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REVIEW PAPER

Mycorrhizal ecology: in the land of the one-eyed king

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Abstract

Unlike most of the other disciplines in microbial ecology, a substantial fraction of the theory on mycorrhizal ecology originates from times when assaying microbes was laborious and inefficient. Most of the resulting hypotheses target, as a result, the plant partner of the symbiosis, or at best treat the two mycorrhizal partners as a unified organism, a holobiont. I here address the legacy of this era of mycorrhizal ecology, as a means of systematizing our understanding of the discipline, but also identifying gaps in knowledge. First, I pair and review hypotheses that align with the holobiont concept with complementary hypotheses that explicitly consider the fitness of the mycorrhizal fungus. Second, I generate a hierarchy of hypotheses in mycorrhizal ecology to showcase the high potential for classifying theory into either hypotheses that treat the mycorrhiza as a holobiont or hypotheses considering mycorrhiza as an association of two individual partners. Third, I identify settings that might dictate when to better abstract mycorrhizas into holobionts and when to consider all their partners individually to foster research progress. I conclude the review with suggestions on how to further unify expectations in mycorrhizal ecology.

Keywords: Diffuse symbiotic associations, ecological theory, Glomeromycota, hierarchies of hypotheses, holobiont, laws in ecology, mycorrhizal responsiveness.

Introduction

Mycorrhizal mutualisms resulting from the association of the roots of most terrestrial plants with fungi are ubiquitous in nature (Brundrett and Tedersoo, 2018). Mycorrhizas have received considerable attention, partly because of the massive alterations they induce in plant host performance (van der Heijden *et al.*, 1998; Klironomos *et al.*, 2011), the functioning of ecosystems (Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2019), carbon, nitrogen, and phosphorus nutrient cycling (Terrer *et al.*, 2021), and the expectation that they could one day be used to sustainably increase crop yield (Oviatt and Rillig, 2021; Veresoglou and Agathokleous, 2023). We have thus witnessed the development of an extensive body of theory addressing mycorrhizas, which renders them some of the best studied mutualisms in microbial ecology (e.g. Kuyper and Jansa, 2023). This body of theory consists of an accrual of testable expectations, which take the form of hypotheses. For clarity I will be using here the terms theory and hypothesis interchangeably (e.g. Fig. 1). Until a few years ago, much of soil ecology remained mostly descriptive, and there were calls for a better integration of general ecological theory in soil ecology (Prosser *et al.*, 2007; Prosser, 2012; Poisot *et al.*, 2013). Mycorrhizal ecology has been no exception to this. Even though the first descriptions of arbuscular mycorrhizal structures date back to the 19th century, it was not until the

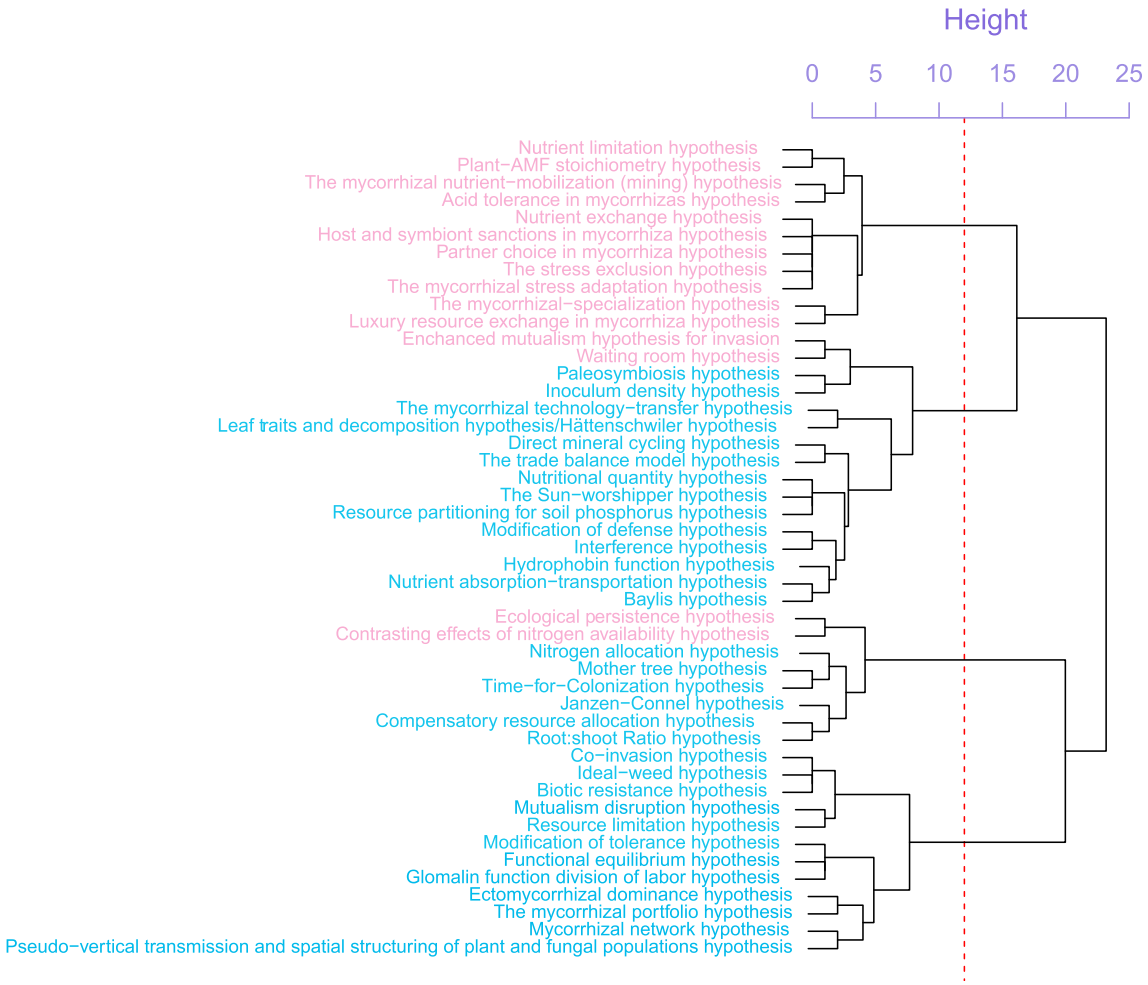

Fig. 1. Dendrogram capturing the classification into four clusters (vertical discontinuous line) of the hypotheses in our hierarchical clustering exercise of alternative and competing hypotheses on mycorrhizal eco-evolutionary structuring and functioning. Hierarchical clustering was based on six classification criteria (i.e. the topic of the hypothesis; the type of mycorrhizas; the type of ecosystem; the discrimination between holobiont-type or individual-symbionts-type hypotheses; universality of the hypothesis; and the type of prediction–for more details consult the section 'A hierarchy of hypotheses in mycorrhizal ecology'). Hierarchical clustering grouped the hypotheses into four groups. The hypotheses are colored based on whether they were holobiont-based (blue) or treated the two symbionts as individual symbiont partners (pink). The specific classification criterion has a Cramer V association value to the four clusters of 82.6% signifying that it has a high (i.e. second highest and considerably higher than the third) discrimination power in relation to the respective ecological theory. The dendrogram was prepared in R (v 4.2.2) with the command *hclust* and was plotted with the core graphics command *plot*. The names of the hypotheses are partially unconventional and have been based on output from Microsoft CoPilot. They are presented in detail, along with associated data and code, at Zenodo (https://doi.org/10.5281/zenodo.14715678; Veresoglou, 2025). The take-home messages of this dendrogram are that there is strong support for the classification of the hypotheses into four clusters, and that there is a clear differentiation between clusters containing holobiont-type and individual-symbionts-type hypotheses. Three hypotheses were named according to their inventors: the Baylis hypothesis (Fitter, 2004), the Janzen–Connel hypothesis (Song *et al.*, 2021), and the Hättenschwiler hypothesis (Hättenschwiler *et al.*, 2011). I refine the distinction between 'holobionts' and 'individual symbionts' in Box 1.

1970s and 1980s that it became common to address the ecology of the symbiosis (Koide and Mosse, 2004). Mycorrhizal ecologists at the time typically focused on the performance of the plant partner and rarely questioned the identity or the quantified fitness of the fungal partners Veresoglou and Johnson, 2023). Much of the early theory on mycorrhizas was disproportionally phytocentric, that is, focused on the plant constituent of the mutualism (but see Fitter *et al.*, 1998; Alberton *et al.*, 2005), which nonetheless allowed the discipline to flourish (Koide and Mosse, 2004) compared with other disciplines in microbial ecology. In the land of the blind (i.e. microbial ecology: Forney *et al.*, 2004), the mycorrhiza was the one-eyed king!

Widespread use of next-generation sequencing tools, in a way comparable to other microbial disciplines, has brought about a fascinating revolution in mycorrhizal ecology and made it possible to address questions targeting specifically the ecology and the biogeography of the fungal partners in the

Box 1. The holobiont concept and how I refer to it here

A pervasive idea in ecology, which has been developed independently across many constituent disciplines, is that oftentimes it pays to abstract multiple individual organisms in the form of a larger superorganism. A characteristic example of this is the pseudo-organismic theory of Clements (1916), which assumes that ecological communities behave in altruistic ways, to facilitate succession towards a climax community. Two related concepts have been those of group selection and eusociality (e.g. Wynne-Edwards, 1962; Ruxton et al., 2014), which picture natural selection as a process that occurs simultaneously between individuals in a group and between different groups of individuals. The 1976 book by Richard Dawkins, *The Selfish Gene*, gave rise to extensive controversy concerning group selection (Wilson and Sober, 1989; Pepper and Herron, 2008). Based on Dawkins (1976), the actual unit of evolution is the gene and not the individual, which obscures a key argument of the proponents of individual selection, that the individual should be used in preference to any larger group as a unit of fitness (Wilson and Sober, 1989). This remains an inconclusive debate (e.g. Godfrey-Smith, 2009) and it is beyond the scope of this review to delve into it. A characteristic example of grouping organisms in microbial symbiotic ecology is the concept of the holobiont, which refers to a non-microbial host and its associated microbial community (Bordenstein and The Holobiont Biology Network, 2024). The holobiont can in some cases be viewed as the unit of selection in symbiotic systems (Theis et al., 2016).

In mycorrhizal ecology, holobiont refers to the association of the plant host with a community of symbiotic fungi that colonize its roots. Here, we often assume as fitness for the holobiont the fitness of the plant host, which was convenient in the early days of mycorrhizal ecology, when it was hard to assay the fitness of the fungi. More often than not, we assume that plant biomass reasonably captures fitness of the holobiont, which also includes the fungal symbionts. The relatively high numbers of fungal propagules in most mycorrhizal systems makes it less critical to explicitly consider the fitness of the mycorrhizal fungi. Nutrient fertilization, shading, and disturbances to the soil and the plant, however, often lower fitness metrics of mycorrhizal fungi such as the number of vesicles and spores in arbuscular mycorrhizal systems (Shukla et al., 2009; Han et al., 2025) and fruiting bodies in ectomycorrhizas (Suz et al., 2021; Bashian-Victoroff et al., 2025). We currently do not understand sufficiently if and under which settings a lower fitness of mycorrhizal fungi could cascade to the functioning of the ecosystem. There could, however, be immense benefits if we account for the identity and functional traits of mycorrhizal fungi in existing frameworks when modelling functions such as contributions to plant biomass gains, host tolerance to pathogens, and decomposition.

symbiosis. For example, Davison *et al.* (2018) addressed the degree to which the ecological concept of island biogeography captures biogeographical features of arbuscular mycorrhizal hypotheses. It has further been possible, along with other exciting ecological ideas, to address phylogenetic host specificity patterns across different types of mycorrhizas (e.g. Jacquemyn *et al.*, 2011; Veresoglou and Rillig, 2014b; Koorem *et al.*, 2025) and scrutinize nutrient transfer dynamics in mycorrhizal symbioses (e.g. Kiers and van der Heijden, 2006; Mayerhofer *et al.*, 2021). It has clearly been an exciting time for mycorrhizal ecology.

The early years of plant-focused (phytocentric) research on mycorrhizas have, nonetheless, left a legacy that is apparent when we consider the postulates of most hypotheses routinely encountered in mycorrhizal ecology: there is a bias towards exclusively describing the plant partner or the plant phenotype in symbiosis (*holobiont-type* approaches; Box 1). This is not surprising, since theory can take considerably longer to catch up with developments in a field of research (e.g. Fox, 2011, 2013). There are some good reasons to focus on the fitness of the plant host and not the mycorrhizal fungus in mycorrhizal ecology, and many new hypotheses remain for this reason phytocentric (Fitter, 1991). For example, ecosystem goods, such as crop yields, depend largely on the fitness of the plant and not the fungus. Modeling the fitness of individuals in a diffuse symbiosis (Box 1), however, might necessitate that we consider the performance of all mutualists (*individual-symbionts-type* approaches; Box 1). Whether further considering the fungal partners in the symbiosis can result in more parsimonious models remains unclear. One possibility is that many questions of mycorrhizal ecology can be addressed with a holobiont approach, whereas individual-symbionts-type approaches contribute an elegant, but not always feasible, extension of existing paradigms.

I review here the prevalence of holobiont-type approaches in mycorrhizal ecology. First, I define the individual and joint types of approaches, and I exemplify through pairing hypotheses how their postulates differ. In this way I introduce how prevalent this distinction is across mycorrhizal theory. There are apparently alternative ways to classify hypotheses. For example, most holobiont-type approaches are phenomenological and describe net effects, whereas individual-symbionts-type approaches tend to be more mechanistic (Johnson and Stinchcombe, 2007; Johnson and Gibson, 2021; but see Fitter, 2006). In my opinion, the classification I use here is the most meaningful and the most likely to foster progress.

Table 1. An exemplary compilation of hypotheses on arbuscular mycorrhiza that either are formulated in relation to the entire symbiosis (holobiont-type approach) or explicitly consider the individual symbionts (individual-symbionts-type approach)

	Holobiont-type approach	Individual-symbionts-type approach
Nutrient exchange	Nutrient exchange hypothesis (Fitter, 2006)	Biological markets (Werner *et al.*, 2014)
Mycorrhizal responsiveness	Trade balance model (Johnson, 2010)	Host selectivity hypothesis (Klironomos, 2003; Frew *et al.*, 2025)
Partner compatibility	Baylis postulate (Fitter, 2004; Bergmann *et al.*, 2020)	Inverse phylogenetic host specificity hypothesis (Veresoglou and Rillig, 2014b; Reinhart and Anacker, 2014)
Net mycorrhizal benefits	Mycorrhizal diversity hypothesis (van der Heijden *et al.*, 1998)	Functional specialization in mycorrhiza hypothesis (Sikes *et al.*, 2010)
Litter decomposition	Direct mineral cycling hypothesis (Hodge *et al.*, 2001; Bunn *et al.*, 2019)	Organic nitrogen transfer efficiency hypothesis (Leigh *et al.*, 2009)

This table is not meant to be exhaustive. For a more systematic attempt to map the literature, see Fig. 1.

Second, I classify theories in mycorrhizal ecology and generate a hierarchy of hypotheses (Heger and Jeschke, 2018). I use the high discrimination potential that our distinction into holobiont-type and individual-symbionts-type approaches provides. At the same time, I present some of the specific benefits and synthesize hypotheses for mycorrhizal ecology. I finish the review with an afterview of our exercise.

Pairing hypotheses

I paired hypotheses that explicitly consider the fitness or the alteration that arbuscular mycorrhizal (AM) fungi induce to hosts or ecosystem functions (Table 1: *individual-symbionts-type* approach) with hypotheses that maintain a phytocentric focus (Table 1: *holobiont-type* approach). To distinguish between the two types of classification, I asked if the identity of the mycorrhizal fungus could alter the predicted outcome, depending on whether the symbiosis partners are considered individually or together. In other words, I differentiated between hypotheses that predicted the phenotype of each symbiotic partner, the plant and the fungus (individual-symbionts-type approaches), and hypotheses that either predicted the phenotype of the symbiosis or focused exclusively on plant fitness, the net symbiotic effect (holobiont-type approaches). I did not produce a comprehensive list of pairs of hypotheses or engage in a systematic mapping with our hierarchy of hypotheses. I wanted, instead, to highlight differences between the two approaches (Table 1), and likely settings that might allow us to approach the symbiosis conventionally from the holobiont concept.

The literature on how the two partners exchange nutrients features two hypotheses aligning with our narrative, the *nutrient exchange hypothesis* and that on *biological markets* (Table 1). Bunn *et al.* (2024) reviewed the specific body of literature on resource exchange between mycorrhizal partners, making some really good points on it, while at the same time proposing a very specific set of terms, which I do not follow here. Fitter (2006) proposed a simple conceptual model (which can be referred to as the nutrient exchange hypothesis) that pictured mycorrhizal fungi as scavengers of carbohydrates in the apoplast of the plant host. To stimulate the local release of carbohydrates in the plant host, AM fungi deliver P (Fitter, 2006). The plant host in this hypothesis does not discriminate among AM fungi but instead reciprocates to the local release of nutrients, and as such I classified it as a holobiont-type hypothesis. There is plenty of evidence that some AM fungal isolates consistently deliver lower nutritional benefits to their plant hosts (e.g. Säle *et al.*, 2021). Werner *et al.* (2014) explored the applicability of the paradigm of biological markets in the case of mycorrhizal systems: plant hosts and mycorrhizal fungi can recognize each other and can preferentially deliver the goods to the partner that maximizes benefits for them (Werner *et al.*, 2014). The idea of exploring the concept of mycorrhizal markets in the case of mycorrhizal systems had been originally proposed by Selosse and Rousset (2011) and has given rise to considerable controversy (Walder and van der Heijden, 2015; Kiers *et al.*, 2016; van der Heijden and Walder, 2016). Two studies that the proponents of the theory on biological markets often cite as evidence in support of the paradigm are those of Kiers *et al.* (2011) and van't Padje *et al.* (2020). The results of studies by Kiers *et al.* (2011) and van't Padje *et al.* (2020) may also be rationalized in terms of the nutrient exchange hypothesis. Clearly, there is plenty of room for additional research on this topic.

A common theme across mycorrhizal studies is analyses of the factors that result in growth benefits (or disbenefits) to the plant host, compared with non-mycorrhizal controls; we refer to this as mycorrhizal responsiveness. Fertilizing the soil with nutrients, for example, reduces benefits from mycorrhizas (Treseder, 2004; Hoeksema *et al.*, 2010). A holobiont-type of expectation (Table 1) in relation to mycorrhizal responsiveness is that adding N indeed makes the plant host less responsive to mycorrhizal colonization, unless the soil is limited in P. Adding N can exacerbate host plant P limitation and render it more dependent on the mycorrhizal symbiosis. The *trade balance model*, in particular, postulates that the leaf C:N:P stoichiometry determines the mycorrhizal responsiveness of the plant host (Johnson, 2010). The expectations of the trade balance model were grounded in observations at the Konza prairie, where

growth is P limited and where upon fertilization with N there was an increase in AM fungal diversity (Egerton-Warburton *et al.*, 2007). Because the hypothesis makes no distinction in relation to the identity of the mycorrhizal fungal partners that colonize the plants, I classify it as a holobiont-type hypothesis. Most of the studies addressing the trade balance model have been supportive of the hypothesis (Grman and Robinson, 2013; Pan *et al.*, 2020; but see Corrêa *et al.*, 2024). A counter-hypothesis, to which I refer here as the *host selectivity* (or *host specificity*) *hypothesis*, attributes variation in mycorrhizal responsiveness to how compatible the plant host is to the respective community of AM fungi. Because this counter-hypothesis considers the identity of the AM fungi, I classify it as an individual-symbionts-type approach. It has so far been possible to pair virtually any plant host with any AM fungus under gnotobiotic conditions, which suggests that host specificity in the symbiosis is relatively low. Some authors prefer for this reason to use the term host selectivity instead, because the symbiotic specificity is context-dependent. An extreme example of host selectivity was observed under field settings by Helgason *et al.* (2002) at a woodland in North Yorkshire. Roots of *Acer pseudoplatanus*, which had been assayed for AM fungi via a cloning–sequencing approach, associated exclusively with *Glomus hoi*. Even though this observation originates from a time when it was challenging to achieve a good sequencing depth, it indicates that under field settings AM fungi indeed exhibit host preferences. To the best of my understanding, to date, the most compelling study addressing the degree to which host selectivity can shape mycorrhizal responsiveness is that by Klironomos (2003). Klironomos (2003) worked with a set of 64 plant hosts, which he experimentally grew either with a single AM fungus, *Glomus etunicatum*, or without any. The mycorrhizal responses that he could subsequently assess ranged from negative (i.e. 46% growth suppression) to strongly positive (i.e. up to a 48% growth stimulation). Mycorrhizal responses can also differ across host cultivars. Kuper-Psenicnik and Bennett (2025) grew nine cultivars of *Medicago sativa* with *Rhizophagus irregularis* in a pot trial and exposed the plants to ambient and high levels of salt stress. Their results showed that there were cultivar-driven differences in growth rates, which, however, fell short of the expectations of the authors.

There is a large body of literature that investigated whether host selectivity is driven by plant traits (i.e. phytocentric—holobiont-type approach) rather by traits in both the plant host and the AM fungus (Table 1). Baylis (1975) proposed that plants with underdeveloped root systems depend more on mycorrhizas for nutrient uptake (Fitter, 2004; Bergmann *et al.*, 2020). The specific expectation does not explicitly consider host preferences and as such it can be classified as a holobiont-type hypothesis. The *Baylis postulate* is reasonably well supported in the literature (Yang *et al.*, 2014; Bergmann *et al.*, 2020; but see Maherali, 2014). A counter-hypothesis that considers mycorrhizal fungi is the *inverse phylogenetic host specificity hypothesis*: in 2014 two independent studies observed that the differences in the structure of the mycorrhizal community increased for hosts that were more closely related phylogenetically (Reinhart and Anacker, 2014; Veresoglou and Rillig, 2014a). Most of the existing literature supports this hypothesis, as well (e.g. Chen *et al.*, 2017; Montesinos-Navarro *et al.*, 2019).

Host plant benefits of the AM symbiosis may increase as the diversity of AM fungal symbionts increases due to fungal complementarity (Table 1). van der Heijden *et al.* (1998) established a series of plant communities simulating North American old-field ecosystems and inoculated them with AM fungal communities ranging in richness from zero to 14 species. Biomass production increased asymptotically with AM fungal richness and peaked in the treatment with the 14 species. Wang *et al.* (2011) replicated those findings over an AM fungal richness gradient from zero to four species, but at the same time further calculated the complementarity and selection constituents of the net biodiversity effects. In this way it was further possible to show that selection effects prevailed in sandy soil substrate, whereas complementarity effects prevailed in the more clay-rich soil substrate (Wang *et al.*, 2011). Selection effects, however, capture expectations in relation to the AM fungal community and could classify as individual-symbionts-type approaches as well. Malicka *et al.* (2021), by contrast, observed that when exposed to hydrocarbons, *Lolium perenne* grew more poorly with mixtures of AM fungi than single AM fungal species. This body of theory does not consider the identity of the AM fungi as a driver of mycorrhizal responsiveness and I thus classify it as holobiont-type theory. Maherali and Klironomos (2007), by contrast, worked with a fixed set of eight AM fungal species and manipulated their phylogenetic relatedness to show that biomass gains of the *Plantago lanceolata* hosts peaked when associated with members of three AM fungal families. In this particular case, the authors considered the identity (i.e. family to which they belonged) of the AM fungal species, and I classify this study as an individual-symbionts-type study. Sikes *et al* (2010) reanalysed data from two studies, one of which was Maherali and Klironomos (2007), to calculate the relative benefits that *Plantago lanceolata* received from *Gigasporaceae* and *Glomeraceae* isolates. The study showed that *Glomeraceae* isolates mainly protected the plant hosts from plant pathogens, while *Gigasporacae* isolates mainly contribute to the nutrition of the plant hosts (Sikes *et al.*, 2010). This study gave rise to the *functional specialization in mycorrhiza hypothesis*, as I refer to it here, postulating that AM fungal taxa contribute distinctively to ecosystem multifunctionality, which also represents a hypothesis that falls under the *distinct-partners* umbrella. Most existing studies working on synthetic AM fungal communities and relatively small gradients of AM fungal richness typically support the *mycorrhizal diversity hypothesis* [e.g. Edathil and Udaiyan, 1996; Gosling *et al.*, 2016; and see Roger *et al.* (2013) on evidence that also genetic diversity can increase plant and possibly fungal fitness]. There is evidence, however, that the relationship between mycorrhizal

richness and plant biomass production is not positive under field settings (Hiiesalu *et al.*, 2014). To the best of my knowledge there are no other studies addressing the functional specialization hypothesis. There are, nevertheless, studies questioning the ability of *Gigasporaceae* to outperform other AM fungi in P nutrition (e.g. Tajini *et al.*, 2009; Lendenmann *et al.*, 2011; Frew *et al.*, 2025; Koorem *et al.*, 2025).

Arbuscular mycorrhizas also inhibit or promote many ecosystem functions, such as decomposition (Hodge *et al.*, 2001), nitrification (Veresoglou *et al.*, 2011), and soil aggregate stability (Rillig and Mummey, 2006), which do not directly cascade to the functioning of the symbiosis. The *direct mineral cycling hypothesis* has been proposed to rationalize why AM fungi proliferate on leaf litter in the tropics (Camenzind and Rillig, 2013; Bunn *et al.*, 2019). The hypothesis postulates that AM fungi indirectly speed up the decomposition of organic litter in the habitats where they occur (Table 1). It is unclear how AM fungi benefit from colonizing litter, but a recent perspective on the topic nicely brought together existing literature and speculated on the likely ecological significance of it, through, for example, nutrient retention in the ecosystem (Bunn *et al.*, 2019). The hypothesis does not differentiate between the effects of different AM fungi, and I thus classify it as a holobiont-type hypothesis. Leigh *et al.* (2009) by contrast, while experimenting with two AM fungal isolates, *Glomus hoi* and *Glomus intraradices*, were able to show that the latter isolate transferred N more efficiently to the plant host, *Plantago lanceolata*, than the former. This is an important finding because it might signify that the relative contributions of different AM fungal isolates to decomposition vary. I took here those results and reframed them in the form of a hypothesis, the *organic nitrogen transfer efficiency hypothesis*, which postulates that there exist large differences in the efficiency with which AM fungal taxa promote decomposition (Bunn *et al.*, 2019). The organic nitrogen transfer efficiency hypothesis has not been integrated sufficiently in the literature (but see Hoysted *et al.*, 2023; Howard *et al.*, 2024; Košnar *et al.*, 2025). The direct mineral cycling hypothesis, by contrast, has received extensive support (e.g. Hodge *et al.*, 2001; Cheng *et al.*, 2012; Xu *et al.*, 2018; Rozmoš *et al.*, 2022).

Sprucing up ecological theory

Constructing hierarchies of hypotheses can bring multifaceted benefits to any discipline (Schurz, 2021). First, organizing knowledge via mapping hypotheses serves as an excellent educational tool, since it confronts opposites and places alternative hypotheses next to each other (Dhami *et al.*, 2019). Hierarchies of hypotheses effectively communicate how the expectations across hypotheses differ and how these relate to each other. Hierarchies of hypotheses also connect empirical results conceptually and graphically generating logic to broader theoretical ideas, which facilitates learning and systematization. This is why we often request young scholars to abstract their understanding of disciplines with visual tools, such as mind maps and concept maps (e.g. Izci and Akkoc, 2024). Mapping hypotheses could further open up opportunities to comparatively assess concepts in the literature and this way identify knowledge gaps and biases in the literature (Heger *et al.*, 2021). The mapping of hypotheses can thereby foster progress in a discipline. Benefits can, nonetheless, go beyond the discipline itself. As the ideas in the discipline become more accessible to other audiences, scholars from other disciplines can benefit from them and can potentially reapply them on different experimental systems or in different contexts, or else in some cases it can bring together scientists from disparate disciplines working at the interfaces of the soil, plant, and microbial sciences. Mycorrhizal ecologists could communicate better this way, for example, with colleagues working on topics such as soil ecology, plant physiology, or agronomy. Maps of hypotheses thus make it easier to reap the benefits of interdisciplinarity (Okamura, 2019).

Some of these benefits are particularly pronounced in relation to mycorrhizal ecology. First, as I stated earlier, a large fraction of the theory has been developed at a time when it was hard to explicitly assess the state of the microsymbiont, which opens up numerous opportunities to synthesize across holobiont-type hypotheses and individual-symbionts-type hypotheses that treat the two partners as *individual mutualists* and thus to pair alternative or complementary, or old and new, hypotheses, which is what I do here. Second, mycorrhizal ecology is also extremely interdisciplinary (e.g. Dahlberg, 2001; Hou *et al.*, 2020), and relies heavily on techniques that have been used in related disciplines, such as biology, soil science, chemistry, computer theory, and bioinformatics. As I mentioned above, multidisciplinarity is subject to effective communication of ideas across the involved disciplines, facilitated by hierarchies of hypotheses. Third, mycorrhizal ecology features an extensive body of theory that has rarely been systematized, and we are occasionally oblivious of the older theory (Koide and Mosse, 2004; Veresoglou and Rillig, 2014b). Mapping hypotheses sheds additional light on the specific theories and thus fosters progress.

A hierarchy of hypotheses in mycorrhizal ecology

To assess how pervasive the distinction between holobiont-type and individual-symbionts-type approaches are in mycorrhizal ecology I carried out a 'hierarchy of hypotheses' analysis (Heger and Jeschke, 2018). I followed to the degree possible an established framework (Heger *et al.*, 2021) on how to integrate the approach, but nonetheless, my interpretation finally only relies on the clustering of the hypotheses into four groups and not the hierarchy *per se*. I therefore use the term hierarchy of hypotheses here in a relaxed, unconventional way to present the clustering based on the association between six classification criteria (Fig. 1).

On the 13 October 2024, I searched the Web of Knowledge core collection with the search string 'hypothes* (Title) and mycorrhiza of arbuscular or ectomycorrhiza or Glomeromycot* (Topic)'. My search yielded 50 hits (Appendix 1, available at Zenodo; Veresoglou, 2025; https://doi.org/10.5281/zenodo.14715678), out of which I was able to derive 47 mycorrhizal hypotheses (Appendix 2, available at Zenodo; Veresoglou, 2025). In many cases (also applicable to most of this contribution), it was hard to identify names for the hypotheses as I considered and named them here. In cases of uncertainty about hypothesis naming, I used an AI tool (Microsoft CoPilot) to name the hypotheses.

For the set of 47 mycorrhizal hypotheses, I used the following six classification criteria with specific levels, each:

(i) The topic of the hypothesis—a categorical variable with eight levels: plant nutrition; stress and pathogen load for the plant host; nutrient cycling; ecosystem services and functions unrelated to nutrient cycling; plant interspecific and intraspecific competition; evolutionary success of the mutualism; evolutionary success of the plant host; seedling success.
(ii) Type of mycorrhizas—a categorical criterion with four levels describing the types of mycorrhizas to which the hypothesis referred: ectomycorrhiza (ECM); AM; both ECM and AM; other.
(iii) Type of ecosystem—a categorical criterion with three levels: agricultural; forests; any.
(iv) Classification as either holobiont-type or individual-symbionts-type of hypothesis—a categorical criterion with two levels.
(v) Universality—a categorical criterion with two levels, describing the settings to which the hypothesis could be applied: no exceptions and some exceptions.
(vi) Type of prediction—a categorical criterion with two levels describing whether the hypothesis was just descriptive or assumed underlying mechanisms that can later be used to make predictions: explanatory and observational.

To calculate the classification tree, I used the three main descriptors of the systems to which the hypotheses applied [criteria (i), (ii), and (iii)] and two out of the three criteria that grant generality to hypotheses [Colyvan and Ginzburg, 2003; criteria (v) and (vi)]. I did not use the third criterion, constraints in Colyvan and Ginzburg (2003), because all the hypotheses framed the expectations in ways independent of plant density. I finally classified the hypotheses [criterion (iv)] as either holobiont-type or individual-symbionts-type. As I mentioned above, I used the distinction criterion in relation to whether the expectations changed (or not) with the identity of the mycorrhizal fungal partners.

I worked towards generating a reasonably factual classification (Appendix 2, available at Zenodo; Veresoglou, 2025), but I understand that there may be reservations in relation to many of the choices. As I discuss later, however, the two top classification criteria generated considerably higher scores than the other four, and I think that any small biases that became integrated into the classification should have had a small impact on the final results (Fig. 1).

The hypotheses were hierarchically clustered (Heger *et al.*, 2021) based on the sums of the pairwise distances across the six criteria as calculated with the command *cat.dist* in the R package *GSDA* (Cao and Pounds, 2021). I used the Ward method (i.e. *ward.D*) of the command *hclust* for the clustering. In the resulting dendrogram (Fig. 1), there are four apparent clusters of hypotheses. To evaluate the degree to which the five categorical criteria contributed to the final classification of the hypotheses, I used the command *cramerV* of the library *rcompanion* (Mangiafico, 2024). The resulting Cramer V values were 91.3% for predictions type, 82.6% for the classification between holobiont type and individual symbionts type, 55.6% for the topic of the hypothesis, 55.4% for the type of the ecosystem, 54% for the type of mycorrhizas, and 25% for the universality of the hypotheses. The Cramer V value for the association between type of prediction and the classification between holobiont type and individual symbionts type was low (i.e. 24.6%), meaning that the results were not driven by a possible collinearity of these two attributes. The take-home message of this classification exercise is the high discrimination power of the six criteria for holobiont-type and individual-symbionts-type approaches in mycorrhizal ecology.

Unifying expectations in mycorrhizal ecology

The categories holobiont-type and individual-symbionts-type approaches form the basis for hypothesis-driven eco-evolutionary investigations on mycorrhizas. I develop here three critical points.

It is important to further explore the settings under which holobiont-type hypotheses perform better than the individual-symbionts-type hypotheses and vice versa. We are clearly in need of further collective reflections on the topic. One consideration should be the scale at which studies take place. The additional statistical power of studies at a global scale might diminish the benefits from separately considering the mycorrhizal symbiosis partners, due to biogeographical patterns. Studies at a small, local scale, by contrast, might benefit from high-resolution mechanistic studies at the scale of the individual symbiosis partners. Another determining factor for the type of investigation is the resolution power of the data available or to be collected: taking the individual symbionts' perspective in meta-analyses may be harder than in primary literature studies, because strict study inclusion criteria can reduce the numbers of eligible studies to address a particular hypothesis. Several additional considerations can be study system specific. Ecosystem processes related to the uptake and cycling of elements might benefit more from paradigms that focus on the individual symbiosis partners than investigations on net primary productivity and plant stoichiometry. Paradigms

considering extensive spatiotemporal scales might be preferably modeled via holobiont-type hypotheses, because of challenges in capturing the transient dynamics of plant–fungus associations and because the resolution of scale for the two partners might show considerable differences since plants are considerably larger than mycorrhizal fungi (e.g. Drakare *et al.*, 2006; Veresoglou and Johnson, 2023). The same applies to studies on lagged responses, such as mycorrhizal respiration in relation to primary productivity (de Luca *et al.*, 2024): in these cases, integrating paradigms considering explicitly both partners may prove tricky. Holobiont-type approaches may be useful to cover the consequences of 'diffuse coevolutionary selection pressure' (Cairney, 2000; Selosse *et al.*, 2006; Hoeksema, 2010). Finally, there may be differences in relation to how well individual hypotheses perform (i.e. idiosyncratic reasons) that could prompt analysts to preferentially use one hypothesis over the other. As investigations on mycorrhizal effects are scaled up to the ecosystem level, integrative holobiont-focused studies may become the matter of choice.

A productive avenue to further propagate discussion on mycorrhizal ecology is to pair hypotheses as suggested here. For the time being, I only focus on pairs of hypotheses that are already promising, which could highlight the potential of the approach. Further exploring pairs can uncover loose links between concepts and give rise to conceptual innovation. Most importantly, exploring further pairs will create sets of counter-hypotheses that can be tested against each other (Chamberlin, 1890; Elliott and Brook, 2007). Extending the existing strong conceptual framework has thus the potential to make primary literature studies even more exciting.

A further aim could be to determine whether some hypotheses may not be particularly well supported and moving beyond their postulates. Oftentimes, it is hard to discredit theory that has already been integrated into the literature, even if there is overwhelming evidence against it (Fox, 2011). This is a widespread problem in ecology, and possibly the only way to solve it is to contribute good alternative explanations (i.e. hypotheses on the same topic) to the scholars working on them. This is something towards which testing of hierarchies of hypotheses contributes. Eventually, abandoning less supported hypotheses would contribute towards tidying up and reorganizing the discipline of mycorrhizal ecology. In the end, it is the study question and purpose that decides whether to focus on the effects and responses of the symbiosis (holobiont-type approaches) or the individual symbionts (individual-symbionts-type approaches).

Non-arbuscular mycorrhizal types

I focused this review on arbuscular mycorrhizas, on the understanding that some of the discussion also applies to other mycorrhizal types, such as ectomycorrhizas, ericoid mycorrhizas, or orchid mycorrhizas (Smith and Read, 2008). The challenges that ecologists face when working on arbuscular mycorrhizas are quite distinct from those that researchers face when focusing on other mycorrhizal types, such as ectomycorrhizas for which it is possible to discriminate morphotypes without sequencing (e.g. Seress *et al.*, 2016; Khokon *et al.*, 2023). The only likely equivalent for arbuscular systems is the classification of the asexual spores into morphospecies, which, however, makes it difficult to assign the fungi to any specific plant host and remains a laborious technique when implemented at large spatial scales. Distinct *Arum*- and *Paris*-type root colonization patterns are largely determined by the plant and not the fungi and need well-stained material and experience to be differentiated, particularly when other fungi are also present, such as mucoromycotinan fine-root endophytes. The study of arbuscular mycorrhizas may thus present a special case, where we can clearly differentiate between older and newer theory, which could give rise to many complementary postulates.

Many of the hypotheses I specified for arbuscular mycorrhizal systems also apply to other mycorrhizal types. For example, Peay *et al.* (2007) questioned species-area paradigms in the ectomycorrhizal symbiosis, in a way comparable to Davison *et al.* (2018), who focused on arbuscular mycorrhiza. In our hierarchy of hypotheses exercise, I included seven hypotheses that are specific for ectomycorrhizal systems. Two of these could be classified in the individual symbionts type. The *contrasting effects of nitrogen availability hypothesis* (Högberg *et al.*, 2003) predicts that at a low N availability, plant investment into mycorrhizal fungi increases, whereas the *ecological persistence hypothesis* predicts that plants facilitate the persistence of mutualistic mycorrhizal fungi by enhancing the mortality of root tips colonized by competitively superior mycorrhizal fungi (Hoeksema and Kummel, 2003). Five hypotheses could be classified into the category of holobiont-type hypotheses, namely the *ectomycorrhizal dominance hypothesis* (Luo *et al.*, 2024), the *mother tree hypothesis* (Bas *et al.*, 2024), the *compensatory resource allocation hypothesis* (Leuschner *et al.*, 2001), the *time for colonization hypothesis* (Torti and Coley, 1999) and the *nitrogen allocation hypothesis* (Wallander, 1995). Further exploration of non-arbuscular mycorrhizal types in relation to holobiont-type and individual-symbionts-type approaches would also be worthwhile.

Conclusion

I discussed here a major differentiation axis of theory in mycorrhizal ecology. Mycorrhizal ecology has commonly been seen as an extension of plant ecology, which in some cases was unfortunate, because there has not been sufficient integration with the pertinent theory in microbial evolutionary ecology. For example, the concept of the holobiont has been discussed more extensively amongst microbial ecologists and general symbiont ecologists (e.g. Triviño and Suárez, 2020) than mycorrhizal ecologists (but see Faure *et al.*, 2018; Biget *et al.*, 2023). Our hierarchy of hypotheses should work towards

integrating better microbial ecology with mycorrhizal ecology. There are immense opportunities to further solidify the theoretical framework that underlies investigations on mycorrhizal interactions, and I hope that I have made a first step with my insights here.

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Conflict of interest

The author declares he has no perceived conflicts of interest.

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Data availability

The Web of Science search results for the mycorrhizal hypotheses data that support the findings of this study are openly available as Appendix 1 in the Excel file Supplement Tables (first sheet) in Zenodo at https://zenodo.org/records/14715678 (Veresoglou, 2025). The respective classification of the hypothesis is presented in the form of a second sheet on the same file (i.e. Appendix 2). The code I used to process the hypotheses is available through the file clustering.R in Zenodo at https://zenodo.org/records/14715678 (Veresoglou, 2025).

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