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Mycorrhizal fungal and tree root functional traits: Strategies for integration and future directions

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Abstract

Plant functional traits offer ecologists quantifiable characteristics that may be used to determine the underlying mechanisms and drivers of processes at scales ranging from individual plants to entire ecosystems. While research on belowground functional traits has increased in recent years, most of this work has not fully considered the traits of mycorrhizal fungi, key symbionts responsible for much nutrient uptake and soil exploration in trees. We argue that, because of the important role of mycorrhizae in resource uptake, the measurement of belowground plant traits without the inclusion of mycorrhizal fungal traits potentially misses key mechanistic factors affecting plant performance, which has implications across ecological scales. In doing so, we provide a synopsis of current and past work on plant root traits and mycorrhizal fungal traits. Finally, we suggest potential key fungal traits to be measured and possible methods for measurement as ways to address the current gaps in our knowledge.

Key Words: belowground traits, functional ecology, fungal traits, mycorrhizal traits, root traits

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Introduction

Functional traits provide ecologists measurable, numerical quantities that can give insight into the mechanisms and drivers of ecological processes at the individual, population, community, and ecosystem level. Understanding these patterns is vital if we hope to anticipate how and why organisms, communities, and ecosystems will respond to expected outcomes of global climate change. Plant functional traits, in particular, have drawn recent attention (Wright et al. 2004, Reich 2014, McCormack et al. 2017), but the majority of studies have primarily focused on aboveground traits – *i.e.,* leaf, stem, and bole (*e.g.,* Wright et al. 2004, 2017, Umaña and Swenson 2019). Research on aboveground traits has offered substantial insight into the ecology of plants across ecological scales; however, aboveground traits pertain primarily to competition for a single resource: light (Wilson and Tilman 1993). More recent work has begun to emphasize belowground traits – *i.e.,* root branching, length, specific mass – that enable plants to forage for multiple soil resources (Withington et al. 2006, McCormack et al. 2012, McCormack and Iversen 2019, Delpiano et al. 2020). Belowground traits offer tremendous potential to explain ecological mechanisms and patterns because, unlike with aboveground plant traits, belowground traits facilitate competition for a broader array of resources, including water and growth-limiting nutrients (Wilson and Tilman 1993, Weemstra et al. 2016). Furthermore, competition for soil resources occurs in both time and space (Schenk 2006), which the belowground portions of plants can integrate across.

Interestingly, the majority of work thus far on belowground plant traits has not considered the extent to which mycorrhizal fungi facilitate the acquisition of soil resources in a manner that is integrated with plant root traits, despite clear evidence of its importance (as discussed in Weemstra *et al.*, 2016; McCormack *et al.*, 2017). Mycorrhizae are responsible for a

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large proportion of soil exploration and nutrient uptake in 80-94% of terrestrial plants (Smith and Read 2008). Here, we argue that the inclusion of mycorrhizal fungal traits, along with the measurement of root traits, is vital to gain an understanding of the belowground foraging strategies of plants. Initial investigations of the coordination of root traits and the presence of mycorrhizal– albeit not traits – has revealed the importance of mycorrhizae on root characteristics at global, interspecific scales, suggesting a potentially strong link between mycorrhizal fungal and plant root function (Bergmann et al. 2020, Carmona et al. 2021, Weigelt et al. 2021). At local and intraspecific scales, nutrient foraging strategies have been shown to alternate between root proliferation and mycorrhizal hyphal growth based upon mycorrhizal type, root diameter, and both nutrient levels and sources (Eissenstat et al. 2015, Chen et al. 2016, Cheng et al. 2016). These patterns at both inter- and intraspecific and global and local scales point to the potential importance of mycorrhizal fungi in resource acquisition, with their subsequent impacts on ecosystem function (Van Der Heijden and Scheublin 2007, Treseder et al. 2018).

The important function that mycorrhizae mediate suggests it is likely that root and fungal traits are not independent of one another in their impact on plant performance. Mycorrhizae potentially represent a cohesive biological unit in which roots and mycorrhizal fungi can respond separately or in unison to environmental conditions (Ostonen et al. 2017, Pellitier and Zak 2021a). Therefore, excluding one or the other in studies of belowground traits potentially leads to missing key factors effecting the belowground competitive characteristics of plants. With plants mediating ecosystem processes like nutrient and carbon cycling, it is important to understand how the functional traits of plants and mycorrhizal fungi combine to influence the acquisition of

soil resources, especially as resource availability continues to shift as a result of climate change (Schulte-Uebbing and de Vries 2018, Terrer et al. 2019, Du et al. 2020).

Here, we address three main points. First, we aim to synthesize the recent thought on root and mycorrhizal traits, identifying our current state of knowledge. We do not, however, provide a comprehensive review of root trait literature, as this has been accomplished numerous times, (McCormack et al. 2015, Weemstra et al. 2016, McCormack and Iversen 2019, Freschet et al. 2020), instead identifying trends in key traits related to resource acquisition that have been highlighted in recent work (Díaz et al. 2016, Carmona et al. 2021, Weigelt et al. 2021). We focus primarily on applications to woody plants, specifically trees, because of their association with both arbuscular and ectomycorrhizal fungi, as well as their important roles as regulators in global nutrient cycles and potential for climate change mitigation via carbon sequestration (Goodale et al. 2002, Luyssaert et al. 2008, Smith and Read 2008, Fowler et al. 2013). Second, we point to what future directions could productively advance this area of plant and mycorrhizal fungal ecology. Finally, using the previous work and potential future directions we propose a novel framework explaining patterns of variation in plant and mycorrhizal fungal traits at the intra- and interspecific level that we believe warrant further testing and exploration.

We use the conceptual framework put forth by Chaudhary et al. (2022) that divides mycorrhizal traits into three categories: 1) plant mycorrhizal traits – those traits specific to the anatomy, morphology, and physiology of plants in mycorrhizal symbioses, 2) fungal mycorrhizal traits – those traits specific to the anatomy, morphology, and physiology of the fungi in mycorrhizal symbioses, and 3) symbiotic mycorrhizal traits – those traits relating to the interaction between plant and fungus in the mycorrhizal symbiosis (Chaudhary et al. 2022). We provide our own framework for research going forward by overviewing observed trends in root

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traits, including the identification of tradeoffs and patterns of variation at both the inter- and intraspecific scale. Owing to the relatively recent development of mycorrhizal trait research, we also summarize studies of fungal traits, in general, with the goal of identifying key findings, promising methods, existing resources, and future directions.

Root and Plant Mycorrhizal Traits

Modern research on plant root function was pioneered by Fitter beginning in the 1980s (Fitter 1987, Fitter et al. 1991). Fitter's initial work (1987) posited that selection acted on, not individual roots, but rather the entire root system. He therefore emphasized the need to examine the entire root system of a plant, and not its individual components. In doing so, Fitter identified a key tradeoff in root architecture between exploration of space and the efficiency of nutrient transport (Fitter 1987, Fitter et al. 1991). More recent research on belowground traits has narrowed focus from the entire root system to quantitative functional traits for fine roots that are responsible for nutrient uptake (McCormack et al. 2015) (Table 1). For the remainder of this article we too will focus our attention on fine roots, specifically those identified as absorptive fine roots, which are responsible for the uptake of nutrients and not simply their transport (McCormack et al. 2015).

At a global scale, when including water and nutrients in the examination of whole plant traits, plants can be categorized along an axis of "slow-fast", with a tradeoff between root lifespan and root tissue density (Reich 2014). "Faster" plants display lower root tissue density and root lifespan, whereas "slower" plants tend to possess roots with higher tissue density and longer lifespans (Reich 2014). Additionally, studies of root traits at the global scale demonstrate that climate appears to be a key driver of root thickness, root nutrients, specific root length, and root tissue density. Plants in temperate and cooler climates displaying thinner roots with higher

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N concentration (*i.e,* ion uptake enzymes) and lower root tissue density compared to roots in warmer, tropical climates (Freschet et al. 2017, Laughlin et al. 2021). However, these studies ignore the global patterns of mycorrhizal associations in which ectomycorrhizae (EM) tend to be more common in cooler and more temperate climates compared to the warmer, tropical regions of the Earth which are dominated by arbuscular mycorrhizae (AM). This observation represents a potentially important driver of root trait variation that may be separate from, or interact with, climate (Soudzilovskaia et al. 2017).

To resolve the differing approaches to explain global variation in fine root traits that are inclusive of mycorrhizal association, others propose that, rather than climate or soil resource availability, it is evolutionary history that underlies the observed variation (Valverde-Barrantes et al. 2017, Ma et al. 2018). Using this framework, an ancestrally conservative strategy characterized by shorter, thicker roots typically associating with AM fungi, with more derived taxa displaying longer, thinner roots tending to associate with EM fungi (Ma et al. 2018, Bergmann et al. 2020).

Environmental variables play important roles in determining root traits at the local and intraspecific level as well as the global, interspecific scale. Small-scale heterogeneity in soil nutrient availability can be influential; roots in N-rich soil patches display different traits compared to individuals of the same species in N-poor patches (Pregitzer et al. 2002, Eissenstat et al. 2015). For example, higher soil N availability results in increased root growth rate, increased branching of higher order roots (i.e. fine roots), longer roots per unit mass, and high root N concentration compared to fine roots in patches with lower N availability (Pregitzer et al. 2002, Eissenstat et al. 2015, Chen et al. 2016). Furthermore, the effects of these local differences in soil characteristics seem to differentially effect species with different trait syndromes – *i.e.*,

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species with long, thin roots compared to species with shorter, thicker roots – reinforcing the important role that phylogenetic relationships play in the determination of root traits (Weemstra et al. 2021). More and more studies have begun to include mycorrhizal symbiotic traits in their analysis of root traits, especially mycorrhizal type and/or the degree of mycorrhizal colonization, in their analysis. Results of this work identified a second axis to the slow-fast continuum above; an axis describing the degree to which plants rely on mycorrhizal fungi for nutrient acquisition ranging from "do-it-yourself" to "outsourcing to mycorrhizae" (Bergmann et al. 2020). However, little work to date has explicitly included mycorrhizal fungal traits while examining plant root traits.

Fungal Mycorrhizal Traits

Broadly across all fungi, the bulk of prior work on fungal functional ecology has focused on classifying fungi into qualitative functional groups (*e.g.,* Rambold & Agerer, 1997; Romero-Olivares *et al.*, 2021). This work has primarily been done via the use of databases storing information compiled from various studies of fungi, with FUNguild being one of the most common (Nguyen et al. 2016). Here, fungi are classified into functional groups such as saprotrophs, mycorrhizae, pathogens, etc. While this certainly has its uses, this process is often complicated by the fact that fungi can function across multiple trophic levels, depending on their current environment (Romero-Olivares et al. 2021); that is, a single fungal taxa can exhibit symbiotic, saprotrophic, and endophytic capacities (Pellitier and Zak 2021b). Furthermore, functional group does not provide quantitative information on resource acquisition and use that can be used to understand and potentially predict an individual's performance and ecosystem processes (Aguilar-Trigueros et al. 2015).

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Specific to mycorrhizae, fungi are typically classified according to how they associate with their plant symbionts, with the two most common types for trees being AM and EM (Smith and Read 2008). AM fungi are the more common of the two types globally, and until recently were thought to have a single evolutionary origin; however, recent works suggests that there may be at least two, but both are hypothesized to be the more ancient of the association types (Smith and Read 2008, Van Der Heijden and Horton 2009, Orchard et al. 2017). EM fungi evolved more recently and represent a polyphyletic group having evolved multiple times (~ 85 times) through evolutionary time (Smith and Read 2008, Pellitier and Zak 2018). Additionally, the two types of mycorrhizae differ in the mechanism by which they colonize roots with AM fungal hyphae appressing plant cell membranes, whereas EM fungi forms a sheath around the outside of roots and enters the root only through the intercellular spaces (Smith and Read 2008). More recent work has begun to emphasize the measurement of functional traits, rather than functional groups. Functional traits are more ideal than simple functional groups, because they allow for additional specificity via the measurement of quantifiable characters especially in regard to performance in differing environmental conditions. For example, mycorrhizal traits commonly measured include hyphal growth (overall and/or rate), hyphal diameter, hyphal nutrient content, distribution of fungal biomass between soil and roots, enzymatic activity, and gene frequency (Table 2) (Crowther et al. 2014, Treseder et al. 2018, Romero-Olivares et al. 2021).

Examining the traits of wood decomposing fungi lead to the discovery of a potential tradeoff like the "fast-slow" continuum suggested in plants by Reich (2014). On one end of the spectrum, fungi have lower hyphal growth rates and lower organic matter decay potential (*i.e.,* genes encoding enzymes that oxidize or hydrolyze plant cell wall constituents or soil organic matter), but are much more tolerant of environments with low resource availability (Maynard et

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al. 2019, Lustenhouwer et al. 2020). On the other end of the spectrum are fungi with high hyphal growth and organic matter decay potential, but a low tolerance for resource-poor environments (Maynard et al. 2019, Lustenhouwer et al. 2020). Because EM fungi evolved from saprotrophic ancestors, it is possible that a similar tradeoff could exist among them, but this aspect of their functional ecology remains to be explored. It is important to note that as this potential tradeoff is explored, researchers identify what qualifies as a resource limited environment for mycorrhizal fungi. Understanding resource limitations for mycorrhizal fungi has implications for not only the fungi, but also the mycorrhizal plant symbiont function and performance. For example, an environment poor in resources vital to mycorrhizal fungal plant symbionts may not necessarily be limiting to fungi if ample carbon (*i.e.,* energy from photosynthate) is allocated by the plant to support fungal function and therefore resource acquisition (Moeller et al. 2014). Alternatively, a light poor environment may switch mycorrhizae from mutualists to parasites, as they become an energy drain on the plant via excess allocated carbon (Ibáñez and McCarthy-Neumann 2016).

Analyses of fungal traits in filamentous fungi in general (a group that includes wood decaying fungi as well as mycorrhizal fungi) have suggested additional tradeoffs. For example, in analyses of filamentous fungi that form networks of mycelial hyphae to forage for nutrients it was discovered that strategies ranged from networks consisting of many hyphal interconnections with multiple pathways for nutrient transport and therefore resilience to damage but with high construction costs, to networks with few interconnections and nutrient transport pathways but with low construction costs (Aguilar-Trigueros et al. 2022).

Gene frequency analysis offers a relatively simple and cost-effective method that has proven to provide reliable results in the analysis of fungal traits (Fierer et al. 2014, Pellitier et al. 2021a). Using functional groups, in tandem with the frequency of genes increasing access to N

bound in soil organic matter, provided insight into the response of various fungi to environmental stressors such as shifts in climate, and also revealed similarities between ectomycorrhizae and brown-rot fungi providing a potential evolutionary link between the two (Romero-Olivares et al. 2021). Furthermore, in examining the gene frequency of fungi across a soil inorganic N availability gradient, Pellitier et al. (2021) observed a similar change in the frequency of genes encoding for enzymes providing access to organic nitrogen in soil in the EM colonizing the roots of *Quercus rubra* (class II fungal peroxidases; Pellitier *et al.*, 2021a).

Mycorrhizal Fungi, Root, and Symbiotic Traits

A relatively small body of work encompasses both plant and mycorrhizal traits in tandem. Those studies have focused almost exclusively on colonization rates or simply the type (*i.e.,* AM compared to EM) of mycorrhizal association. From these studies, it appears that plants associating with AM fungi trend towards shorter and thicker roots, whereas EM associating plants tend to have longer and thinner roots (Moeller et al. 2014, Chen et al. 2016, Cheng et al. 2016). Furthermore, recent work including both mycorrhizae and plant roots has identified a tradeoff in the use of mycorrhizae or roots as the primary source of nutrient acquisition (Bergmann et al. 2020). Specifically, plants either use a "do-it-yourself" strategy and invest in longer, thinner roots to exploit soil for nutrients or an "outsource" strategy in which shorter, thicker roots associate with more mycorrhizae, using the fungi as the primary means to exploit soil for limiting resources (Bergmann et al. 2020). This axis is orthogonal to the resource-use axis, which defines the degree to which a plant is acquisitive or conservative (Bergmann et al. 2020). While Bergmann et al. (2020) identify the importance of a second axis of variation depending on mycorrhizae, further work is necessary to investigate the function of the mycorrhizae simply beyond quantity, including functional groups and traits.

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We use the Bergmann et al. (2020) framework to propose patterns of variation in root and mycorrhizal fungal traits at the inter- and intraspecific scale. We suggest that at both scales, AM plant roots appear to have a greater potential for altered morphology in traits defining the resource-use axis – root N and root tissue density – than do EM plant roots, potentially owing to a more intimate association with their mycorrhizae that has developed via the long evolutionary history between them (McCormack et al. 2015, Eissenstat et al. 2015, Cheng et al. 2016). As a result, we expect large degrees of variation in plant traits related to the resource acquisition axis, but less variation in traits related to the collaboration axis. Counter to this, EM plants potentially have a greater range of root traits due to the more recent, and polyphyletic nature of EM associations (Smith and Read 2008, Pellitier and Zak 2018). We therefore suggest that traits related to a resource use axis should have less variation than is seen in AM plants, but there should be comparatively greater degrees of variation in plant traits related to the collaboration axis. While more work is certainly needed, initial studies found that AM plants showed greater root proliferation and exploration of nutrient patches via roots, while EM plants tended to rely more on their fungal partners to exploit nutrient patches (Cheng et al. 2016).

While it is possible that patterns of mycorrhizal fungal and plant trait variation are consistent at inter- and intraspecific scales, we recognize that it is also possible and potentially more likely that patterns may, in fact, differ between these scales. Indeed, work on aboveground traits, specifically those associated with the leaf economic spectrum that describe the degree of resource conservation in leaves, has found a breakdown of the strong interspecific relationships at the intraspecific scale (Messier et al. 2017, Umaña and Swenson 2019). As a result, future work in the field should address the impact of scale on patterns of trait variation.

Future Directions

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It is vital that we begin to include mycorrhizal functional traits for plants, fungi, and symbiosis in our assessment of belowground plant traits, because these organisms are an integral component of how plants forage for limiting soil resources, and knowledge of the traits impacting these strategies can improve understanding of plant – and therefore ecosystem – response to climate change. Preliminary work reveals that mycorrhizal fungi are linked with root traits; however, it is uncertain to what extent and how tight these relationships occur across both plant and mycorrhizal lineages (Romero-Olivares et al. 2021). The lack of understanding of the degree of fidelity of the identified relationship potentially owes to the lack of information we currently have on the functional characteristics of mycorrhizal fungi.

To help tackle how to approach variation in mycorrhizal fungi and plant root traits, we propose a framework that emphasizes the unique phylogenetic history of the two most common mycorrhizal types in trees: EM and AM fungi (Figure 1). Specifically, because EM have evolved multiple times from saprotrophic ancestors, the variation present in terms of functionality, both morphologically and physiologically, is substantially higher than in the monophyletic AM fungi (Powell et al. 2009, Pellitier and Zak 2018). EM fungi have a wider array of genes encoding enzymes that mediate nutrient acquisition (*e.g.,* peroxidases and glucosidases), in addition to hyphal exploration types ranging from contact-type with limited hyphae extending only short distances into the soil to long-distance types with extensive hyphae extending into the soil far from the colonized root tip (Agerer 2001, Brundrett and Tedersoo 2018, Pellitier and Zak 2018). Counter to this, AM fungi contain a drastically constrained gene repertoire (*i.e.,* absence of genes encoding enzymes mediating organic matter decay), relative to EM fungi. Furthermore, while AM morphotypes – *i.e.* the allocation of hyphae to inside and outside of the root – found associating with roots can vary between phylogenetic groups and across environmental gradients

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(Hart and Reader 2002, Treseder et al. 2018), these morphotypes tend to be constrained phylogenetically (Powell et al. 2009, Chagnon et al. 2013). As a result, we expect opposite patterns of variation in the roots of plants associating with EM or AM fungi; because EM fungi have higher levels of functional plasticity, the plant roots themselves should have lower levels of plasticity, instead relying on their mycorrhizal symbionts to adapt and adjust to shifting conditions. On the other hand, plants associating with AM fungi should have greater root functional plasticity, because AM mycorrhizal fungi have limited ability to shift function in response to different soil conditions. Preliminary work has hinted at this pattern. EM plants have a greater reliance on mycorrhizal fungal partners for foraging in nutrient patches, whereas AM fungi relied more on their own roots, increasing root branching and proliferation more than EM plants (Cheng et al. 2016). Additionally, EM plants displayed greater shifts in root biomass and total length in response to N-enrichment in a global meta-analysis of plant and mycorrhizal fungal resource use strategies (Ma et al. 2021).

For EM, gene frequency via shotgun metagenomics offers a relatively straightforward method that has provided promising initial results to begin to examine patterns of root and mycorrhizal trait variation within this framework; it, of course, requires *a priori* knowledge of the genome content, which is gained by the complete sequencing of these fungal taxa. Because plants are often colonized by numerous species of mycorrhizal fungi, gene frequency analysis at the metagenomic scale, as opposed to the individual fungus level, may be a more effective approach for assessing mycorrhizal fungal traits. Prior work on metagenomics reveals that community weighted means (CWMs) calculated via metagenomic analysis can be an effective estimate of community function in microbes and fungi (Fierer et al. 2014, Pellitier et al. 2021a). Examining the metagenome is especially useful in mycorrhizae, because multiple different

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mycorrhizal fungi can associate with a single plant, and likewise the same mycorrhizal fungi can associate with multiple plants making it difficult to disentangle the effects of the two on each other (Smith and Read 2008, Fierer et al. 2014).

Coupling gene frequency analysis in EM with work across environmental gradients that support similar plant communities throughout allows for the control of key factors impacting root traits; including climate and phylogenetic history coupled with variation in key environmental variables such as water and nutrient availability (Pregitzer et al. 2002, Withington et al. 2006, Valverde-Barrantes et al. 2017). Initial studies across environmental gradients show promising results with either root traits or mycorrhizal traits, but none to date of combined the two in a single perspective of root function (Defrenne et al. 2019, Pellitier et al. 2021b, 2021a). For example, Pellitier et al (2021a,b) found that, across an N mineralization gradient in northern Lower Michigan, USA, the frequency of EM genes encoding enzymes that liberate N from soil organic matter (*e.g.,* peroxidases and glucosidases) increased as N mineralization decreased, and that this coincided with additional N from organic sources being assimilated by plants. However, this work did not address potential shifts in plant traits that may occur concurrently. Gene frequency is, however, not without limitations. More work is needed on the effectiveness of gene frequency in relation to function, specifically work is needed to ensure that gene frequency is related to the actual expression of genes. This could be accomplished by employing transcriptomics or actual physical measurements of growth and enzyme activity in the field and/or lab using assays and/or isotopic labeling.

Furthermore, gene frequency is not applicable to all fungal guilds and types. AM fungi – due to its inability to access soil organic N – cannot be analyzed for changes in gene frequency of enzymes across gradients of soil resource availability (Smith and Read 2008). However, it is

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conceivable that AM fungi accomplish a similar task via morphological and physiological changes that affect the foraging ability of plant roots for limiting soil resources as has been suggested by limited prior work (Treseder et al. 2018). For this more traditional measurement, traits may be more useful like those used to measure plant morphological traits. For example, measurements of fungal biomass in plant root and soil may be useful for determining soil exploration strategies (Hart and Reader 2002). Other measurements such as hyphal growth rate, hyphal and arbuscule/vesicle nutrient content, and enzymatic activity are traits that, while potentially difficult to measure, may offer insight into variability in mycorrhizal fungal strategies (Hart and Reader 2002, Van Der Heijden and Scheublin 2007, Chaudhary et al. 2022). Alternatively, because measuring fungal traits *in situ* can be difficult, more work can be done to identify links between genes and functional performance trends in AM fungi.

Conclusion

Including mycorrhizal traits with the measurement of plant root traits provides the potential for gaining deeper insight into plant communities, as well as the belowground competitive abilities of individual plants composing those communities. This includes how plant communities form, coexist, and grow. Furthermore, knowledge of how plants take up nutrients and translate that into growth, survival and reproduction can provide vital information that can be scaled up to understand important ecosystem processes such as nutrient cycling and carbon sequestration.

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Author Contributions

Dr. Donald Zak planned the literature review, provided text editing, and provided equal input into the conceptual framework developed.

Sam Schaffer-Morrison wrote the text, reviewed literature, and provided equal input into the framework developed.

Data Availability Statement

No data were collected for this study.

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Tables

Table 1 – Commonly measured root traits, their units, and the pattern observed at various levels of that trait value.

Trait	Common Units	Pattern
Specific Root Length	length · $mass^{-1}$	higher: longer and thinner roots, lower levels of mycorrhizal fungal colonization (Bergmann et al. 2020)
Root Diameter	mm or cm	higher: thicker roots, higher levels of mycorrhizal fungal colonization (Bergmann et al. 2020)
Root Tissue Density	mass · $volume^{-3}$	higher: lower tissue nutrient content, increased root lifespan (Freschet et al. 2010)
Root Nitrogen, Phosphorus	ppm or % or g · $mass^{-1}$	higher: less dense roots, shorter root lifespan (Freschet et al. 2010)
Root Growth Rate	mm or cm · $time^{-1}$	Variable, but tends to be higher when nutrients availability is higher (Eissenstat et al. 2015)
Root Branching	number of branches · $length^{-1}$ or structural description or angle of branching	Variable, but tends to be higher when nutrient availability is higher (Liese et al. 2017)
Resource Uptake Rate	resource amount · root volume $^{-1}$ or root area $^{-1}$ or root length $^{-1}$ · unit time $^{-1}$	Variable, but tends to be higher when nutrient availability is higher (Freschet et al. 2021)

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Table 2 – Commonly measured fungal traits and their units. Adapted from van der Heijden & Scheublin (2007) with additional sources as noted.

Trait	**Impacts on Plant Performance**
Hyphal Length	Nutrient acquisition
Mycelia Structure	Nutrient acquisition
Exploration Type	Nutrient acquisition (Agerer 2001)
Hyphal Biomass Distribution in Roots and Soil	Nutrient acquisition (Jörgensen et al. 2022)
Hyphal Life Span	Nutrient acquisition
Speed of Colonization	Plant establishment
Degree of Colonization	Nutrient acquisition; protection against pathogens
Spore Production	Seedling establishment
Nitrogen, Phosphorous, and Micronutrient Uptake	Nutrient acquisition
Carbon Acquisition	Carbon Storage
Hyphal Enzymatic Activity	Nutrient acquisition (Lindahl et al. 2005)
Gene Frequency	Nutrient acquisition

Figure 1. Theoretical framework for variation in ectomycorrhizal (EM) fungi and plants (left) and arbuscular mycorrhizal (AM) fungi and plants (right). In EM plants greater phylogenetic diversity of fungi leads to greater variation in fungal traits both morphologically and physiologically and less variation in root traits as plants rely more on their fungal symbionts to adapt to different environments. In AM plants less phylogenetic diversity of fungi leads to less variation in fungal traits and greater variation in plant roots traits to adapt to different environments. This pattern carries over to environmental gradients as well where we expect stronger shifts in EM fungal traits compared to AM fungi, and greater changes in root traits in AM plants compared to EM plants.

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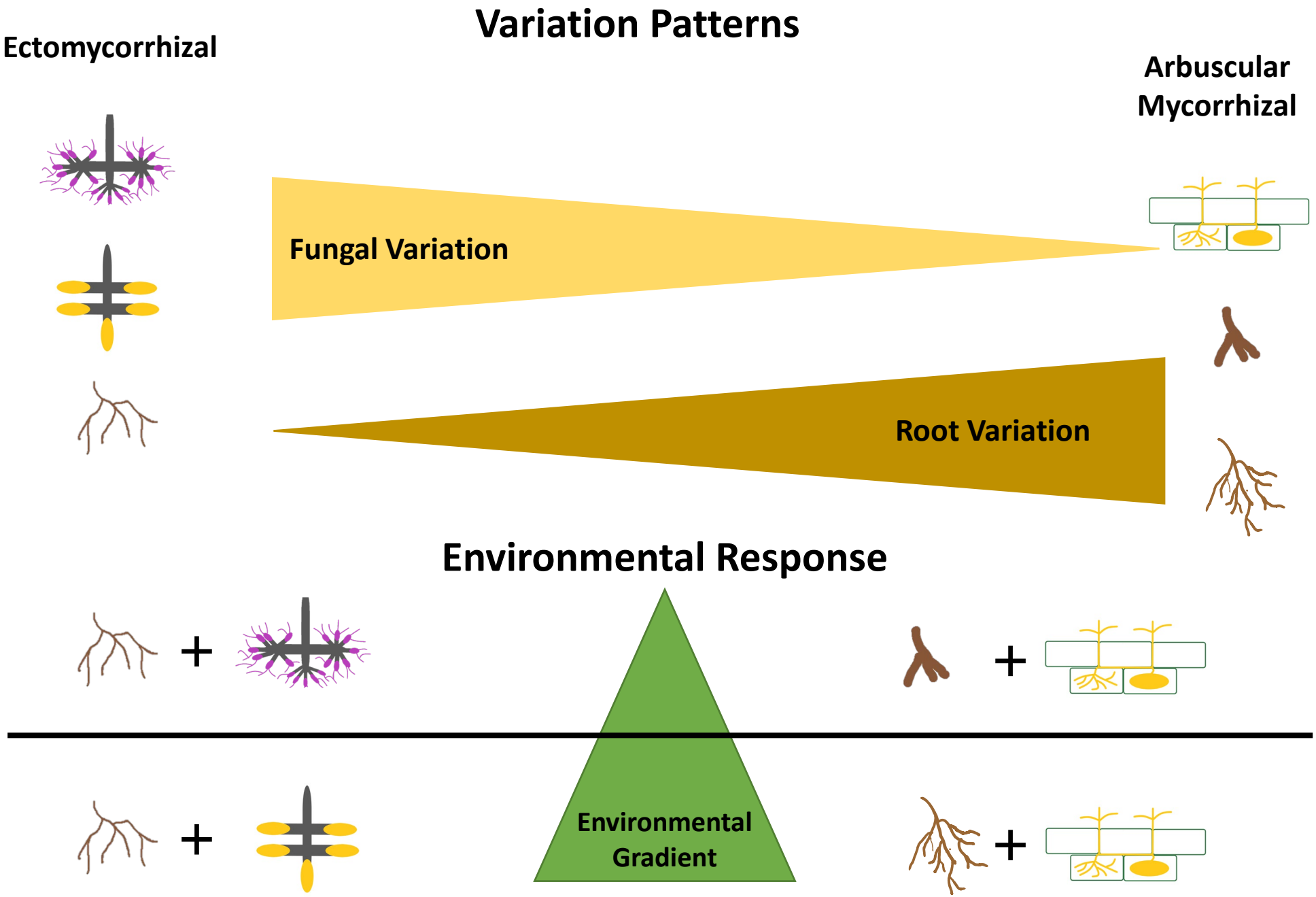
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