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# Biodiversity and Ecosystem Function of Arbuscular Mycorrhizal Fungi

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## Abstract

Arbuscular mycorrhizal (AM) fungi play important functional roles in ecosystems, including the uptake and transfer of nutrients, modification of the physical soil environment and alteration of plant interactions with another biota. Several studies have demonstrated the potential for variation in AM fungal diversity to also affect ecosystem functioning, mainly via effects on primary productivity. Diversity in these studies is usually characterized in terms of the number of species, unique evolutionary lineages or complementary mycorrhizal traits, as well as the ability of plants to discriminate among AM fungi in space and time. However, the emergent outcomes of these relationships are usually indirect, and thus context dependent, and difficult to predict with certainty. Here, we advocate a fungal-centric view of AM fungal biodiversity–ecosystem function relationships that focuses on the direct and specific links between AM fungal fitness and consequences for their roles in ecosystems, especially highlighting functional diversity in hyphal resource economics. We conclude by arguing that an understanding of AM fungal functional diversity is fundamental to determine whether AM fungi have a role in the exploitation of marginal/novel environments (whether past, present or future) and highlight avenues for future research.

**Key words: arbuscular, biodiversity, ecosystem, global change, multifunctionality, stoichiometry, trait-based ecology**

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## Introduction: Pathways of Influence and Pervasiveness of Effects

The arbuscular mycorrhizal (AM) symbiosis is unique among the various interactions in which plants engage because of its ubiquity from perspectives both geographic (its occurrence on all continents and in most biomes) and evolutionary (the ability to engage in the symbiosis is lost, not gained). It is fundamentally a nutritional symbiosis, in which nutrients (phosphorus and others) are traded with plant hosts for carbon (sugar and lipids). This very exchange, with all its physiological, biochemical, molecular and ultrastructural intricacies, has captured the imagination of many researchers and explains the prominence of work at the organismal level, i.e., the examination of individual plant–fungal modules. Observations that inoculation with AM fungi could increase host biomass and phosphorus content triggered a flurry of early studies aiming to demonstrate the effects of these fungi across a broad range of plant species, including those of economic importance, in a variety of environmental contexts (Koide & Mosse, 2004; Fig. 1a). Detailed examinations of AM fungal diversity came later (Fig. 1b), particularly facilitated by advances in environmental DNA sequencing. For example, in a global assessment of AM fungal diversity, Davison et al. (2015) observed approximately five-fold variation in virtual taxon (VT; a proxy for 'species') richness among their sampled plots. However, when looking at roots associated with individual plants, they observed extensive variation in diversity in each root sample, ranging from a single VT to as many as 66 (median = 14, 25%/75% quantiles = 8/24). Given the extensive variation in VT richness, which represents a reasonable proxy for species richness, these studies provide further evidence for AM fungi being especially relevant with respect to the ecology of their hosts.

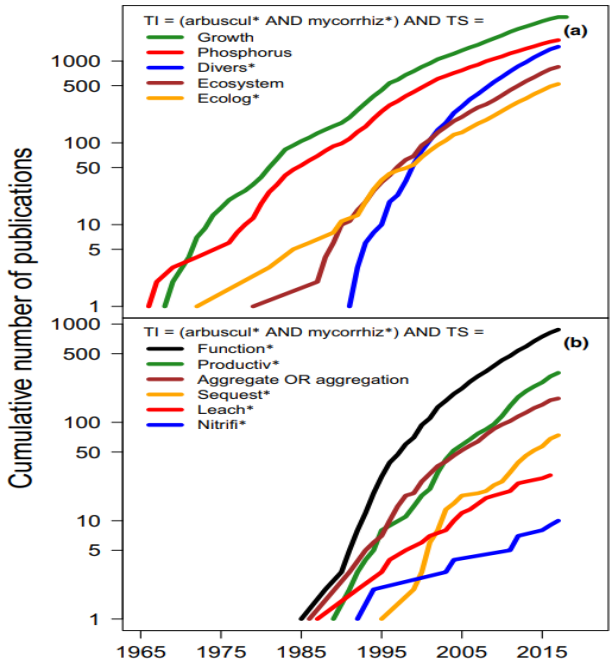


**Fig. 1 (a)Interest in the functional roles of arbuscular mycorrhizal (AM) fungi from an ecosystem perspective has increased rapidly in the last 40 yr. (note y-axis scaling). Before this, work on the symbiosis focused mainly on host plant-level research. More recently, work on diversity within the symbiosis has exhibited rapid growth, largely as a result of advances in environmental DNA sequencing methods. (b) Interest in the diverse functional roles played by AM fungi in**

**ecosystems has also grown in the last 30 yr. Each search was performed on the Web of Science Core Collection on 10 November 2017**

The direct experimental investigation of effects at the plant community and ecosystem levels is a relatively more recent endeavor (Fig. 1b). This lag is, in part, a result of the fact that the examination of the role of the symbiosis at the ecosystem scale requires a different focus, different methods and a different perspective. Many of these methods and much of this perspective arose out of extensive work in the fields of plant and ecosystem ecology, aiming to empirically demonstrate the value of biodiversity by estimating its contribution to ecosystem functioning (Schulze & Mooney, 2012). Integration of AM fungi into this work then became a focus of researchers, who demonstrated that the inclusion of AM fungi in experiments could lead to changes in the properties of ecosystems, some of which were recognized as important for ecosystem functioning (Rillig, 2004). Recognizing that not all AM fungi were equivalent, and that plant fitness outcomes within the symbiosis could be highly variable (Johnson et al., 1997), researchers also began probing the extent to which more diverse communities of AM fungi could contribute to variation in these key functions (e.g., van der Heijden et al., 1998).

Our aim here is to provide an overview of what is known about functional diversity of AM fungi, starting from the perspective of whether more diverse communities promote ecosystem functioning (in the sense of affecting biogeochemical processes within an ecosystem; Schulze & Mooney, 2012). From this, we show that there is general (but not universal) support for the existence of positive biodiversity–ecosystem function relationships, but little understanding of why these relationships exist, and no consensus on their strengths. Thus, we then focus on another aspect of functional diversity, the degree to which AM fungi differ in characteristics that affect their fitness in the environment. Through this, we highlight proposed and potential frameworks that may advance this work beyond the description of phenomena and towards a mechanistic understanding of AM fungal functional diversity and its role in the regulation of ecosystem function. We then propose types of environments for which an understanding of AM fungal functional diversity might be particularly important and where research could be directed, as well as opportunities for progressing this research.

## 1.Pathways of Influence:

Fundamentally, AM fungal communities can influence ecosystem functioning at different hierarchical levels in an ecosystem (Fig. 2; Rillig, 2004). The mycelium can have direct effects on an ecosystem function by interacting with its abiotic environment. Examples of mycelium effects are soil structure, which AM fungi affect through their role in soil aggregation (Leifheit et al., 2014), and soil chemistry, which they can affect via direct uptake of nutrients (Li et al., 1991). AM fungi can indirectly affect ecosystems via their effects on individual plants, which then propagate to the level of an ecosystem function. Data on the range of effects pertaining to individual hosts have been broadly synthesized (Hoeksema et al., 2010; see database: Chaudhary et al., 2016). The fungi can also indirectly influence functioning by affecting plant or microbial community composition, both of which represent ecosystem properties that, in themselves, can affect functioning. AM fungi can affect communities of other soil

microbes and their activities, such as microbes involved in the nitrogen cycle (Veresoglou et al., 2012), and can exert effects on plant community composition on a par with that of many other studied factors (Klironomoset

al., 2011) by modifying, for example, plant–plant (Bever, 2002), plant– pathogen (Wehner et al., 2010) and plant–herbivore (Gehring & Whitham, 2002) interactions. The indirect influences of AM fungi via effects on the biotic environment are complex and can be several steps removed from their direct effects on the physical properties of soil and the chemical properties of soil and host plants. Therefore, we provide context by referring broadly to the evidence that AM fungi (here) and AM fungal diversity (Sections II, VI and VII) play (or could play) functional roles in ecosystems, but focus on the direct effects of AM fungi, explicitly linked to their roles in biogeochemical processes, to further our mechanistic understanding of these roles.

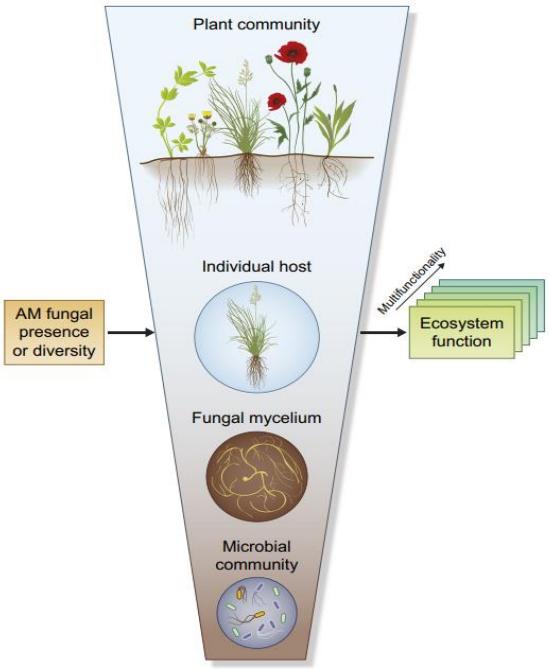


**Fig. 2 Arbuscular mycorrhizal (AM) fungal presence and diversity can affect ecosystem functions at different hierarchical levels. For example, if AM fungal diversity effects on an ecosystem function are to be examined at the level of the plant community, all lower levels are also relevant. This is because AM fungi can influence the composition of the plant community, with rippleon effects to the lower levels in this hierarchy. AM fungi typically have a range of effects on ecosystem functioning, such that multifunctionality is a useful concept (and computational tool) for the capture of such simultaneous effects. AMF, arbuscular mycorrhizal fungi.**

## 2.Pervasiveness of Effects:

Through these different pathways, AM fungi have a pervasive influence on a number of different ecosystem functions (Rillig, 2004; van der Heijden et al., 2015), perhaps a broader influence than that of many other groups of soil microbes. This is, in part, because they are not defined by a function in the first place (unlike, for example, nitrifiers or root pathogens), but rather through a structure formed in plant roots, the arbuscule. Another reason is that they inhabit simultaneously two habitats: the host plant root, the basis for direct effects on the

plant, and the soil, with the potential to influence soil-borne microbes and physico-chemical characteristics. This feature positions AM fungi, for example, at two key points in the carbon cycle: the entry of carbon into terrestrial ecosystems (via the influence on primary productivity)

and the loss of carbon through respiration (via the influence on soil microbes, nutrient levels and soil aggregation).

Given this unique position in terrestrial ecosystems, AM fungi have been postulated or observed to be relevant in the contexts of water balance, energy balance and nutrient/element cycling (Rillig, 2004), with the focus of research having traditionally been placed on the latter. Many effects hypothesized over a decade ago still remain without empirical support, such as changes in light reflectance and absorbance within the canopy as a function of AM colonization, leading to altered energy balance; or AM influences on transpiration at the ecosystem scale, leading to changes in the retention of heat within an ecosystem. However, there has been progress in many areas. For example, AM fungi have been shown to affect soil hydrophobicity (Rillig et al., 2010), with potential consequences for water fluxes (e.g., the partitioning between runoff and infiltration). Mardhiah et al. (2016) has experimentally documented decreased soil erosional losses by surface water flow in the presence of AM fungi. Moreover, much progress has been made in the empirical demonstration (van der Heijden, 2010; K€ohl & van der Heijden, 2016) and conceptual capture (Cavagnaro et al., 2015) of effects of AM fungi on nutrient loss via leaching. In addition, the potential effects of AM fungi on the stability of ecosystem functions have also recently been demonstrated. Yang et al. (2016) found that the presence of AM fungi reduced variation in community productivity across a strong gradient of phosphorus and nitrogen limitations, and increased plant community-level stoichiometric homeostasis (the degree to which plant tissue nutrient content varies independently of soil supply rates). This complements previous work by Yang et al. (2014) that demonstrated reduced temporal stability of community productivity, possibly as a result of the suppression of AM fungi, following benomyl application to plots in a dry grassland.

Overwhelmingly, studies on AM fungal effects on ecosystem functions and stability have manipulated the presence/absence of this entire microbial group. Although useful for demonstrating the potential for the symbiosis to affect these functions, this work provides relatively little insight into how much AM fungi contribute to variation in these functions in real environments, given the ubiquitous nature of AM fungi in terrestrial ecosystems and the vast taxonomic breadth of potential hosts. However, as stated above, large gradients in AM fungal diversity exist both within and between ecosystem types – we review the evidence that this variation is of functional consequence for ecosystems in the next section.

## AM fungal richness effects on ecosystem functions:

There are fundamentally different avenues one can take to tackle the role of AM fungal biodiversity in ecosystem functions and, ideally, these can be combined to generate mechanistic insight. First, one can characterize and compare the effects mediated by different species, learning about the traits responsible for such effects (Sikes et al., 2010; Yang et al., 2017) and supporting the development of mechanistic hypotheses regarding how biodiversity facilitates function. Second, one can co-inoculate with combinations of different AM fungal isolates to study the effects of increasing diversity. This latter step is essential to demonstrate these mechanisms conclusively; such approaches have been taken (Table 1) and they form the basis of our understanding of biodiversity (richness) effects on ecosystem functions to date. Many of these studies have operated for relatively short times (typically a growing season or less), have been conducted in mesocosms using disturbed soils, have used a limited suite of plants, and also have often used a relatively low AM fungal richness (Table 1); this does, to some extent, limit the external validity of these studies. Care must also be taken when interpreting the outcomes of each study, as increasing diversity can result in complementarity among species, leading to overyielding responses, but can also lead simply to a higher probability of an influential (with respect to an ecosystem function) species being present (a 'sampling' or 'selection' effect, discussed by Wardle, 1999). If differentiating among overyielding and selection is an aim of any experiment, it must be designed with the appropriate monoculture and mixture treatments to estimate the effects associated with each mechanism (e.g. Wagg et al., 2011a). In addition, effects of reducing diversity may not be ecologically relevant if manipulations do not reflect real communities or non-random extinction processes (Wardle, 2016). Although competition may lead to a greater likelihood of a functionally similar species becoming locally extinct (Maherali & Klironomos, 2007), beyond this we know little about the drivers of extinction in AM fungal communities (or for soil biota in general; Veresoglou et al., 2015).

A third approach, complementary to the others, is to ask questions about changed communities in real ecosystems (e.g. taking inoculum from soils reflecting different treatments and using them in experiments) and to tease apart AM fungal effects from those of other soil biota along gradients of diversity (for example, using path analysis; Wagg et al., 2014). This latter approach appears to be heavily underutilized relative to studies of other groups of microbes (e.g. Rigg et al., 2016).

Compared with the evidence associated with AM fungal removal, there is much more limited evidence for the importance of AM fungal diversity on ecosystem functions (Table 1). Although generally positive trends between AM fungal diversity and ecosystem functions can be observed in Table 1, the results among studies are often inconsistent, the effects sometimes appear to be associated with individual species, and even variation within studies can be large. As such, it is difficult to draw firm conclusions about when and where we expect biodiversity to promote ecosystem functions. Is it more likely for some aspects of ecosystem functioning than others? Under what contexts (including soil and climate parameters) are the mechanisms underlying these observations based on complementary interactions among AM fungi (whether among species or at higher/lower levels of taxonomic resolution; Hazard & Johnson, 2018) or a result of an increased likelihood of important taxa being present (sampling effect)? In particular, it is important to look at aspects of biodiversity that go beyond species richness, which has been the primary focus, and to look at those that relate more mechanistically to functional diversity. In the following section, we explore these and other aspects of biodiversity.

# Other Dimensions of Biodiversity:

## 1.Aspects of Alpha Diversity

Alpha-diversity focuses on the diversity that exists within a community. It is often used as a proxy for functional diversity in that communities with high diversity are more likely to contain: (1) genotypes that are complementary in their effects on an ecosystem function and/or (2) a genotype that exerts a strong effect on an ecosystem function. Richness has received the most attention from researchers (Table 1), probably because it is easiest to manipulate or measure, but is only one aspect of alpha-diversity and an imprecise proxy of functional diversity (Table 2). Another aspect focuses on the frequency or biomass distributions among taxa given a constant richness (evenness). These are rarely studied, even though they have been demonstrated for bacteria (in principle) to affect ecosystem functioning and stability (Wittebolle et al., 2009; Powell et al., 2015), possibly as a result of an increased likelihood that perturbed communities will remain diverse or retain important taxa when frequency or biomass distributions are even. The study of evenness effects is challenging given the imprecise definition of 'abundance' for AM fungi (e.g. biomass estimation from observations in the soil or in the root), but multiple operational definitions are workable, for example, by using different amounts of inoculum to achieve gradients in realized evenness. Such an approach would work well with simple communities containing species exhibiting different hyphal characteristics, so that the frequency and intensity of colonization by each species could be measured (Abbott, 1982), or for species that can be quantified using quantitative polymerase chain reaction (qPCR) (Thonar et al. 2012).

Yet another aspect of alpha-diversity focuses on the degree of similarity among taxa of a given community based on their shared evolutionary history (phylogenetic – another imprecise proxy for functional diversity) or based on their traits (actual functional diversity if these traits have a mechanistic link to an ecosystem function). Phylogenetic patterns in AM fungal communities vary extensively, exhibiting phylogenetic clustering (closely related taxa frequently observed; Egan et al., 2017), overdispersion (distantly related taxa frequently observed; Maherali & Klironomos, 2007), or both (Maherali & Klironomos, 2012). Maherali & Klironomos (2007) varied phylogenetic diversity by inoculating individual plants with combinations of AM fungal isolates that were closely (low diversity) or distantly (high diversity) related, keeping the number of isolates the same, and found that realized AM fungal richness and plant growth were greater under higher phylogenetic diversity. In this case, phylogenetic diversity was a good proxy for functional diversity for two aspects of function – uptake of phosphorus from soil (extensive hyphal length in one family) and reduction of root colonization by pathogens (extensive intraradical colonization in one order) – because these traits were observed in different clades of AM fungi. However, although a useful model to demonstrate the potential for evolutionary history impacting on an ecosystem function (in this case, productivity), it is unclear to what extent these patterns can be generalized across other ecosystem functions, as there is no evidence that other functional traits are strongly phylogenetically conserved. Therefore, it is premature to suggest that phylogenetic diversity on its own is a useful predictor of any aspect of ecosystem functioning in real environments. That said, Yang et al. (2017), in a meta-analysis of pot experiments involving inoculation with a variety of species of AM fungi, provided additional evidence that different aspects of mycorrhizal function are conserved within clades of AM fungi. In their case, phosphorus uptake was observed to be greater in the presence of species from the Glomeraceae, which is inconsistent with the observations of Maherali & Klironomos (2007). Members of the Glomeraceae also improved plant outcomes with respect to drought tolerance. The observed members of the Gigasporaceae improved

plant outcomes when facing heavy metal stress, whereas members of the Claroideoglomeraceae were beneficial for plants dealing with plant-feeding nematodes.

To understand the mechanisms underlying these differences among AM fungal taxa and the inconsistencies among study outcomes, a more focused, trait-based approach is required, which would also be very useful to address questions of species richness effects on ecosystem functioning (van der Heijden & Scheublin, 2007). One example is the process of soil aggregation (sometimes taken as a part of the broader process of soil formation; Mace et al., Table 1 2012) to which AM fungi contribute in a variety of ways. In this case, as in many other instances, it is helpful to conceptualize the ecosystem function of soil aggregation as consisting of a number of component processes, such as aggregate formation, aggregate stabilization and disintegration (Rillig et al., 2015). A goal is to then experimentally identify the traits of AM fungi that contribute to these component processes, typically by examining a suite of suitable traits among a wide range of isolates. Once these traits are identified, it then becomes possible to perform experiments that examine the additive and non-additive effects of increasing species diversity on soil aggregation. The effects of multiple species that contribute to the same component process will presumably saturate with few added species, whereas the addition of those species that contribute to different component processes will lead to additive (or synergistic) effects on soil aggregation as a whole. Similar exercises are also possible for other ecosystem functions, such as decomposition, for which component processes could be the removal of nutrients, the selective favouring of certain microbial groups or priming, or, for primary production, for which component processes include the supply of various nutrients, pathogen protection and carbon sink activity. Lists of relevant traits and references to methods appear in multiple papers (e.g. van der Heijden & Scheublin, 2007; Aguilar-Trigueros et al., 2014, 2015; Behm & Kiers, 2014; Rillig et al., 2015).

## 2.Community Variation in Space and Time:

Another dimension of diversity is the degree to which communities differ in space and time, referred to as beta-diversity. Valyi et al. (2016) provide an overview of the various scales at which betadiversity manifests, and provide hypotheses as to the most important drivers of community assembly at these scales. One way in which beta-diversity has been proposed to be of functional importance is in facilitating the ability of individual plants to interact independently with different communities of AM fungi. For example, Bever et al. (2009) and Kiers et al. (2011) both provided examples of plants being able to discriminate among spatially separated isolates of AM fungi that vary in their ability to promote plant growth or to supply phosphorus. There are few studies of within-root system variation in AM fungal communities (Wolfe et al., 2009), and the importance of small-scale spatial structure in the distribution of symbionts has a theoretical basis in the evolution and ecology of the mutualistic symbioses (West et al., 2002; Verbruggen et al., 2012). These developments provide a basis for the development of an understanding of why the AM fungal symbiosis has persisted on evolutionary timescales despite observations that plant–fungal interactions sometimes do not reflect mutualistic outcomes and that cheating might occur in certain contexts (Johnson et al., 1997).

Given the three-dimensional nature of soil, community turnover can also be considered in terms of soil depth. In terms of sheer volume, subsoil (often defined as the soil beyond the plough layer or below the topmost soil horizon) is a dominant feature in ecosystems. Nevertheless, our knowledge of AM fungal communities is very limited when it comes to subsoil, and our understanding of their contribution to ecosystem functioning is virtually non-existent. This is despite a growing realization that nutrient reservoirs from the subsoil could be quite important, at least in agroecosystems (Kautz et al., 2013). For example, although effects are variable, nitrogen, phosphorus and potassium uptake from the subsoil can amount to over two-thirds of plant nutrition. Clearly, the study of subsoil AM fungal communities comes with unique logistic challenges, but this is an aspect of biodiversity we cannot afford to ignore. Recently, Sosa-Hernandez et al. (2018) found, using high-throughput sequencing, that subsoil communities of AM fungi are not merely a subset of the topsoil

community, and data hinted at the existence of subsoil specialist taxa; this suggests that these communities may also contribute different ecosystem roles.

Temporal patterns of AM fungal communities can be meaningfully studied at a range of scales, from diurnal to seasonal, interannual and successional. We know of only one study of diurnal dynamics, albeit not resolved to species composition (Hernandez & Allen, 2013). This timescale is certainly not at the top of researchers' lists; however, this level of resolution may offer unique insights into temporal niche separation in activity within the AM fungal community that could also be functionally relevant. Phenological variation among taxa and seasonal dynamics of communities have been frequently documented (e.g., Pringle & Bever, 2002), more recently also using high-throughput sequencing methods (e.g. Dumbrell et al., 2011; Helgason et al., 2014). A clear connection to function has not been made, however, and it would be exciting to test whether such AM fungal-mediated functions shift during the course of a growing season. Successional dynamics have been used to link AM fungal community composition to stoichiometric patterns and shifting needs of the host plant community (e.g., Roy et al., 2017), and also to place occurrence and relative abundance in context with that of other mycorrhizal types (Read, 1991; Read & Perez-Moreno, 2003).

| Diversity dimension | Definition | Relationship with functional diversity |
|---|---|---|
| Richness | Number of taxonomic units, whether species, genotypes or otherwise; defined using morphological and/or genetic approaches | More taxa means greater probability of complementary/contributing traits being present |
| Evenness | Abundance/frequency distribution among taxonomic units at a given richness | More even distribution means greater probability of complementary/contributing traits being present following disturbance |
| Phylogenetic | Extent of shared evolutionary history among taxa present within a community | If traits are constrained within lineages, more lineages means greater probability of complementary/contributing traits being present |
| Trait | Number of unique characters (morphological, biochemical, anatomical or otherwise) present within a community | If traits have a mechanistic link to ecosystem functioning or stability, more traits means greater functional diversity |

Traits may act independently (contributing to the rate or stability of an ecosystem function) or interactively and synergistically (complementing each other and leading to further enhancements to rates or stability).

**Table 1: Dimensions of alpha-diversity (within community) and their relationships with functional diversity, defined as the presence or frequency of organismal traits that mediate ecosystem functioning**

## Back to basics – primary axes of niche differentiation by AM fungi:

### 1.Complementarity and competition among AM fungi

There are some very simple questions that have not yet been satisfactorily answered for AM fungi, yet are relevant for the ecological processes and environmental functions mentioned above. Research tends to focus on complementarity in terms of differing contributions to primary production by associated plants or other functions, but not in terms of the interactions among fungi themselves. For instance, is there a relationship between AM fungal diversity and AM fungal biomass production? This is the first question that the initial large-scale plant diversity–ecosystem function studies addressed (although other functions were also addressed in

those early studies; e.g. Naeem et al., 1994), and all tended to do so as productivity is measured on the same trophic level that is being manipulated. Such a relationship would be expected for AM fungi if taxa differed in their abilities to take up and transfer nutrients or in the forms of nutrients that they take up and transfer. For example, Hawkins et al. (2000) observed that isolates differed in their abilities to take up and transfer nitrogen, whether as nitrate, ammonium or glycine. Hodge & Fitter (2010) found that an isolate of Glomus hoi could obtain proportionally more nitrogen from an organic source than could an isolate of 'Glomus mosseae' (species name as used in the source), although this was not consistently observed between experiments. A few studies have measured AM fungal productivity in relation to diversity, such as that of van der Heijden et al. (1998), where hyphal length was observed to increase with increasing richness of AM fungi. Such a response has consequences for resource availability in soil as carbon and nutrients are sequestered in plant or fungal biomass; for instance, van der Heijden et al. (1998) observed that AM fungal richness led to increased phosphorus concentrations in plant tissue and reduced levels in the soil. However, these responses appear to depend on the identities of the taxa that are included: Jansa et al. (2008) found that hyphal lengths in soil sometimes decreased, and were never observed to increase, when plants were inoculated with multiple species of AM fungi compared with single inoculations. Environmental context may also be important for the determination of the outcomes of inoculations with diverse mixtures of AM fungi. Wagg et al. (2011a) found that inoculation of multiple AM fungal species generally had negative effects on root colonization by each species (measured using qPCR) compared with colonization following monospecific inoculation, suggesting interspecific competition. However, these interactions appeared to be weaker when less sand was mixed into the soil, with potential complementarity in colonization responses observed for some combinations. In another study, Wagg et al. (2011b) also found that colonization by these AM fungal species depended on the relative abundance of a grass and legume species in each pot. Roger et al. (2013) found that closely related genotypes of Rhizophagus irregularis were more likely to exhibit symmetrical colonization patterns of plant roots (measured using relative frequencies of marker genes) than were distantly related genotypes, but total abundance (measured using qPCR) was too variable to demonstrate complementarity.

These patterns suggest that niche differentiation exists, but the mechanisms underlying this differentiation are poorly understood. Most work has focused on drawing inferences based on broad biogeographical patterns. For example, soil texture may be an important determinant of whether species in the Gigasporaceae or the Glomeraceae are abundant within AM fungal communities (Lekberg et al., 2007). However, even with evidence that environmental filtering can be an important driver of AM fungal community composition (Davison et al., 2011; Caruso et al., 2012), extensive variation remains within these communities which has not yet been accounted for (Powell & Bennett, 2016), and might result from strong interactions among taxa sharing a similar niche. Variation in outcomes among co-inoculated AM fungi in some of the studies described above (Maherali & Klironomos, 2007; Jansa et al., 2008; Wagg et al., 2011a) indicate that the strengths of interactions among AM fungal taxa are not constant and suggest opportunities for the identification of the mechanism(s) underlying relationships between species composition and hyphal productivity within AM fungal communities. There are a few examples that suggest axes of niche differentiation based on colonization strategy (whether the bulk of fungal biomass is invested into root or soil colonization; Hart & Reader, 2002) and hyphal spread (the distance from the root at which hyphal production occurs; Jakobsen et al., 1992). As described above for the evaluation of relationships between AM fungal diversity and plant productivity, care must be taken to design experiments to distinguish between complementarity and selection effects (Wardle, 1999, 2016).

## 2. Life history, environmental filtering and functional diversity

Hart et al. (2001) and Chagnon et al. (2013) made cases for the classification of AM fungi into functional groups that differentiate among life history strategies based on the 'r–K' axis (Pianka, 1970) and the 'C–S–R' triangle (Grime, 1979). Taxa are classified into those that are capable of persisting in environments with strong competition for resources and exhibiting phenotypes linked to efficient resource access and use ('competitors' or 'K-selected'), those able to tolerate abiotic stress and exhibiting phenotypes indicating maintenance ('stress tolerators'), and those effective at colonizing new or disturbed environments and exhibiting rapid growth phenotypes ('ruderals' or 'r-selected'). Therefore, taxa can be classified either by their attributes when grown under particular environmental conditions (e.g. hyphal production and turnover rates, sporulation rates, frequency and timing of root colonization events) or by the type of environment in which they are commonly found (e.g. within stages of plant community succession, levels of land use intensity or in the presence of an abiotic stressor). Comparative analyses across many taxa are essential for the former, requiring cultured isolates or the ability to identify organisms from which traits are measured in situ (e.g. genomic traits). The inference of traits based on shared evolutionary history is sometimes proposed as a means to extrapolate traits to understudied AM fungi, but is problematic as the explanatory power of phylogenetic relationships, although statistically significant, is quite low (Powell et al., 2009; Koch et al., 2017).

Basing life history assessments on the type of environment in which AM fungal taxa are found has advantages, particularly in how community data arising from environmental DNA sequencing can be used to inform these assessments. However, these assessments are often based on environmental characteristics that are clearly relevant for plants and animals, such as vegetation clearing, but may have less direct relevance for AM fungi, other than via effects on the pool of available hosts. Because of this, we may be overlooking other important axes of environmental variation. For example, what are relevant 'disturbances' for an AM fungus? These may vary depending on the life history stage of interest. Disturbances such as tillage (Bowles et al., 2017) and vegetation clearing (van der Heyde et al., 2017) are among the most frequently studied, and ruderal strategies involving frequent dispersal and rapid growth may be successful for the recolonization of these environments (van der Heyde et al., 2017). However, the comparison of fungi in these environments with those in sites that have not experienced these large-scale events implies that disturbance is unimportant in these reference sites. Ruderal strategies may also be successful in these seemingly undisturbed environments if roots turn over frequently, root mortality is high, earthworms or other burrowing animals are active or the availability of photosynthate is ephemeral. This might explain why, for example, Hartet al.(2016) did not find that frequencies of putative disturbance-tolerant AM fungal taxa differed between logged and unlogged old-growth forest, despite compositional differences in AM fungal communities on the whole.

## Functional diversity of AM fungi – a role for biological stoichiometry?

The issues raised in the previous section need to be addressed to reach a mechanistic understanding of AM fungal community assembly in natural and managed systems, which may indirectly inform predictions of how ecosystem functions are likely to respond to changes in AM fungal diversity. However, an alternative approach

that explicitly links functional diversity of AM fungi to variation in ecosystem functions via growth strategies and resource economics (Johnson, 2010) may provide more concrete answers to questions regarding the functional importance of AM fungal diversity. Using a global database of plant traits, Dıaz et al. (2016) demonstrated that plants exhibit growth strategies that can be collapsed down to two main axes differentiating form and function: (1) representing plant size, and (2) representing leaf economics. The latter axis is largely associated with differentiation between leaves representing 'acquisitive' (high specific leaf area and nitrogen concentration, indicating high photosynthetic capacity) and 'conservative' (low specific leaf area and nitrogen concentration, with reduced photosynthetic capacity but longer lifespan) types. The application of such a framework to AM fungi would be valuable given the prominence of resource exchange in the symbiosis and its relevance for hyphal economics, but this is, in practice, not straightforward. First, AM fungi are heterotrophic and so there is no direct corollary between nitrogen concentration as an indicator of carbon acquisition in plants (as a major component of rubisco in leaves) and fungi (as a major component of chitin in cell walls). In addition, the size of an AM fungus is a difficult concept to define operationally given their filamentous nature and the potential for anastomosis to lead to the connection of previously separate colonies. However, it may be possible to address this indirectly based on theorized aspects of biological stoichiometry (Sterner & Elser, 2002).

The 'growth rate hypothesis' reflects the variable stoichiometric constraints on organisms depending on how rapidly they grow, as fast-growing organisms are required to transcribe phosphorus-rich RNA in the process of producing more protein. The hypothesis predicts lower tissue nitrogen : phosphorus (N : P) and protein : RNA ratios for fast-growing organisms, and patterns consistent with this prediction have been observed for comparisons among (e.g. Wright et al., 2004) and within (e.g. Matzek & Vitousek, 2009) species of plants. This hypothesis has not been tested on AM fungi, which can vary extensively both within and between species in their rates of root colonization, hyphal extension and spore production (Graham & Abbott, 2000; Hart & Reader, 2002; Koch et al., 2004), and can exhibit temporal patterns of hyphal growth and decline (Miller et al., 1995; Hernandez & Allen, 2013). There are few examples of nitrogen (Hodge & Fitter, 2010) or phosphorus (Hammer et al., 2011a,b) being measured on AM fungal hyphae, and only one to our knowledge in which both were measured (at least certain isotopes: 14N, 15N and 31P; Kaiser et al., 2015).

An extension of the growth rate hypothesis accounts for the variation in the extent to which organisms alter their growth rates in response to changing supplies of nitrogen and phosphorus. Under conditions in which certain nutrients are not limited, plants (and presumably AM fungi) can accumulate higher concentrations of these nutrients, referred to as 'luxury consumption'. This results in tissue N : P ratios that change in a manner resembling soil N : P ratios, and thus these plants exhibit low stoichiometric homeostasis. High stoichiometric homeostasis is reflected in relatively small changes in tissue N : P with changing soil N : P, and is an outcome of the allocation of supplied nutrients to growth. Thus, plants (and, presumably, AM fungi) that exhibit 'acquisitive' strategies, allocating resources to resource acquisition and rapid growth, are less likely to luxury consume, and exhibit higher stoichiometric homeostasis, than those that exhibit 'conservative' strategies.

Given that the AM symbiosis is primarily a nutritional symbiosis, the role of soil fertility in the AM symbiosis has been widely studied and is of general interest to researchers looking at all aspects of mycorrhizal research, from molecules to ecosystems. Soil fertility plays an important role in the context dependence of

mycorrhizal outcomes (Johnson, 2010; Johnson et al., 2010), its impact on mycorrhizal fungal abundance in ecosystems (Treseder, 2004) and its effects on individual AM fungal taxa (van der Heyde et al., 2017). The definition of functional diversity of AM fungi within a conceptual framework based on biological stoichiometry is especially promising for relating AM fungi to ecosystem functioning, particularly to aspects directly related to carbon and nutrient dynamics, for several reasons.

(1)The framework is reconcilable with that of hypotheses predicting that the direction and strength of mycorrhizal growth responses depend on the type and degree of nutrient limitation (Johnson, 2010). Johnson et al. (2015) demonstrated that positive plant growth responses to inoculation with AM fungi were more likely to be observed in soils that were naturally phosphorus limiting than nitrogen limiting. AM fungal demand for nitrogen (3–5% of fungal tissue; Hodge & Fitter, 2010) is probably stronger than that of the host plant suggesting that competition for nitrogen among symbionts might be an

important determinant. AM fungal-mediated transfer of nitrogen to host plants has been demonstrated in carefully controlled experiments (e.g. Hodge & Fitter, 2010; Fellbaumet al., 2012), but whether this represents an appreciable proportion of nitrogen under real conditions still needs to be determined (Veresoglou et al., 2012).

(2)The framework may also be reconciled with biological market theory, and further emphasizes the important role of phosphorus in the acquisition of carbon from the host plant. If differential allocation of carbon from plants to fungi is based on rules consistent with biological markets, fitness outcomes of symbiotic interactions will also be guided by trade-offs in phosphorus allocation by the fungus. If too much phosphorus is allocated to the host plant, the carbon rewards received in return may not be converted into growth because insufficient phosphorus is available for RNA synthesis. The correct balance of phosphorus allocation may depend on a number of factors, such as the availability of phosphorus in soil and potential variation among AM fungi and their host plants in phosphorus use efficiency

(3)The distributed nature of the mycelium and the formation of common mycelial networks (CMNs) mean that the dynamics of resource allocation and exchange could be quite complex (Walder et al., 2012). A fungus forming a CMN needs to be responsive to the possibility of receiving carbon from multiple hosts and commit resources to hyphal growth, gene expression and protein production in these locations. Acquisitive and conservative fungi may differ in the degree to which they respond to carbon availability, the extent to which they asymmetrically commit resources to different hosts or even the ability to integrate information among different hosts to optimize resource allocation. If this is the case, CMNs formed by acquisitive fungi might be less likely to lead to the asymmetric trade outcomes and apparent facilitation observed by Walder et al. (2012) if they are more likely to allocate resources to exchange with a host that supports rapid and efficient fungal growth.

(4)Biological stoichiometry and its related hypotheses are fundamental to our understanding of niche differentiation and biodiversity maintenance. Thus, interspecific and intraspecific variation among AM fungi in their allocation of resources to growth and their ability to regulate N : P homeostasis with changing supply may help to explain the variation in AM fungal diversity within particular environments as well as the compositional turnover in space and time.

(5)Basing a framework of functional diversity for AM fungi on N : P stoichiometry allows for direct, tangible relationships to be made between the community ecology of AM fungi and aspects of their functionality relating to plant nutrition and soil fertility (Fig. 3). This will allow the inclusion of parameters representing ecological

interactions among AM fungi, and with their chemical environment, into models of resource exchange between plants and fungi (Schnepf & Roose, 2006; Schnepf et al., 2008), or pools and fluxes of organic matter and

nutrients in soil (Orwin et al., 2011).

(6) Although AM fungal N : P is not a widely measured parameter, methods exist to obtain these measurements on bulk samples of collected mycelium (e.g. mass spectrometry – Hodge & Fitter, 2010) or on individual spores or hyphae (e.g. particle-induced Xray emission – Hammer et al., 2011a,b; secondary ion mass spectrometry – Kaiser et al., 2015). Similarly, RNA and protein concentrations could be measured on AM fungal mycelium provided that sufficient material is obtained. Pepe et al. (2017) described a plate-based system for collecting AM fungal extraradical mycelium, observing averages between 2.7 and 5.4 mg of mycelium per plant for three AM fungal species. Pepe et al. (2017) also extracted RNA from these mycelia and observed extensive variation among species (15.7, 65.5 and 87 lg mg1 of mycelium for Funneliformis mosseae, Rhizophagus irregulare and Funneliformis coronatus, respectively). Alternatively, hyphal traps (Wright & Upadhyaya, 1999; Olsson & Wilhelmsson, 2000; Neumann & George, 2005) could be employed to select for AM fungal mycelium in pots or field soils, although measurements would only be valid if it could be ensured that AM fungal biomass was sufficiently greater than that of other fungi.

## Opportunities and the way forward

Understanding the role of AM fungal communities in ecosystem functions is clearly a major current and future focus in mycorrhizal research, particularly given the impact of various factors of global change and the need to sustainably manage agroecosystems. In particular, ecosystem modellers are increasingly looking to mycorrhizal ecologists for ways to include mycorrhizal parameters in their frameworks in order to capture major dynamics. As we have outlined above, much progress has been made in recent decades, but much fundamental work still remains to be carried out. Notwithstanding these gaps, we see major opportunities for future research (see Table 4).

One important area will be the discovery of markers indicative of function: prokaryotic molecular ecologists have an ever-increasing arsenal of target genes at their disposal with which they can dissect potential functionality. AM fungal ecology lags behind, and no functional gene markers are available as yet. Similarly, metabolic markers of AM fungal functionality would be of tremendous value for the measurement of the actual contributions of AM fungi to ecosystem functions. These would be particularly useful for testing biodiversity–function relationships in AM fungal communities in space and time, particularly when markers can be used to distinguish between different component processes to which AM fungi contribute, or to compare contributions to multiple ecosystem functions. Multifunctionality is a concept of increasing prominence in biodiversity–functioning studies. Given the many functions that AM fungi mediate, perhaps this concept is uniquely suited for the study of the ecosystem contribution of this group of fungi (van der Heijden et al., 2015).

Mycorrhizal ecologists, especially those working at the ecosystem interface, are aware that AM fungal communities do not act in isolation. Clearly, AM fungi are part of the soil foodweb, and participate in a number of other interactions with organisms other than their host plants, including associated and endosymbiotic bacteria, with evidence that these relationships can vary among AM fungi (e.g. Rillig et al., 2005, 2006). This of course creates one of the main challenges in attributing any proportion of ecosystem function to AM fungi. Just as an example, one of the better researched functions of AM fungi at the ecosystem scale, soil aggregation, is also carried out by a plethora of other soil biota, who all contribute directly and interactively to the soil aggregation process (Lehmann et al., 2017). In all such cases, the challenge is to disentangle the unique portion of variability attributable to AM fungi under any given set of conditions. For this task, data synthesis, such as meta-analyses and machine-learning algorithms, and path analysis techniques can be used. These latter approaches, although ultimately based on observational data, take a step towards making causal inferences based on prior knowledge (Eisenhauer et al., 2015) or, when this is unclear, are still useful for estimating the strength of relationships between biodiversity and function (Delgado-Baquerizo et al., 2017).

An important consideration is that most studies of the role of AM fungal biodiversity on ecosystem function have been conducted in or focused on grassland systems (see Table 1). Further research can address this bias by focusing on understudied systems, such as temperate (Hart et al., 2016), Mediterranean (Brundrett & Abbott, 1991) and tropical (Janos, 1980) forests. For instance, the study of the responses of slower growing and/or longer lived species provides opportunities to characterize how temporal dimensions of AM fungal diversity (Husband et al., 2002) may contribute to temporal variation in ecosystem functions (Bardgett et al., 2005), and to target traits of hosts that have consequences for ecosystems at large scales (Powell et al., 2013, 2017). It may also be important to overcome cognitive biases: for example, the documentation and acceptance that AM fungi have no noteworthy contribution to a given ecosystem function in a given situation is just as valuable as the documentation of (positive) effects. This realization has already become paradigm at the level of individual host plant effects (e.g. Johnson et al., 1997).

To summarize, we have identified several opportunities to advance our understanding of how AM fungal biodiversity has contributed, and will continue to contribute, to the functioning of terrestrial ecosystems. In particular, we argue that this can be achieved with work that addresses dimensions of diversity other than AM fungal richness, allows better predictions of outcomes among co-occurring AM fungi and makes explicit linkages between the ways in which AM fungi interact with their environment.

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