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# Trends in Ecology and Evolution

## What are mycorrhizal traits?

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| **Corresponding Author:** | Bala Chaudhary<br>Dartmouth College<br>Hanover, NH UNITED STATES |
| **First Author:** | V. Bala Chaudhary |
| **Order of Authors:** | V. Bala Chaudhary |
| | E. Penelope Holland |
| | Suw Charman-Anderson |
| | Aidee Guzman |
| | Lukas Bell-Dereske |
| | Tanya E. Cheeke |
| | Adriana Corrales |
| | Jessica Duchicela |
| | Cameron Egan |
| | Manju M. Gupta |
| | S. Emilia Hannula |
| | Rachel Hestrin |
| | Shabana Hoosein |
| | Amit Kumar |
| | Genet Mhretu |
| | Lena Neuenkamp |
| | Pushpa Soti |
| | Yichun Xie |
| | Thorunn Helgason |
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# What *are* mycorrhizal traits?

V. Bala Chaudhary[1*], E. Penelope Holland[2], Suw Charman-Anderson[3], Aidee Guzman[4], Lukas Bell-Dereske[5], Tanya E. Cheeke[6], Adriana Corrales[7], Jessica Duchicela[8], Cameron Egan[9], Manju M. Gupta[10], S. Emilia Hannula[11], Rachel Hestrin[12], Shabana Hoosein[13], Amit Kumar[14], Genet Mhretu[15], Lena Neuenkamp[16,17], Pushpa Soti[18], Yichun Xie[19], Thorunn Helgason[2]

[1]Department of Environmental Studies, Dartmouth College, Hanover, NH, USA

[2]Department of Biology, University of York, York YO10 5DD, UK

[3]Finding Ada Network, Bournemouth, UK

[4]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720 USA

[5]Laboratory of Environmental Microbiology, Institute of Microbiology of the Czech Academy of Sciences, Vídeňská 1083, 142 20 Prague, Czech Republic

[6]School of Biological Sciences, Washington State University, Richland, WA, USA

[7]Centro de Investigaciones en Microbiología y Biotecnología-UR (CIMBIUR), Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia

[8]Departamento de Ciencias de la Vida, Universidad de las Fuerzas Armadas ESPE, Ecuador

[9]Department of Biology, Okanagan College, 1000 KLO Rd, Kelowna, BC, Canada V1Y 4X8

[10]University of Delhi, Sri Aurobindo College, Delhi, India

[11]Institute of Environmental Sciences, Leiden University, Leiden, The Netherlands

[12]Physical and Life Sciences Directorate, Lawrence Livermore National Laboratory, Livermore, CA, 94550, USA

[13]Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA
[14]Institute of Ecology, Faculty of Sustainability, Leuphana University of Lüneburg, 21335 Lüneburg, Germany
[15]Mekelle University, Ethiopia
[16]University of Bern, Institute of Plant Sciences, Switzerland
[17]Department of Ecology & Multidisciplinary Institute for Environment Studies "Ramon Margalef", University of Alicante, Spain
[18]Biology Department, University of Texas Rio Grande Valley, Edinburg, TX, USA
[19]School of Life Sciences, The Chinese University of Hong Kong, Hong Kong SAR
*Corresponding author, email: bala.chaudhary@dartmouth.edu, Twitter: @balachaudhary

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**Abstract**

Traits are inherent properties of organisms, but how are they defined for organismal networks such as mycorrhizal symbioses? Mycorrhizal symbioses are complex and diverse belowground symbioses between plants and fungi that have proved challenging to fit into a unified and coherent trait framework. We propose an inclusive mycorrhizal trait framework that classifies traits as morphological, physiological and phenological features that have functional implications for the symbiosis. We further classify mycorrhizal traits by location - plant, fungus, or the symbiosis - which highlights new questions in trait-based mycorrhizal ecology designed to charge and challenge the scientific community. This new framework is an opportunity for researchers to interrogate their data to identify novel insights and gaps in our understanding of mycorrhizal symbioses.

**Fitting mycorrhizal symbioses into existing trait-based ecological frameworks**

A **trait** (see Glossary) is defined as a measurable characteristic (morphological, physiological, phenological, behavioral, or cultural) of an individual organisms that is measured at either the individual or other relevant level of organization [1, 2]. Plants and animals typically have many distinguishable morphological traits and, after decades and/or centuries of research, their life histories are generally well described. As a result, conceptual frameworks for trait-based ecology were developed for and are primarily applied to plants [3, 4] and animals [5, 6] with a proportionate number of plant- and animal-trait databases emerging to support these efforts [7].

Trait-based approaches are increasingly applied broadly across disciplines within ecology and evolution. Advantages include the ability to make ecological inferences across temporal, spatial, and organizational scales and a predictive understanding of communities and ecosystem processes [8, 9]. Commonly used methods employ species traits in order to understand mechanisms behind responses of species to variation in environmental conditions (i.e. response traits) and traits that link species to patterns in ecosystem processes and functioning (i.e. effect traits) [10]. For microbes, a trait-based approach to ecological studies is particularly crucial as many individuals and species are not easily identifiable or culturable for in-depth laboratory studies [11]. Trait-based approaches are a key to solving 'big picture' problems in ecology such as community responses to anthropogenic global change [5, 12] that depend on complex interactions between species and environments, both above and belowground [13, 14].

**Mycorrhizal symbioses** (synonymous with "mycorrhizas") are close associations between roots and certain fungi [15] and, in terrestrial ecosystems, the dominant belowground structures responsible for shuttling the resources (e.g. nutrients, water) that drive primary productivity [16]. In mycorrhizal symbioses, plants provide photosynthetically derived carbon to fungal partners in exchange for increased access to soil resources such as nitrogen, phosphorus, and water, though the degree of mutual benefit is context dependent [17]. Mycorrhizal symbioses are most well known for their role in nutrient exchange, but are also recognized for their key roles in ecosystems across a range of organizational scales such as promoting plant establishment, plant pathogen protection, plant resistance to heavy metals, drought tolerance, interspecific community interactions, soil aggregation, and global carbon cycling [18]. Mycorrhizal symbioses represent the interface between two different types of modular lifeforms; in nature, most plant roots are associated with more than one mycorrhizal fungus. Furthermore, one mycorrhizal fungus can be associated with multiple plants to form non-random assemblages of physical networks of **hyphae** that are connected belowground [19, 20]. As such, mycorrhizal symbioses are root-mycelial networks of modular lifeforms with varying degrees of complexity ranging from one plant-one fungus to multiple plant-fungal connections.

Applying concepts from, and drawing parallels to, trait-based ecological theory developed for individual organisms with more definable traits can be challenging for symbioses that are inherently defined as associations between multiple organisms. Traits are often defined for the purpose of a specific study, so terminology, semantics and interpretations vary across datasets [7, 21], even for well-studied and easily identifiable organisms. For organisms with high species-level diversity but few distinguishable morphological traits such as fungi [22], trait-based ecology often takes a more mechanistic approach, particularly for species that are cryptic or microscopic [23, 24]. For symbioses that are not discrete species units but in fact emergent properties of complex root-mycelial networks such as mycorrhizal symbioses (but see also [25]), trait-based ecology poses an even greater challenge.

**Prior morpho-physio-phenological trait definitions for mycorrhizas**

Mycorrhizal ecologists, whether invoking the word 'trait' or not, have long studied various

**mycorrhizal traits** to gain insight into predictors or proxies of mycorrhizal performance [26]. Table 1 lists examples of previously used definitions of morphological, physiological, or phenological traits that have led to considerable advances in our understanding of mycorrhizal ecology. Mycorrhizal type is an emergent property of the plant and fungal taxa involved in the symbiosis and likely the most commonly studied mycorrhizal trait. The major types of mycorrhizas - **arbuscular mycorrhizas** (AM), **ectomycorhizas** (EcM), **ericoid mycorrhizas** (ErM), and **orchid mycorrhizas** (OrM) - are similar in that they are all symbiotic root-mycelial networks of fungi and plants with varying degrees of complexity. However, mycorrhizal types vary substantially with respect to plant and fungal taxa involved in the association, morphological form, ecophysiological function, and their comparative roles in biogeochemical cycling [16, 27]. Research on mycorrhizal type, among other mycorrhizal traits, is increasingly being conducted with large global databases (e.g. MycoDB, FungalRoot, FUN$^{FUN}$, FungalTraits) aimed at making broad inferences about the biogeography and functioning of mycorrhizas [24, 28-31].

The application of existing ecological conceptual frameworks has also led to advances in trait-based mycorrhizal ecology, in particular the application of Grime's C-S-R (competitor, stress tolerator, ruderal) framework [32, 33]. A fungal-centric perspective characterizes variation in AM fungal traits such as hyphal growth rate, hyphal turnover rate, **spore** phenology, and dispersal ability as alternative competitive strategies for different AM fungal species [34]. Efforts have also been made to classify AM fungi into edaphophilic or rhizophilic guilds related to differential allocation to soil hyphae or root colonization, respectively, and how that relates to mycorrhizal function [35, 36]. In EcM fungi, previous work has defined mycorrhizal traits as differences in morphology and physiology of mycelial [37] and reproductive structures [38] that produce differences in species' capacity for carbon storage, enzymatic activity, nutrient uptake and translocation, dispersal, and habitat colonization [27, 39-42]. Alternatively, plant-centric perspectives have shown how mycorrhizal symbioses explain significant variation in plant life history strategies [43] and multivariate root trait space [44] accounting for different C-S-R and resource utilization strategies of plants across the globe.

Methodological limitations (e.g. culturing bias) certainly impair empirically derived knowledge of mycorrhizal traits [45], but disparate definitions across a diversity of trait-based mycorrhizal research efforts also hinder productive scientific discourse. Often, different definitions of mycorrhizal traits are specific to mycorrhizal type, focused on either a plant- or fungal-centric perspective, or borrowed from existing ecological theories based on distinct unitary organisms that cause confusion for network-based symbioses between modular organisms. A unified language for mycorrhizal traits that spans mycorrhizal types and morpho-physio-phenological characteristics is sorely needed.

**Controversy and disagreement in what constitutes mycorrhizal traits**

Thus far, the body of research on trait-based mycorrhizal ecology has used different definitions of traits with organismal divides that stem from different morphological metrics that are a proxy for functions, direct measures of functions, or measures of mycorrhizal plant and/or mycorrhizal fungal growth that may also approximate function. In many ways, these organismal divides are a result of researchers coming from different disciplinary backgrounds and perspectives [46, 47]. A plant-centric perspective can result in studying different types of traits and the use of varied vocabularies that don't easily translate to those using a fungal-centric perspective (and vice versa). Many microbes have relatively few measurable or easily observable features and thus functional measures are translated into traits. For example, the presence or abundance of saprotrophic fungi may be correlated with litter decomposition rates. Plant traits on the contrary are observable but their relevance for the ecosystem functioning may be ambiguous. For example, specific leaf area can be an indication of plant longevity and thus biomass turnover and photosynthetic rates [10].. Geographic region of study can also drive miscommunication as certain regions of the world, particularly the tropics, are comparatively understudied [48] resulting in a greater need to incorporate local terminologies into globally-accepted paradigms. Indeed, inconsistencies in terminology surrounding traits are as diverse as trait ecologists suggesting the need to keep trait definitions broad, malleable, and identified independently from the environment [2].

Divides also exist between researchers that primarily work in EcM-dominated systems compared to those working in AM or ErM-dominated systems. Certain systems have also been studied for longer, as EcM symbioses were identified in the 1880s [15], but the functional significance of the AM symbioses was not discovered until the 1950s [49]. Less is known about AM symbioses compared to other mycorrhizal groups [50] resulting in a lack of the basic biological and taxonomic framework to integrate ecological research with general mycology. This affects the study of mycorrhizal symbioses as there are significant differences in the focus of AM vs EcM studies which hampers the generation of a unified language to describe them [11, 47]. Applying trait-based methods to highly context-dependent mycorrhizal symbioses without a standardized vocabulary is challenging and can result in "locked-in debates" among researchers that hinder scientific advances [51].

## An inclusive and unified framework for mycorrhizal traits

It is the opinion of the authors that a common framework and standardized vocabulary will help to further our understanding of the trait-based ecology of mycorrhizal symbioses. As traits are characteristics of organisms, mycorrhizal traits must be inclusive of all organismal components that make up mycorrhizal symbioses, recognizing that the mycorrhizal functions we observe in nature are the imprint of all mycorrhizal traits working together. Therefore, **mycorrhizal traits are morphological, physiological or phenological characteristics of mycorrhizal fungi, plants, and mycorrhizal associations that have functional implications for the mycorrhizal symbiosis.** Because this definition is based on symbiotic function and the inherent root-mycelial network nature of all mycorrhizas, it is applicable across all mycorrhizal types. Our definition emphasizes traits that have functional implications for the mycorrhizal symbiosis to further a mechanistic understanding of mycorrhizal performance and fitness. We aim to link trait-based mycorrhizal ecology to the work of defining mycorrhizal niches and understanding the mechanisms of community assembly [9]. Some mycorrhizal traits *are* functions (e.g. plant productivity response to mycorrhizal symbiosis)), but some are **functional markers**, traits that don't measure a function directly but instead are indicators of mycorrhizal functions (e.g. hyphal production by mycorrhizal fungi that influences soil aggregate formation)[11, 52].

Although there are benefits to using inclusive terminology, an overly broad definition of mycorrhizal traits can also cause confusion during scientific discourse when researchers universally refer to "mycorrhizal traits" but mean different things. We propose to further qualify mycorrhizal traits using language that references their physical location within mycorrhizal networks (Table 2). Therefore, mycorrhizal traits fall into one of three categories: plant mycorrhizal traits (plant-MT), fungal mycorrhizal traits (fungal-MT), and symbiotic mycorrhizal traits (symbiotic-MT).

Plant-MT are mycorrhizal traits that are largely driven by the morphological, physiological, or phenological characteristics of the plant partner. Many root traits, for example, represent important plant-MTs as they have functional implications for the symbiosis [44]. Fungal-MT are mycorrhizal traits that are dependent on the morphological, physiological, or phenological characteristics of the mycorrhizal fungal partners. Both fungal response and fungal effect traits [23], particularly physiological traits relating to fungal ecosystem functions, are components of fungal-MT. Finally, symbiotic-MT are morphological, physiological, or phenological characteristics that lie at the intersection of both partners and are dependent on both the plant and fungal partners present. Figure 1 diagrams examples of plant-MT, fungal-MT, and symbiotic-MT across morphological, physiological, and phenological traits.

This framework both accommodates existing trait-based research and identifies gaps in knowledge due to data limitations. For example, considerably more research has been conducted on morphological mycorrhizal traits than on physiological mycorrhizal traits with phenological traits by far the least studied. More research into how plant-MT, fungal-MT, and symbiotic-MT shift with seasons or ontogeny will give greater insight into the range of variation in traits. This trait-based framework also highlights how little we understand about interspecific and intraspecific variation as well as plasticity in many mycorrhizal traits, particularly at the physiological level. Computational methods linking genes to traits [53] could be employed to explore relationships between plant-MT, fungal-MT, and/or symbiotic-MT and either plant or mycorrhizal fungal gene frequencies. Further exploration of relationships between traits, particularly those that illuminate symbiotic partner resource sharing and connections between mycorrhizal form and function, is warranted as mycorrhizas are models for studying resource exchange and stability in symbioses [54].

## Concluding remarks

There is already consensus across scientists using traits in ecology that standardized definitions and data structures are required to make the most of trait data and to address challenges at the community and ecosystem levels [7, 21]. Microorganisms influence almost all ecosystem processes, and a common framework for researching how microbial processes affect ecosystem-level function is crucial for advancing our understanding [55]. Mycorrhizal symbioses occupy a unique and complex position in ecological communities with a pivotal role in the maintenance of ecosystem function [56], and will be fundamental to meeting United Nations Sustainable Development Goals in the medium to long term [57].

The Cha-Cha-Cha theory suggests that scientific discoveries can be classified as Charge, Challenge or Chance [58]. Charge problems are obvious to the observer, but require a new way of thinking to devise a solution, Challenge problems require us to devise a new theory to bring unexplained and diverse anomalies together, and Chance discoveries require a "prepared mind" to recognize the importance of something that happens by chance. **Our framework for mycorrhizal traits raises numerous Outstanding Questions as Charges and Challenges to the ecological community in order to be better prepared to recognize future Chance discoveries.** By acknowledging how our position of observation flavors our analyses and understanding of mycorrhizal traits through the very language we use to pose research questions [59], we can, as a community of scientists, be better prepared to recognize serendipitous discoveries. A common framework for mycorrhizal traits may engage scientists around the world to collect more trait-based data, especially in understudied areas, generating Chance discoveries. It is the authors' opinion that a common framework for mycorrhizal trait-based ecology will facilitate the next generation of discoveries in this field. This paper describes only a small portion of the exciting work tackling Charges at the present time. Shared terminology allows us to better identify synergy between studies approaching similar questions from different angles and take on the Challenges.

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**LIST OF ELEMENTS**

Table 1: Previously published and highly varied definitions of “mycorrhizal traits”

Table 2: An inclusive and unified framework for mycorrhizal traits including definitions and examples.

Box 1

Figure 1: Schematic diagram of plant mycorrhizal traits, fungal mycorrhizal traits, and symbiotic mycorrhizal traits with graphical depictions of example morphological, physiological, and phenological traits for each.

Glossary

**Table 1. Examples of previously published and highly varied definitions of "mycorrhizal traits"**

| **Definitions of mycorrhizal traits** | **Relevant citations** |
|---|---|
| Traits as the type of mycorrhizal symbiosis (e.g. AM, EcM, ErM) or frequency of occurrence (e.g. obligate, facultative) of mycorrhizal symbiosis in a plant species. | Wang and Qiu [60], Hempel et al. [61], Moora [62], Soudzilovskaia et al. [31], Bergmann et al. [44], Shi et al. [63], Bueno et al. [64] |
| Traits as the context dependent benefits that plants derive from mycorrhizal symbioses. | Hoeksema et al. [17], Johnson et al. [65] |
| Traits as spore morphology (e.g. size, shape, color) of mycorrhizal fungi | Norros et al. [66], Pringle et al. [67], Deveautour et al. [68], Chaudhary et al. [69] |
| Traits as root and/or soil colonization strategies of mycorrhizal fungi, including fungal biomass allocation and hyphal production. | Agerer [70], Hart and Reader [71], Ekblad et al. [72], Powell et al. [73], Weber et al. [36] |
| Traits as soil aggregation and stabilization capabilities of mycorrhizal symbioses | Rillig et al. [74], Lehmann et al. [75] |
| Traits as C-S-R characteristics of mycorrhizal fungi | Chagnon et al. [34], Treseder and Lennon [76] |
| Traits as mycorrhizal fungal behaviors such as movement, communication, and decision making. | Bielčik et al. [77], Aleklett and Boddy [78] |
| Traits as mycorrhizal symbiosis properties related to nutrient flux and ecosystem functioning | Van Der Heijden and Scheublin [79], Phillips et al. [80], Behm and Kiers [81] |

**Table 2.** An inclusive and unified framework for mycorrhizal traits. Examples given are categorized as morphological, physiological, or phenological traits; the framework is intended to stimulate thought and discussion, so dynamic classifications are encouraged.

| | **Plant mycorrhizal traits (Plant-MT)** | **Fungal mycorrhizal traits (Fungal-MT)** | **Symbiotic mycorrhizal trait (Symbiotic-MT)** |
|---|---|---|---|
| **Definition** | *Mycorrhizal traits dependent on the morphological, physiological, or phenological characteristics of **plant partners*** | *Mycorrhizal traits dependent on the morphological, physiological, or phenological characteristics of the **fungal partners*** | *Traits that lie at the organismal intersection of mycorrhizal symbioses and are dependent on both plant **and fungal partners*** |
| **Morphological traits (form)** | -Root characteristics (e.g. diameter, architecture, surface area:volume, root hair density)<br>-Root:shoot ratio<br>-Growth form (e.g. tree, grass)<br>-Resource allocation (e.g. root:shoot).<br>-Seed size<br>-Phylogenetic history | -Fruiting body (e.g. size, shape, color)<br>-Spores (e.g. size, color, shape, ornamentation, wall thickness)<br>-**Mantle** (e.g. color, cell morphology)<br>-Hyphae (e.g. specific length, architecture)<br>- Biomass allocation strategy (e.g., rhizophilic, edaphilic)<br>-Culturability | -Mycorrhizal type (AM, EcM, ErM, OrM, NM, **Dual**)<br>-Colonization intensity (e.g. abundance of inter- and intracellular structures)<br>-Structures induced by colonization (e.g. Hartig net, arbuscules, vesicles, **Paris vs Arum form**)<br>-Species-specificity between plant and fungal symbionts<br>-Network indices (e.g. nestedness, modularity, connectivity) |
| **Physiological traits (function)** | -Plant mycorrhizal status (obligate vs. facultative)<br>-Photosynthetic pathway<br>-Immune responses (e.g. herbivores induced responses)<br>-Growth and transpiration rates<br>-Quantity and quality of root exudates<br>-Plant nutrient requirements | -Hyphal/spore productivity and turnover<br>-Nutrient acquisition strategy (e.g. inorganic vs organic sources, extracellular enzyme production, acid exudation)<br>-Melanin content<br>-Carbohydrate metabolism and conversion<br>-Facilitative/antagonistic interactions | -Plant mycorrhizal response (e.g. increased productivity or nutrient status)<br>-Exchange rates for resources (e.g. N, P, C, $H_2O$)<br>-Gene expression changes induced by symbiosis<br>-Plant-fungal influences on metabolic products<br>-Functional specificity between plant |

| | | | |
|---|---|---|---|
| | | with microorganisms | and fungal symbionts |
| **Phenological traits** | -Life history (e.g. annual, perennial)<br>-Flowering time and seed production<br>-Changes in root exudate quality and quantity | -Temporal dynamics in production of fruiting bodes, spores, and hyphae<br>-Hyphal/spore persistence and longevity<br>-Temporal dynamics in fungal community structure | -Shifts in mycorrhiza type over plant lifespan<br>-Temporal shifts in colonization structures and/or symbiotic exchange |

**Glossary**

Arbuscular mycorrhiza (AM) – Mycorrhizal association where plant roots display intracellular colonization by fungi of the subphylum Glomeromycotina.

Arbuscule - A specialized mycorrhizal structure present inside plant cells and the common site of nutrient exchange in arbuscular mycorrhizas (AM). Other nutrient exchange sites in arbuscular mycorrhizas include hyphal coils.

Dual colonization - Colonization of plant roots by two different mycorrhizal types (i.e. AM and EcM), generally demonstrating ontological shifts in particular plant species (e.g. *Quercus* sp., *Salix* sp., *Populus* sp.).

Ectomycorrhiza (EcM) – Mycorrhizal association between plant roots and fungi characterized by an intercellular interface consisting of a branched hyphal lattice and mantle.

Ericoid mycorrhiza (ErM) – Mycorrhizal association between plants in the family Ericaceae and certain fungi characterized by intracellular coils.

Functional markers - Traits that don't measure a function directly but instead are indicators of functions (e.g. hyphal production by mycorrhizal fungi that influences soil aggregate formation).

Hyphae - The branching filaments of mycorrhizal fungi that make up the mycelium and conjoin to plant roots either intra or extracellularly. Hyphae differ with respect to morphology, environmental persistence, and function (e.g. nutrient absorption versus transport).

Mantle - Sheath of fungal hyphae enveloping plant roots in EcM associations.

Mycorrhizas - Symbiotic associations between plant roots and certain fungi. Synonym: mycorrhizal symbioses.

Mycorrhizal fungi - The fungal symbiotic partners of mycorrhizal associations.

Mycorrhizal traits - morphological, physiological or phenological characteristics of mycorrhizal fungi, plants, and mycorrhizal associations that have functional implications for the symbiosis.

Orchid mycorrhiza (OrM) - Mycorrhizal association between plants in the family Orchidaceae and certain fungi characterized by intracellular coils called pelotons.

Paris/Arum - Alternative root colonization strategies in arbuscular mycorrhizas. Paris-type is characterized by coiled hyphae that spread intracellularly from plant cortical cell to cell while Arum-type spreads in the plant root cortex via intercellular hyphae.

Spore - Fungal cells specialized for asexual or sexual reproduction and dispersal. Can be born from specialized fungal fruiting bodies or directly from mycelial networks.

Symbiosis – association between organisms that live in close physical contact

Trait - Any measurable characteristic (morphological, physiological, phenological, behavioral, or cultural) of an individual organism that is measured at either the individual or other relevant level of organization.

**Box 1**

Our framework for mycorrhizal traits can be applied to easily incorporate trait-based methods into empirical and theoretical ecological research. Adopting a trait-based framework for mycorrhizal symbioses benefits ecologists from a variety of disciplinary backgrounds.

**Plant Ecologist**

Plant ecologists use existing frameworks for measuring traits and incorporating trait-based methods into ecological studies [32, 82, 83]. Plant ecologists already measure many plant mycorrhizal traits (plant-MT; Table 2) such as root architecture, photosynthetic pathway, and phenology. By also including symbiotic mycorrhizal traits (symbiotic-MT) such as colonization intensity, plant mycorrhizal response, or resource exchange rates, plant ecologists could further increase their understanding of plant functioning. For instance, examining mycorrhizal colonization intensity in plant roots would facilitate inferences about carbon and nutrient transfer between plant and fungal symbionts, with links to functioning such as plant productivity or pathogen resistance [54, 84].

**Fungal Ecologist**

Fungal ecologists have long used traits to categorize fungi according to guilds, and continue to use trait-based perspectives to research the numerous functional roles that fungi play in ecosystems [24]. As methodologies to assess fungi *in situ* continue to improve, we can better measure many fungal mycorrhizal traits (fungal-MT; Table 2) such as mycelial traits and enzyme activity [11]. Many fungal-MT can be measured using standard laboratory equipment (e.g. centrifuge, filters, microscope) that researchers already have access to. For example, spore size is an indicator of AM fungal aerial dispersal ability and thus could improve predictions of landscape management impacts on local AM fungal diversity and composition [69]. Just as leaf traits have expanded knowledge of plant life-history strategies [85], the incorporation of important fungal-MT such as spore morphology will expand our understanding of life history strategies of mycorrhizal fungi.

**Data Synthesizer**

Large team science to compile and analyze global ecological datasets increase our understanding of biodiversity and ecosystem functioning. Ecologists examining ecological phenomena across spatial and temporal scales can incorporate mycorrhizal traits to improve understanding of global trends in mycorrhizal symbioses. For example, merging data on symbiotic mycorrhizal traits (symbiotic-MT) like mycorrhizal type or plant mycorrhizal response from FungalRoot [31] or MycoDB [29] into other ecological synthesis efforts could reveal novel ways to predict global ecological biodiversity and ecosystem function. Furthermore, because many ecological data comprise repeated sampling (e.g. LTER, NEON), they represent an opportunity to monitor understudied phenological mycorrhizal traits, such as shifts in mycorrhizal type or mycorrhizal influences on plant reproductive phenology.

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**Highlights**

- Applying trait-based approaches to ecological research on mycorrhizal symbioses broadens ecological inferences, but a single unified framework is lacking to unite disparate language, terminology, and methods across the multitude of multidisciplinary scientists studying mycorrhizas.
- We propose an inclusive framework for trait-based mycorrhizal ecology aimed to stimulate scientists around the world to collect and use more mycorrhizal trait data, particularly in understudied areas. This would widen our understanding regarding the ecological role of mycorrhizal symbioses at individual, species, community, and ecosystem scales.
- Analyzing how mycorrhizal symbioses fit within existing trait definitions highlights significant theoretical and empirical knowledge gaps, novel questions, and new research directions to improve our understanding of trait-based mycorrhizal ecology.

**Outstanding Questions**

- Where are the research gaps in trait-based mycorrhizal ecology? What new ecological knowledge about mycorrhizal symbioses can be generated by examining multiple mycorrhizal traits across multiple categories, plant-MT, fungal-MT, and symbiotic-MT. Future theoretical and empirical work must consider traits inclusive of all components of mycorrhizal root-mycelial networks that are relevant to the ecological question at hand.
- Can a trait-based framework drive novel approaches to linking plant and fungal measurements that are meaningful for the biology of mycorrhizal symbioses? What new experimental systems can be imagined to better measure mycorrhizal traits and understand mycorrhizal ecology *in situ*? What accessible (and affordable) methods can be broadly used across systems to fill knowledge gaps, particularly in understudied regions of the world?
- What is the relationship between form and function in mycorrhizal symbioses? Do morphological traits of mycorrhizal plants, mycorrhizal fungi, or the symbiosis predict mycorrhizal functions or behaviors?
- Are mycorrhizal traits positively or negatively related to each other? Are tradeoffs more likely to exist between traits belonging to the same mycorrhizal trait category? A trait framework helps differentiate the origins of trade resources, which can reveal tradeoffs that may exist between traits with shared resource allocation strategies.
- Temporal changes in plant traits are well studied, but how do fungal-MTs and symbiotic-MTs interact with plant-MT phenology? How do relationships between mycorrhizal traits vary temporally? Certain mycorrhizal traits shift phenologically, but temporal

patterns are underexplored for most mycorrhizal traits, particularly in long-lived plants, long-lived fungi, and their mycorrhizal associations.

- Are plant-MT, fungal-MT, and symbiotic-MT phylogenetically conserved? What is the degree of interspecific and intraspecific variation in mycorrhizal traits and can mycorrhizal function be predicted by plant or fungal partner phylogeny?
- Can knowledge of mycorrhizal traits influence the conservation and management of mycorrhizal symbioses in natural and managed ecosystems? Using traits to predict mycorrhizal species distributions, dispersal, and survival will improve our ability to protect and restore these important interaction networks in a changing world.

Figure

**Figure 1.** Schematic diagram of plant mycorrhizal traits, fungal mycorrhizal traits, and symbiotic mycorrhizal traits with graphical depictions of example morphological, physiological, and phenological traits for each.