Review

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Coupling of plant and mycorrhizal fungal diversity: its occurrence, relevance, and possible implications under global change

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Summary

First principles predict that diversity at one trophic level often begets diversity at other levels, suggesting plant and mycorrhizal fungal diversity should be coupled. Local-scale studies have shown positive coupling between the two, but the association is less consistent when extended to larger spatial and temporal scales. These inconsistencies are likely due to divergent relationships of different mycorrhizal fungal guilds to plant diversity, scale dependency, and a lack of coordinated sampling efforts. Given that mycorrhizal fungi play a central role in plant productivity and nutrient cycling, as well as ecosystem responses to global change, an improved understanding of the coupling between plant and mycorrhizal fungal diversity across scales will reduce uncertainties in predicting the ecosystem consequences of species gains and losses.

I. Introduction

Biodiversity loss is rapidly occurring globally, with far-reaching consequences for ecosystem processes and the ecosystem services that they provide. Despite decades of research on the causes and consequences of biodiversity loss, we still know little about how shifts in species richness (i.e. alpha diversity) at one trophic level affect diversity patterns at another. First principles predict that communities with high species richness at one trophic level *should* have higher species richness at another level, with the strongest relationships occurring between trophic levels that interact most strongly (Duffy *et al.*, 2007; Eisenhauer *et al.*, 2010). Despite the intuitive nature of a 'coupled diversity hypothesis', empirical tests of the hypothesis are uncommon.

Symbiotic associations between plants and their mycorrhizal fungi present an excellent testbed for evaluating the coupled diversity hypothesis. Plants are highly dependent on belowground microorganisms for the acquisition of nutrients (Phillips *et al.*, 2013; Sulman *et al.*, 2019) and amelioration of environmental stressors (Kivlin *et al.*, 2013); and the symbiosis between plants and

various mycorrhizal fungi is one of the oldest, most stable and most ecologically consequential in nature (Smith & Read, 2008). This leads to the prediction that in communities where plant richness is high, mycorrhizal fungal richness should also be high (i.e. the diversity patterns are coupled). And if greater species richness results in enhanced resource use, speciose communities of plants and mycorrhizal fungi may be more productive than species-poor communities (van der Heijden *et al.*, 1998). However, there have been few direct tests of this idea beyond a limited set of site-specific studies. As such, we have a limited understanding of how common aboveground–belowground diversity couplings are across different biomes, and whether such couplings have the potential to affect ecosystem functions across space and over time.

A central challenge to the characterization of patterns of plant–mycorrhizal fungal coupling is that the two dominant types of mycorrhizal fungi globally – arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi – differ in various aspects. Striking differences in the biogeography of AM-associating plants (dominant in low latitude biomes) and EM-associating plants (dominant in high latitude biomes) suggest mycorrhizal fungal type could shape plant–mycorrhizal diversity patterns. In general, AM and EM fungi differ in their diversity (Zanne *et al.*, 2020), plant host dependence, breadth, and specificity (Brundrett & Tedersoo, 2018; van der Linde *et al.*, 2018; Kokkoris *et al.*, 2020; Toussaint *et al.*, 2020) (Table 1). It is widely reported that EM fungi are more diverse, less dependent on plant hosts, and somewhat more plant host-specific (Allen *et al.*, 1995) than AM fungi. However, new tools for sequencing AM fungi have called into question some of these patterns. For instance, there is emerging evidence that AM fungi may have greater host-specificity than previously recognized (Kokkoris *et al.*, 2020). Moreover, no discussion of AM and EM fungal diversity is complete without mentioning that species definitions of these fungi are still fluctuating. Because fungal species concepts are defined via molecular barcoding, species of fungi may not be analogous to definitions of plant species (e.g. AM fungal species may contain as much genetic variation as plant families; Öpik *et al.*, 2016).

Given emerging evidence of the role of mycorrhizal fungi in plant productivity, nutrient cycling and stress amelioration/buffering, understanding the coupling of plant–mycorrhizal fungi diversity patterns is likely to be increasingly important in the wake of human-accelerated environmental change. The goals of this paper are as follows: to identify the critical knowledge gaps in our understanding of patterns of plant–mycorrhizal diversity couplings for AM and EM plants; to articulate how and why such couplings may have consequences for ecosystem functioning in the wake of global changes; and to propose a data-driven research agenda that can help enhance our understanding of this critical issue.

Table 1 Differences in arbuscular mycorrhizal and ectomycorrhizal plant and fungal diversity patterns.

	Arbuscular mycorrhizas	Ectomycorrhizas
Fungal diversity	Low	High
Host plant diversity	High	Low
Dependency on plant host	High	Low/intermediate
Specificity to plant host	Low	Intermediate/high

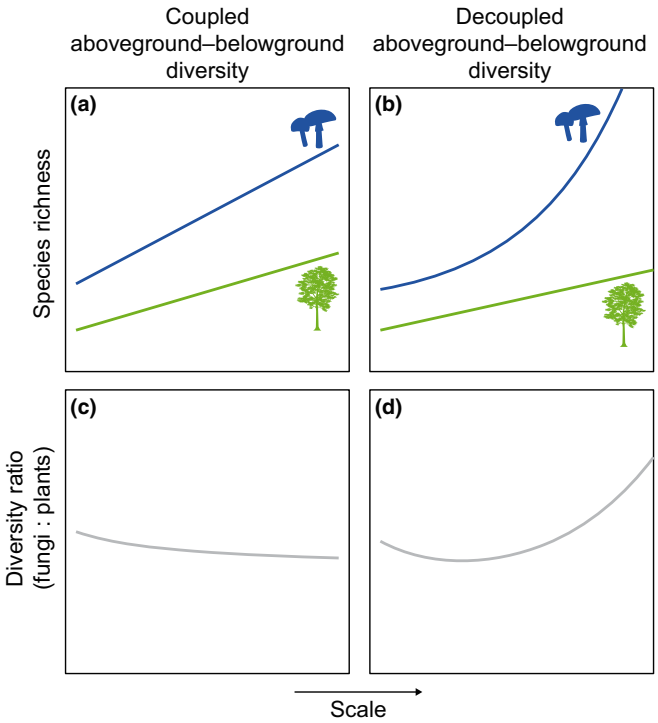
II. Association between plant and mycorrhizal fungal diversity

There is a relatively rich body of literature on the patterns, drivers, and consequences of plant diversity across scales (Stein *et al.*, 2014) and some recent advancements on belowground microbial diversity distributions (Davison *et al.*, 2015). However, far less is known about how patterns of aboveground diversity are coupled to patterns of belowground diversity, if at all. A key challenge in understanding plant–mycorrhizal fungal diversity coupling is that there is limited knowledge about whether plant–fungal relationships change at different spatial scales (e.g. plot, stand, region, and continent) and across temporal scales (e.g., annual, decadal, century). It is well-known that ecological patterns can change across spatial and temporal scales due to changes in key ecological processes (Gonzalez *et al.*, 2020), and the use of different statistical approaches can affect our understanding of such patterns (Dixon Hamil *et al.*, 2016). Therefore, it is important to understand turnover in plant and mycorrhizal fungal taxonomic identity across space and over time (Box 1).

At the local scale, numerous studies have reported positive correlations between mycorrhizal fungal richness and plant species richness. Manipulative studies show that plant diversity is linked to belowground AM (Kivlin & Hawkes, 2011) and EM fungal diversity (Gao *et al.*, 2013; Nguyen *et al.*, 2016) and function (Eisenhauer *et al.*, 2010). In glasshouse trials, plant performance is often optimized when plants associate with highly diverse AM fungal communities (Maherali & Klironomos, 2007), perhaps owing to complementarity in function among AM fungal clades (Powell *et al.*, 2009). However, other studies have reported no such relationship between plant and AM (Wagg *et al.*, 2015) or EM fungal diversity (Lang & Polle, 2011), and some studies have reported negative relationships (Li *et al.*, 2020).

Matters are further complicated by the role of common mycorrhizal networks (CMNs) – hyphal networks in soil that connect host plants of the same or different species (Selosse *et al.*, 2006). Common mycorrhizal networks have the potential to affect plant–mycorrhizal diversity couplings. In forests, CMNs may weaken coupled diversity patterns if CMNs support the establishment of understory seedlings that increase plant richness but do not affect mycorrhizal richness. Likewise, the effects of CMNs on diversity couplings may differ between EM- and AM-dominated stands. Common mycorrhizal networks are presumed to be more common in EM-dominated communities owing to the greater length and slower turnover of EM mycelium relative to AM hyphae (Courty *et al.*, 2010). However, plant–soil feedbacks in EM-dominated forests are typically 'positive', meaning that conspecific seedlings are often promoted; by contrast, plant–soil feedbacks in AM-dominated stands are typically 'negative', which results in the promotion of heterospecific seedlings that can increase plant richness but have no effect on mycorrhizal richness *per se* (Bennett *et al.*, 2017; Teste *et al.*, 2017; Kadowaki *et al.*, 2018; Chen *et al.*, 2019). Thus, AM-dominated stands with CMNs may experience a

Box 1



Plant–mycorrhizal fungi diversity coupling patterns may vary across spatial and temporal scales. Species-area relationships (SARs) for fungi (blue) and plants (green) may be similar over space (a) or may diverge (b). If SARs are similar among the two groups, the ratio of alpha diversity between mycorrhizal fungi and plants (i.e. alpha diversity coupling) will be similar between the two groups across space and time (c). However, if, for example, mycorrhizal fungal species richness accumulates faster than plant richness, then alpha diversity coupling will diverge over space and time (d). Note, relationships depicted here represent two of many cases and these relationships may shift in response to global change. Discovering trends in plant and mycorrhizal fungal diversity across scales is not trivial because it requires spatially- and/or temporally-explicit sampling regimes that account for environmental variation. However, elucidating these scaling relationships can inform when and where aboveground or belowground biodiversity loss will impact ecological communities and ecosystems the most.

greater decoupling of plant–mycorrhizal diversity than EM-dominated stands at local scales.

At larger spatial scales (e.g. continental to global), plant and AM and EM fungal diversity couplings are often weak (Tedersoo *et al.*, 2014). Diversity patterns for mycorrhizal fungi in general often differ from those of plants (Cameron *et al.*, 2019). It is well-known that plant diversity is highest in the tropics where AM-associating trees are dominant. However, congruent patterns of elevated AM fungal richness in the tropics have rarely been detected or reported (Toussaint *et al.*, 2020). In the case of EM plants, richness tends to be greatest in temperate latitudes, which corresponds to where EM fungal richness is also greatest (Tedersoo *et al.*, 2014). A recent study reported that both AM and EM fungal diversity were highest where host densities were maximized (Toussaint *et al.*, 2020), suggesting that the biogeographic diversity mismatch reported in earlier studies may be related to incomplete (or nonrepresentative) sampling records. There are a relatively small number of sites (< 2000 globally) where fungal diversity has been characterized with molecular methods (Guerra *et al.*, 2020); whereas plant diversity information is available for hundreds of thousands of sites. Moreover, we know even less about the degree to which fungal diversity patterns change over time, although numerous studies have demonstrated temporal variation in AM and EM fungal diversity locally (Averill *et al.*, 2019).

Fortunately, researchers have already started building continental and global maps of mycorrhizal host plants (Jo *et al.*, 2019), but similar mycorrhizal fungi maps are relegated to predicting distributions of fungal guilds (Sulman *et al.*, 2019) and contain very large uncertainties (Pärtel *et al.*, 2017). For example, in the United States, although there are a large number of systematic sampling efforts investigating plant diversity, there were < 200 sites examining AM and EM fungal diversity using accurate next-generation sequencing (Fig. 1). Thus, our ability to accurately characterize plant–mycorrhizal fungal diversity associations requires 'filling in the map' at different scales (spatial and temporal) and with high mycorrhizal fungal diversity resolution. In particular, more sampling efforts in historically under-sampled areas of the globe (e.g. tropical ecosystems, the global south; Toussaint *et al.*,

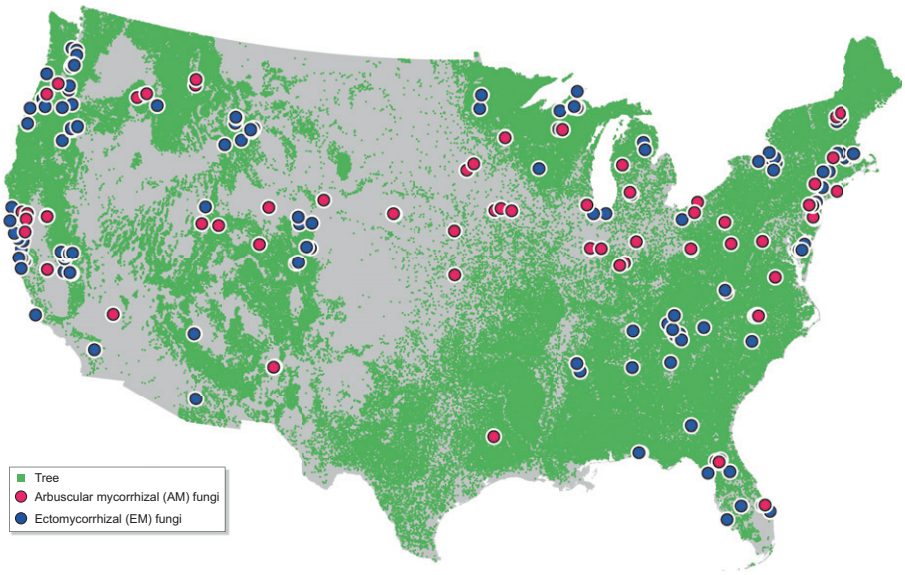


Fig. 1 The spatial coverage of data available to measure mycorrhizal fungal richness is limited in comparison to the national coverage of plant data. Mycorrhizal host plant distribution data are based on 0.067 ha Forest Inventory and Analysis (FIA) plots (Jo *et al*., 2019). Locations of fungal data collection for the two most dominant types – arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (EM) fungi – were obtained from archived fungal DNA sequences in the NCBI GenBank repository. Sequencing methods and depths vary among mycorrhizal fungal studies, complicating diversity comparisons across space and time. Note that the mycorrhizal fungal richness study sites do not include the large number of traditional studies focusing on the aboveground surveys of fruit bodies of EM fungi, which often do not include a complete assessment of all EM fungi presented in the soil.

2020) are necessary to understand global patterns of plant and mycorrhizal fungal coupling.

III. Influences of plant–mycorrhizal fungal diversity on ecosystem function

A rich body of literature exists on the role of plant diversity in determining ecosystem functioning, yet few studies have investigated the consequences of plant–mycorrhizal diversity coupling. Plant diversity has been linked to increased productivity in forests (Zhang *et al*., 2012; Ratcliffe *et al*., 2017), but the magnitude and form of the relationship is context-dependent and relatively weak (Fei *et al*., 2018). One factor that may affect this relationship is mycorrhizal diversity. An assumption central to our current understanding of how plant richness increases primary production is that greater resource partitioning can be achieved with more species (Hooper *et al*., 2005). Given that mycorrhizal fungi provision resources to plants yet differ in their ability to acquire said resources (Johnson *et al*., 2012), greater fungal diversity could lead to steeper tree richness–productivity relationships. This leads to the question of whether accounting for mycorrhizal diversity (e.g. statistically or experimentally) can account for some of the variance in tree richness–productivity relationships.

In most forests, nitrogen (N) and phosphorus (P) limit productivity, which means that the positive relationship between tree richness and productivity may be driven by how N and P are taken up, cycled, retained, and lost. With the exception of N-fixing species, differences in N and P use between tree species are related to root traits and mycorrhizal symbioses. Most root traits are phylogenetically conserved (Valverde-Barrantes *et al*., 2013) and many trees rely heavily on mycorrhizal fungi for N and P foraging and mining. This leads to the prediction that nutrient partitioning should be greatest in stands with the most dissimilar species (tree and fungal), which is supported by evidence of root 'overyielding' in diverse forests (Valverde-Barrantes *et al*., 2015). Further, given that variation in mycorrhizal types or taxa can affect nutrient foraging and partitioning (Johnson *et al*., 2012), trait dissimilarity between roots and their mycorrhizal fungi should lead to the most complete resource use and hence the greatest enhancement of productivity.

Likewise, the percentage of AM vs EM-associating trees in a stand may affect forest productivity. AM and EM symbioses are believed to differ in their acquisition of nutrients (Read, 1991), with AM fungi acting as scavengers of inorganic nutrients and EM fungi acting as miners of organic nutrients (Lambers *et al*., 2008; Phillips *et al*., 2013). Therefore, investigations that quantify mycorrhizal fungal diversity, as opposed to plant diversity, may produce more accurate predictions about the ecosystem consequences of diversity change. In ecosystems where AM and EM trees co-occur (e.g. temperate forests), there may be complementary resource use, leading to elevated productivity (Ferlian *et al*., 2018). To date, these ideas have rarely been tested, but they highlight important knowledge gaps that affect our ability to understand the potential consequences of biodiversity loss.

In addition, if greater couplings elevate primary production, this could lead to greater litter inputs, increased heterogeneity in litter quality and enhanced soil carbon (C) storage. There is some evidence of positive links between plant diversity and soil C stocks in grasslands (Lange *et al*., 2015) and forests (Chen *et al*., 2018) but the role of mycorrhizal richness in this relationship is unexplored.

In forests, EM trees also produce slow-cycling litter that results in the formation of particulate organic matter (POM) at the soil surface; whereas AM trees produce fast-cycling litter that promotes mineral-associated organic matter (MAOM) at depth (Craig *et al.*, 2018). Given that plots with both large stocks of POM at the surface and large stocks of MAOM at depth should hold more total C, mixed mycorrhizal stands with a high diversity of AM and EM taxa may lead to maximal soil C storage. Moreover, different mycorrhizal fungi types and diversity can regulate C storage by stimulating or hampering rates of decomposition (Frey, 2019). To date, empirical assessments of how mycorrhizal diversity affects soil C storage via inputs and/or effects on decomposition are still limited.

IV. Impacts of global changes on plant–mycorrhizal fungal associations

Biodiversity increases the likelihood of ecosystem resistance and resilience to global change. Therefore, understanding how plant and mycorrhizal fungal diversity may individually and jointly respond to global change has many ramifications for future ecosystem function. Global change affects plant diversity in terrestrial ecosystems in many ways since plant responses to the global change drivers vary depending on species identity, community characteristics, and the intensity of the change drivers (e.g. warming, drought, N-deposition; Fei *et al.*, 2017). However, ongoing climate change along with other global change drivers over the long-term can significantly decrease plant diversity (Sommer *et al.*, 2010; Komatsu *et al.*, 2019).

Similarly, mycorrhizal fungal diversity is often impacted rather quickly by global change, but the effects are not consistent. For example, warming can increase (Deslippe *et al.*, 2012), have no effect on (Fernandez *et al.*, 2017), or decrease (Geml *et al.*, 2015) EM fungal richness. Similarly, AM fungal richness sometimes increases (Yang *et al.*, 2013; Kim *et al.*, 2015), but also decreases (Cao *et al.*, 2020) under long-term warming. Experimental shifts in precipitation can both increase and decrease AM fungal richness (Gao *et al.*, 2016; Deveautour *et al.*, 2020). There are few studies of EM fungal richness response to drought, but in one manipulation of drought and warming, the combined effects of both global change drivers decreased EM fungal richness more than either driver alone (Gehring *et al.*, 2020). These idiosyncratic mycorrhizal fungal responses to imposed climate change may depend on the historical climate legacy of both plants and mycorrhizal fungi at a given location (Hawkes *et al.*, 2017), the starting species richness and identity of the mycorrhizal fungal community, the associated plant community and its tolerance to the global change driver, and the duration and intensity of the global change driver itself (Pec *et al.*, 2021).

It is even less clear how the coupling of plant and mycorrhizal fungal diversity responds to global changes. There is no doubt that both abiotic and biotic drivers can affect plant–mycorrhizal fungal associations, but will the existing patterns of plant and microbial diversity remain coupled or become decoupled by these global changes? If plants and mycorrhizal fungi are weakly linked, mycorrhizal fungi that have faster generation times than plants may respond more quickly to global change than plants (*sensu* Smith *et al.*, 2009; Hawkes & Keitt, 2015), effectively decoupling plant and mycorrhizal fungal richness under global change. However, if plants and mycorrhizal fungi are already tightly linked, mycorrhizal fungi buffer plants from extreme environmental stress (Kivlin *et al.*, 2013) and thus maintain diversity relationships between plants and mycorrhizal fungi under global changes.

V. Conclusion

As ecosystems world-wide are experiencing rapid global changes, understanding these fundamental facets of mycorrhizal fungal and plant diversity relations will advance our ability to formulate sound management practices that ensure the sustainability of ecosystems. Given the uncertainty of mycorrhizal fungal and plant diversity relationships across scales, a fundamental question remains as to what factors control the coupling between plant and mycorrhizal fungal diversity patterns. In addition, unraveling how patterns, variation, and complementarity in plant–mycorrhizal fungal communities affect ecosystem functioning, as well as a mechanistic understanding of the factors and processes that contribute to the emergence of such patterns, are critically needed.

To better understand the patterns and dynamics of plant–mycorrhizal fungal association under global change, we need sophisticated experimental manipulations and coordinated sampling efforts at regional, continental, and global scales, with paired plant and mycorrhizal fungal diversity data, ideally with repeated sampling over an extended period. Taking advantage of these coordinated networks of spatial and temporal samplings, the availability of other biodiversity metrics (e.g. phylogenetic, functional, and structural diversity), the inclusion of other mycorrhizal fungal types (e.g. ericoid mycorrhizal fungi), and the consideration of CMNs, along with new computational tools and capacities, we can harness the data revolution to advance key topic areas in plant–mycorrhizal fungal diversity associations. Suggested new research frontiers include, but are not limited to, the following: elucidation of patterns of plant and mycorrhizal fungal diversity coupling in ecosystems across spatial and temporal scales, determination of the key abiotic and biotic drivers (within and across scales) of plant–mycorrhizal fungal coupling patterns, and forecasting of the effects of plant–mycorrhizal fungal couplings on ecosystem functioning under global changes.

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SF, RP and SK drafted the manuscript. All authors contributed to the writing of the manuscript.

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