal associations by host plants (Field & Pressel, 2018; Treseder, 2004). Most natural environments are nutrient limited to one degree or another, thus plants associating with mycorrhizal fungi stand to gain a competitive advantage over non-mycorrhizal plants of the same species (Chen, Arato, Borghi, Nouri, & Reinhardt, 2018). The interconnectedness of plants via below-ground common mycelial networks (CMN) may also bestow a selective advantage on the plants that draw resources from it, whether they contribute or not (see Bidartondo et al., 2002). By providing access to shared resources, CMNs may promote seedling recruitment and establishment (van der Heijden & Horton, 2009) and thus play an important part in maintaining plant community structure. Given the widespread nature and critical function of mycorrhizal fungi, and therefore CMNs, across ecosystems, it is increasingly recognized that in order to construct and implement effective strategies for conservation and restoration of vulnerable and diminishing habitats, attention must be paid to the mycorrhizal fungal associations that tie the plant communities, and the human communities that rely on them, together.

An important factor for consideration is specificity between mycorrhizal symbionts. The presence of compatible soil fungi may play an influential role in the success of establishment for rare species; orchids for example tend to associate with a single fungal symbiont

and the absence of that species will result in a failure of seeds to germinate. When the species involved are rare, endangered or declining, it may pay dividends to consider fungal diversity as part of a larger strategy for conservation and restoration. A central aim then of such strategies should be to promote fungal biodiversity, particularly important given that only a fraction of the Earth's fungal species have been positively identified to date (Willis, 2018).

Symbiotic fungal diversity may be influenced by anthropogenic activities. A recent survey across European forests has shown that the diversity of the ectomycorrhizal fungi that form associations with forest tree roots is driven by a combination of host identity and environmental factors, such as nitrogen availability (van der Linde et al., 2018). As such, nitrogen deposition and plantation forestry resulting from anthropogenic activities could have a dramatic impact on mycorrhizal associations, in turn affecting the distribution of associated plants. Agricultural practices also serve to reduce the diversity of mycorrhiza-forming fungi (Helgason et al., 1998; Verbruggen et al., 2013; Verbruggen & Toby Kiers, 2010; Williams, Manoharan, Rosenstock, Olsson, & Hedlund, 2017). However, it is possible to increase fungal diversity through careful management and potentially thereby restore soil and wider ecosystem function (Hijri et al., 2006).

In order to generate more comprehensive conservation strategies, greater importance should be placed on mapping fungal diversity, both functional and phylogenetic, understanding the relationship between plants and their partners both beneficial and non-beneficial, and linking it to environmental and biotic factors and then consider these within the future strategies. Significant attention is needed to enumerate the fungal diversity of the Global South, as research in these areas remains patchy at best. It is likely restoration strategies for degraded landscapes would also benefit from consideration of mycorrhizal fungi, either as agents of bioremediation or as restoration targets themselves.

4 | MYCORRHIZAS AND SOCIETY

The edible mushroom industry is worth US\$42 billion annually (Knowledge Sharing Intelligence, 2017), many species of which, for example, porcini (*Boletus edulis*), chanterelles (*Cantharellus sp.*), and various truffles (Mello, Murat, & Bonfante, 2006), form mycorrhizal associations with plants. The diversity of these edible mushroom-forming mycorrhizal fungal species remains unclear. Indeed, a packet of dried Chinese porcini was recently found to contain three species of fungi previously completely unknown to science (Dentinger & Suz, 2014).

There has been increasing interest and awareness across society of the benefits of mycorrhizal colonization of plants, be that in natural ecosystems (Read, 1991; van der Heijden & Horton, 2009), horticulture (Azcón-Aguilar & Barea, 1997; Roupheal et al., 2015), or in the agricultural industry (Gianinazzi & Vosátka, 2004; Thirkell et al., 2017). This growing awareness has resulted in an increase in the manufacture and marketing of mycorrhizal fungal inoculum to commercial and home growers (Vosátka, Látr, Gianinazzi, & Albrechtová,

2012) and rising urgency to develop a deeper understanding about how the way in which land is managed by farmers, foresters, or recreational gardeners may affect the functioning of the wider mycorrhizal network. Such changes in practice and attitude have potential to make significant and lasting impacts on economies and the direction and rapidity of future research if collaboration between the scientific community and industry is fostered. This is particularly pertinent with ongoing emphasis from governments on reducing environmental impact by reducing usage of chemical inputs in agriculture and horticulture.

5 | CONCLUSIONS

It is clear that mycorrhizas of all types are an essential component of ecosystem biodiversity, that also deliver, through their roles in plant nutrition and protection, significant ecosystem services that have potential to play an important role in sustainability agendas. Thus the applications of mycorrhizal fungi in sustainable systems, in addition to their own economic and cultural significance, are areas of rapid research progress and increasing attention. However, significant knowledge gaps remain covering the multitude of interactions between plants, fungi, people, and the environment. It is in this context that we are delighted to announce a forthcoming Special Issue of *Plants, People, Planet*, which will bring together an exciting body of creative new research, reviews, reports and opinion pieces exploring the relationships and significance of mycorrhizas in human society and development, and how they might contribute toward the global goals of food security, sustainability and well-being. We welcome suggestions from the community for potential articles covering all aspects of mycorrhizal research in the context of global change. In particular, we welcome articles within (but not limited to) the following broad themes:

- Agriculture, horticulture, and forestry
- Conservation
- Climate change
- Cultural and societal significance
- Ecosystem services
- Restoration and remediation

KEYWORDS

agriculture, climate change, conservation, ecosystem services, horticulture, mycorrhizas, restoration, remediation, society

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