A trait-based framework to understand life history of mycorrhizal fungi

Pierre-Luc Chagnon[1], Robert L. Bradley[1], Hafiz Maherali[2], and John N. Klironomos[3]

[1] Université de Sherbrooke, Département de Biologie, 2500 boul. de l'Université, Sherbrooke, QC, J1K 2R1, Canada
[2] Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, ON, N1G 2W1, Canada
[3] Department of Biology, University of British Columbia, ASC 373-3333 University Way, Kelowna, BC, V1V 1V7, Canada

Despite the growing appreciation for the functional diversity of arbuscular mycorrhizal (AM) fungi, our understanding of the causes and consequences of this diversity is still poor. In this opinion article, we review published data on AM fungal functional traits and attempt to identify major axes of life history variation. We propose that a life history classification system based on the grouping of functional traits, such as Grime's C-S-R (competitor, stress tolerator, ruderal) framework, can help to explain life history diversification in AM fungi, successional dynamics, and the spatial structure of AM fungal assemblages. Using a common life history classification framework for both plants and AM fungi could also help in predicting probable species associations in natural communities and increase our fundamental understanding of the interaction between land plants and AM fungi.

Functional diversity in arbuscular mycorrhizal fungi: the need for a conceptual framework

The symbiosis between plants and arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota; see Glossary) originated some 450 million years ago [1] and is thought to have facilitated the transition of plants from water to land. This symbiosis occurs in a majority of species in the plant kingdom and may be a major driver of the assembly, dynamics, and productivity of plant communities (e.g., [2,3]). Therefore, there is a need to understand the mechanisms through which AM fungi influence a wide range of plant responses in different environmental contexts.

The historical notion that AM fungi are a functionally homogeneous group specialized in the provision of phosphorus (P) to their host plants [4] has been expanded to consider other types of functions. It has been known for some time that AM fungi can confer plant pathogen protection as well as improve plant tolerance to drought and heavy metal contaminants (e.g., [5–7]). More recently, it has been demonstrated that AM fungi may alter plant hormone dynamics [8] as well as stabilize soil aggregates, which could have physical and resource benefits for the plant [9]. There is also interspecific variation for these

functions and their attendant traits, suggesting the existence of functional trade-offs among AM fungal species [10]. For instance, different AM fungal species can vary in their carbon demand from host plants [11], P translocation to roots [12], carbon storage [13], and relative investment into extraradical versus intraradical biomass [14]. To understand the origin of this variation and to predict its ecological consequences, it is necessary to develop a conceptual framework that organizes AM fungal species according to functional groups.

Several advantages arise from classifying AM fungal species according to broad functional groups. Identifying

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Glossary

Arbuscular mycorrhizal (AM) fungi: soil fungi forming a mycorrhizal symbiosis with a majority of vascular plants by colonizing roots and providing various benefits in exchange for plant carbon. These fungi belong to the phylum Glomeromycota and develop arbuscules (finely branched hyphae within the plant cell) when colonizing plant roots. Fossil evidence indicates that they are more than 400 million years old and lived as endophytes in ancestral vascular plants. The Glomeromycota are made up of several families, of which the most speciose are the Gigasporaceae, Acaulosporaceae, and Glomeraceae, the latter subdivided in the subgroups (or clades) *GlomusGroup A* (*GrA*) and *GlomusGroup B* (*GrB*).

Autogenic succession: successional changes that are driven by the biotic components of communities (i.e., living organisms).

β-Diversity: degree of species turnover between local communities.

Carbon sink strength: degree to which the metabolic demands of heterotrophic AM fungi can increase plant carbon flow to regions of the root colonized by the fungus.

Deterministic/niche-based mechanisms: ecological mechanisms of community assembly associated with the niche of organisms, and situations in which community assembly can be predicted by niche requirements.

Environmental filter: feature of the environment that can exclude or include organisms displaying specific traits or characteristics (e.g., recurrent drought in a prairie ecosystem may filter out drought sensitive plants).

Functional trait: a physiological or morphological aspect of the phenotype of an organism that influences survival, growth, and reproduction.

Life history strategy: describes how an organism acquires resources and invests them into growth and reproduction, and includes trade-offs associated with these investments.

Obligate biotroph: symbiotic (parasitic or mutualistic) organism that cannot complete its life cycle without colonizing a living host organism.

Ontogenetic development: ontogeny traces the various successive developmental stages of an organism.

Phyllosphere: plant leaf surface (sometimes extended to all aboveground surface) that can serve as a habitat for various microorganisms.

Resource use efficiency: amount of biomass or energy that can be produced per unit resource acquired.

Root system architecture: characterization of the relative allocation of a plant to different components of the root system (i.e., tap root, lateral roots, root diameter classes, root hair length, and density). One can simplify root architecture description by dichotomizing coarse versus ramified root systems; the former refers to large diameter roots with few branches and the latter to small diameter and highly branched roots.

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sets of correlated functional traits within each group could help us to define major life history strategies. Those strategies, in turn, could be used to predict biodiversity patterns and successional trajectories in a tractable way. For example, ecologists have been using r and K selection strategies [15] to describe the early establishment of populations with a short generation time, rapid growth, and low resource use efficiency (i.e., r strategy), and their eventual replacement by populations with delayed reproduction, high parental care, and a few large offspring (i.e., K strategy) [16]. In the case of AM fungi, as obligate plant biotrophs, an additional challenge would be to develop a common framework that categorizes both plant and AM fungal life history strategies, because the level of matching between the life histories of interacting plant and fungal symbionts may predict the relative benefit that each partner will derive from the interaction.

Frameworks that group species into functional groups along a few trait axes have helped to summarize biological variation and has led to the development of hypotheses to explain the origins of functional diversity [15], the distribution and abundance of species [17], and the consequences of functional traits for ecosystem functioning [18]. Of the many frameworks that have been proposed, the r–K selection model [15] has probably been the most influential. Nevertheless, this framework has been criticized for its oversimplification of life history strategies along a single axis that combines both disturbance and resource availability [17]. Other models that integrate additional axes have thus been proposed to more completely characterize diversity while at the same time remaining simple and tractable. One example in aquatic science is the Winemiller–Rose triangular model [19], which integrates both disturbance frequency and predictability, thus defining three main strategies: opportunistic (highly disturbed systems), seasonal (periodically disturbed systems), and equilibrium (undisturbed systems). One limitation of the triangular model, however, is that even though it provides a clearer role for two different qualitative aspects of disturbance in selecting for distinct life histories, it does not account for additional and potentially major aspects of life history, such as resource availability and abiotic stressors.

In plant science, Grime's C-S-R (competitor, stress tolerator, ruderal) framework overcomes some limitations of other models by classifying plant life history strategies according to the functional traits associated with responses to two major environmental filters, namely stress and disturbance [20]. Stress refers to persistent adverse environmental conditions (e.g., low soil fertility and limited light availability), whereas disturbance refers to events leading to significant loss of functional biomass (e.g., fire and windthrow). The C-S-R framework identifies three main life history strategies. 'Competitors' thrive in low stress and low disturbance environments, where they gain a competitive advantage by delaying reproduction so as to invest in structures that optimize the acquisition of resources [21]. 'Stress tolerators' endure suboptimal environments owing to resource conservation strategies, such as the production of long-lived biomass, which increases resource use efficiency in the long term [22,23]. 'Ruderals' cope with frequent disturbance by relying on high colonization ability, rapid production of low cost biomass, and short reproductive cycles [20,21]. According to the framework, no species can withstand both high levels of stress and disturbance, thus preventing the existence of a fourth life history strategy. As a whole, the C-S-R framework has been useful for understanding the assembly of plant communities undergoing land-use change [24], and for predicting successional trajectories of plant communities after disturbance events [25,26]. In addition to plant studies, the C-S-R framework has been used to study functional variations in coral reef communities [27], and it has also been proposed as a means of studying life history strategies of phyllosphere microorganisms [28], thus supporting its generalizability to various systems. In this opinion article, we employ the C-S-R framework as an example of how trait-based classification approaches can advance our knowledge of the relationship between AM fungal life history traits, plant life history traits, and environmental abiotic filters.
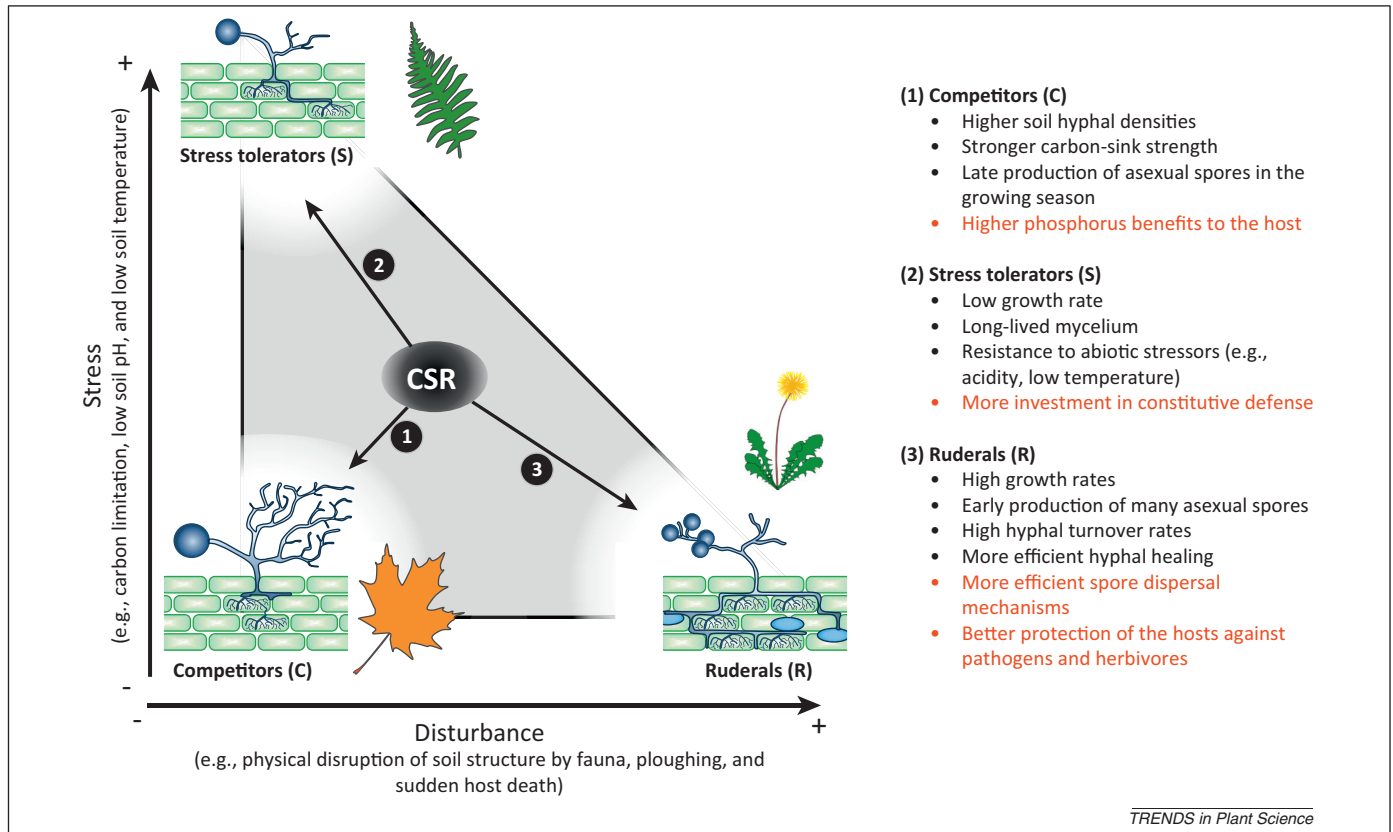
Applying the C-S-R framework to AM fungi
To better understand the biology and life history of AM fungi requires a mycocentric perspective, that is, an appreciation of AM fungi not only as plant symbionts but also as organisms that have developed traits that maximize their own fitness in different environments [29,30]. We must recognize, therefore, that what benefits the plant is not necessarily what benefits the AM fungus, and vice versa. For example, high soil P availability may promote the growth of the plant, but will in turn reduce the amount of carbon transferred to the AM fungal symbiont [31]. Thus, when applying a C-S-R framework to AM fungi, we must consider which environmental conditions cause stress or disturbance to AM fungi, and then explore which functional traits improve the AM fungal response to those environmental filters (Figure 1).

Competitive AM fungi
The competitive ability of an individual derives from its capacity to acquire growth-limiting resources. Considering previous work on AM fungal foraging strategies, the main growth-limiting resource for AM fungi appears to be plant-derived carbon [32]. Consequently, competitive AM fungi should be those with functional traits that improve carbon acquisition from the host plant. It is generally recognized that soil P deficiency increases the flow of plant carbon to AM fungi [33]. Furthermore, it has also been shown that the flow of plant carbon to the fungus is proportional to the amount of P that the fungus returns to its host [34], thus supporting models of metabolic coupling between carbon and P transfer [35,36]. A high rate of P transfer to the host is related to extraradical hyphal production [37,38] rather than to the intensity of root colonization [12]. Hence, competitive AM fungi are likely to be those that allocate large quantities of carbon to growing mycelial biomass for soil exploration and soil P solubilization. In this situation, the trade-off traits are likely to be a lower investment in root-borne carbon storage structures (e.g., vesicles) and a delay in the reproductive effort.

There is evidence that AM fungi in the Gigasporaceae family show traits associated with a competitive life

(1) Competitors (C)
- Higher soil hyphal densities
- Stronger carbon-sink strength
- Late production of asexual spores in the growing season
- Higher phosphorus benefits to the host

(2) Stress tolerators (S)
- Low growth rate
- Long-lived mycelium
- Resistance to abiotic stressors (e.g., acidity, low temperature)
- More investment in constitutive defense

(3) Ruderals (R)
- High growth rates
- Early production of many asexual spores
- High hyphal turnover rates
- More efficient hyphal healing
- More efficient spore dispersal mechanisms
- Better protection of the hosts against pathogens and herbivores

Figure 1. A C-S-R triangle identifying stress and disturbance factors as well as phenotypic traits of arbuscular mycorrhizal (AM) fungi classified as competitors, stress tolerators, or ruderals. Empirical evidence is lacking for the suggested traits highlighted in red. On the triangle, we also illustrate the corresponding plant life history strategy that would match each fungal strategy given that preferential associations are likely between plants and fungi with similar C, S, or R strategies.

history strategy. For example, members of the Gigasporaceae invest more biomass in extraradical hyphae than in root-borne structures, compared with other phylogenetic groups [14,39]. Moreover, members of the Gigasporaceae increased dramatically in abundance in nitrogen (N)-fertilized plant communities where P availability in the soil was limited [40]. In this case, added N increases the carbon-fixing potential of plant hosts, which exacerbates P limitation and consequently prompts them to provide more carbon to their fungal symbionts. Several isotope tracer studies have also provided direct evidence of a 'competitive' strategy among the Gigasporaceae, revealing that these fungi are stronger carbon sinks for plant carbon than other lineages [11,41]. Finally, the Gigasporaceae in temperate ecosystems sporulate later in the growing season than AM fungi from other taxa [42,43], which is consistent with a competitive life history. Taken collectively, these traits indicate that AM fungal communities in low P, or high N-to-P, environments should favor members of the Gigasporaceae family owing to their shared traits related to high carbon acquisition from their host plants.

Plant species that would benefit most from competitive AM fungi are likely to be those with high soil P requirements and high carbon-fixing potential. This is likely to exclude ruderal plants, owing to their short life cycle and lack of nutrient limitation on disturbed, early successional soils. Likewise, stress-tolerant plants would not fully benefit from competitive AM fungi because of their low growth rate and high resource use efficiency. Preferential

associations between competitive AM fungi and competitive host plants are, therefore, likely, particularly under low soil P supply. Besides their matched nutritional benefits, their matched delay in reproduction effort would allow both organisms to invest in vegetative growth so as to derive reciprocal nutritional benefits for an extended period of the growing season. According to functional equilibrium models [44], this matching of functional traits should create a positive feedback favoring dominance and stability of both organisms in their respective communities, and delay ecological succession.

Stress-tolerant AM fungi

AM fungi are stressed, for example, when the carbon supply from their host is consistently low. Under such conditions, successful AM fungi may be those that use carbon most efficiently, through the slow production of high cost, long-lived biomass. Reduced turnover rates should then reduce carbon costs in the long term [22]. To date, hyphal turnover rates in the order of a week have been measured for a few AM fungal strains belonging to the Glomeraceae [45]. Measuring turnover rates across a broader phylogenetic spectrum may reveal that some taxa use plant carbon more efficiently than the Glomeraceae and, thus, correspond to a 'stress-tolerant' strategy. Efficiency in the use of host carbon could also be expressed by the ability of the fungus to complete its life cycle with low biomass production, because this would reduce metabolic maintenance costs. Producing little extraradical biomass

would also reduce exposure to abiotic stress agents such as soil acidity or heavy metals.

There is some evidence that stress-tolerant strategies do exist among AM fungal species. For example, shading experiments have shown reduced root colonization by whole AM fungal assemblages [46], suggesting a competitive advantage for carbon-efficient strains. This is corroborated by data from [47] who reported a shift in AM fungal community structure in response to shading. Likewise, abiotic stress such as high soil acidity has frequently been shown to drive AM fungal community structure [48–50]. Specifically, AM fungi belonging to the Acaulosporaceae family are commonly reported in lower pH environments (e.g., [48,50,51]). Also, high elevation sites with harsher climatic conditions frequently show a higher proportion of species belonging to the Acaulosporaceae family than is commonly seen in grasslands. Moreover, some Acaulosporaceae species are found exclusively in alpine environments [52]. Consistent with the expectation of stress tolerance, members of this family produce less biomass (both extraradical hyphae and internal root structures) than members of the Glomeraceae and Gigasporaceae [14,39].

As with competitive AM fungi, we propose that there are likely to be preferential associations between stress-tolerant fungi and specific plant functional groups. For example, shade-tolerant plants will sparingly invest carbon in AM fungal symbionts because of their low rates of photosynthesis [47]. Indeed, plants growing under any adverse condition that limits carbon fixation are likely to limit the amount of carbon supplied to the AM fungal symbiont. Given that stress-tolerant AM fungi may be slow to provide nutritional and other benefits to their hosts, the initial cost of a fungal symbiont to their host may be high, although these could be offset by their long-term benefits. Thus, the plants that are likely to benefit the most from stress-tolerant AM fungi are those with slow growth rates, long life spans and resource conservation strategies: in other words, stress-tolerant plants. It is important to note that the predicted matching between stress-tolerating plants and AM fungi strictly relates to the life histories of the partners. Although AM fungi can improve plant tolerance to various stresses such as drought or heavy metals [5–7], the potential ability of AM fungi to alleviate host stress is not the basis for our prediction. Instead, we suggest that similarity in resource allocation to various components of the life history (i.e., growth and reproduction) may lead preferential associations between stress-tolerant plants and AM fungi.

Ruderal AM fungi
From a mycocentric perspective, disturbance occurs when hyphal networks are broken, either by physical disruption of the soil structure or by faunal grazing. Disturbance could be an ecological filter selecting for ruderal traits that enable the rapid re-establishment of functional hyphal networks and symbiotic interactions with a plant host. A ruderal life history could be achieved through high growth rates and efficient hyphal fusion mechanisms by which fragmented hyphae can be reconnected to form functional mycelia [38]. Another way for ruderal AM fungi to re-establish a symbiosis following disturbance is by

maximizing *de novo* colonization of roots by propagules. Thus, a short life cycle leading to an early and constitutive investment in asexual spores could be a strategy by which ruderal AM fungi cope with disturbance. Likewise, efficient healing mechanisms that prolong the viability of colonized roots and soil hyphae that have been severed (e.g., [42,53]) would be consistent with an AM ruderal strategy.

Frequently tilled agricultural soils are likely to select for ruderal AM fungal strategies. Studies have shown that these soils tend to have low AM fungal diversity, and are dominated by species belonging to the Glomeraceae, more specifically to the *Glomus* group (Gr.) A clade (e.g., [54–56]). Compared with other AM fungal families, *Glomus* Gr. A species (i) grow faster [57], (ii) fuse hyphae more readily [53], (iii) invest earlier and more abundantly in spore formation [43], and (iv) form cross-walls that enable infected root pieces and severed hyphal fragments to heal and recolonize host roots [42,53]. All of these traits are consistent with a ruderal life history strategy. Also, the ratio of intraradical relative to extraradical hyphal abundance appears to be higher in the Glomeraceae than in other AM fungal families [14], which may comprise a disturbance avoidance strategy.

Ruderal AM fungi with high growth rates and short life cycles should produce low cost, although nonenduring, biomass. The cost of having to replace this short-lived biomass represents, therefore, a disadvantage to long-lived plants. Hence, ruderal plants with a similar short-term investment in low cost biomass should preferentially interact with ruderal AM fungi. Given that ruderal plants colonize early successional habitats where soil nutrients are rarely limiting [26], the primary benefit they derive from AM fungi may not be P uptake, but rather an increased protection against phytopathogens [58]. This is supported by the finding that early successional ruderal plant species may be more prone to pathogen attacks than other plant functional groups (e.g., [59]). Accordingly, *Glomus* Gr. A strains are more efficient at providing protection to plant hosts than other AM fungal lineages [39]. It has been suggested that this protection relies partly on a jasmonate-based plant hormonal pathway that also activates several anti-herbivore mechanisms [60]. Hence, it is possible that ruderal AM fungi are involved in priming plant responses against herbivores as well [61].

Despite our use of the C-S-R framework to organize functional variation in AM fungi, we emphasize that the aim of this opinion article is not to simplistically allocate species or even families to C, S, or R strategy, nor to promote the C-S-R framework as the best way to make sense of functional diversity in the AM fungi. Rather, our aim is to identify the traits that are likely to be the most important components of AM fungal life histories. Likewise, preferential associations between plants and fungi may not follow the idealized cases where C, S, and R plants would interact with C, S, and R AM fungi, respectively. Associations in nature will likely be much more complex because (i) plants and AM fungi involved will rarely be at any of the three extremes of the C-S-R triangle, but most of the time will rather have an intermediate life history and (ii) many factors, other than preferential partner selection,

will influence the assembly of fungal assemblages in plant roots (e.g., plant neighborhood, spatial constraints on fungal species' availability, stochastic events). Still, the C-S-R framework offers a basis from which to develop a trait-based approach for AM fungi and advance our understanding of their life history strategies. In the following section, we identify five research areas where such a better understanding of AM fungal life history strategies would be particularly useful.

Potential advances in AM fungal ecology using a trait-based approach

Preferential association patterns with host communities
Some plants and AM fungi are known to interact preferentially in natural communities (e.g., [62]); however, it is as yet unknown whether those overrepresented interactions in communities are between symbionts that share compatible life history strategies. If so, this would suggest a strong influence of niche-based (i.e., deterministic) processes underlying the assembly of plant–AM fungal communities. Such determinism could arise either from the matching of functional traits that optimize mutual benefits, or from both partners being similarly filtered along environmental gradients. Evidence for such determinism has been found [63] in a previously described plant–AM fungal community [64]: AM fungi from different families interacted preferentially with different plant species. Given the apparent phylogenetic conservatism of AM fungal traits at the family level [57], these results would suggest a strong influence of deterministic (i.e., niche-based) mechanisms driving plant–AM fungal community assembly. Nevertheless, the pattern described in [63] was mainly the result of one plant species that interacted with distinct fungal species compared with the rest of the community. Hence, more field surveys are needed to test this hypothesis. One fruitful avenue would be to couple data on interaction patterns at given sites with a characterization of plant and fungal traits from those sites, to test for correlations between the two.

Succession patterns in AM fungal communities
A major debate in plant ecology over the past century has been the theoretical basis for ecological succession (e.g., [65–68]). Although the C-S-R framework was mainly focused on describing plant history traits in contrasting environments, it implicitly drew linkages between plant traits and autogenic succession, particularly when reconciled with a resource-based theory of competition and succession [69,70]. From these two frameworks, the paradigm of secondary succession that has evolved is one whereby short-lived ruderal plants colonize newly disturbed environments, to be replaced by competitive plants that optimize resource-use over the longer term, which are themselves eventually replaced by stress-tolerant plants once the demand for resources exceeds supply. By extension, a C-S-R approach could provide a trait-based explanation of temporal patterns that have been reported in AM fungal communities. For example, in a microcosm succession experiment, the early stage communities were dominated by *Glomus mosseae* [43], which is often found dominating in agricultural fields (e.g., [54]). Similarly,

later successional AM fungal inocula produced relatively more soil hyphae than early successional ones [71], which is consistent with a switch from ruderal towards competitive life history traits. Finally, late successional fungi tended to form either larger spores or sporocarps [52,72]. More studies that link AM fungal traits and succession would help us to understand the potential interplay between plant and fungal succession and its implications for ecosystem function.

Specificity of responses in plant–AM symbioses
A paradox of AM fungal ecology is that, although the specificity of association between different plant and AM fungal species is low [73], the specificity of the response to such associations is relatively high. Thus, the fitness consequences for both partners are highly dependent on the identity of the species involved (e.g., [74,75]). This is likely to be related to the compatibility of measurable traits in each partner. For example, plants with coarse root systems may be more apt to derive a P benefit, whereas those with ramified root systems may rather derive pathogen protection from their AM fungal symbionts [58,76]. This is only one example of how trait matching may promote mutualistic benefit in the symbiosis, and many possibilities can still be explored [36]. By integrating several functional traits into discrete life history strategies, a C-S-R framework would provide a more predictive approach for studying the specificity of response of various associations. Such predictive power would be valuable for agriculture or horticulture where best matches between various plant and AM fungal genotypes would enhance production.

Linkages between plant and AM fungal diversity
A trait-based approach could also provide insights to link plant and AM fungal diversity at fine spatial scales (i.e., within site β-diversity). It is known that AM fungal community structure is highly heterogeneous at a 1-m scale (e.g., [77]). Given the specificity of the response of plants towards different AM fungal species, such a spatial structure in AM fungal communities may influence plant recruitment [78] and contribute to the fine-grain spatial structure in plant communities. If there is preferential matching between AM fungi and plant hosts with analogous life histories, then it is probable that the spatial distribution of plants and fungi are tightly linked. There is thus an opportunity to test for such linkages in the spatial distribution patterns of plants and AM fungi that share similar life history strategies.

Phylogeny as a proxy for life history traits in AM fungi
We suggested above that life history traits of AM fungi may drive their biogeography and interaction patterns with host plant species [79]. To study the importance of this phenomenon, we must characterize the life history strategies of AM fungal species based on their functional traits. The obvious way to achieve this is by collecting AM fungal strains from a wide range of environments, cultivating these strains in pure cultures, and measuring a standardized set of traits. Given the enormity of this task, and considering that many AM fungal species are difficult to cultivate, it may be preferable to validate an established

Table 1. Examples of comparative studies with AM fungal isolates[a]

Trait measured	AM fungal taxa	Trait value	C-S-R	Explanation	Refs
Healing ability	*Glomus* Gr. A	Efficient healing, rapid regrowth	R	Reestablish functional mycelium after disturbance	[53]
	Gigasporaceae	Efficient healing, moderate regrowth	–		
Growth rate	*Glomus intraradices*	High	R	Replace biomass loss after disturbance	[93]
	Glomus etunicatum	Intermediate	–		
	Gigaspora gigantea	Low	C/S		
Hyphal turnover rate	*Glomus* spp.	High	R[b]	Low resource use efficiency (i.e., high tissue turnover rates)	[45]
Carbon sink strength	*Gigaspora rosea*	Strong	C	Relates to the ability of AM fungi to compete for plant carbon	[41]
	Glomus mosseae	Weak	S/R		
	Glomus intraradices	Weak	S/R		
Hyphal fusion	*Glomus* Gr. A	Frequent	R	Reestablish functional mycelium after disturbance	[53]
	Gigasporaceae	Infrequent	C/S		
Timing to sporulation	Glomeraceae	Early and constitutively	R	Short generation time	[43,94,95]
	Gigasporaceae	Fall in temperate systems	C	Delayed reproduction to favor resource acquisition	
	Acaulosporaceae	Spring in temperate systems	–		
Biomass allocation	Glomeraceae	Low in soil, high in roots	R	Reduced exposure to soil disturbance	[14,39]
	Gigasporaceae	High in soil, low in roots	C	High P acquisition and transfer to host	
	Acaulosporaceae	Low in both soil and roots	S	Low metabolic costs and exposure to soil stressing agents	

[a]We present functional trait values and their associated life history strategy. No C-S-R strategy is assigned to a trait value when it does not constitute an explicit prediction of the C-S-R framework.

[b]Measured turnover rates are thought to be high, but comparisons with other taxa are needed. Ruderals are likely to have the highest turnover rates.

classification scheme that might correlate with AM fungal life histories. As we have alluded to in previous sections, many functional traits of AM fungi appear to be similar among close relatives within broad phylogenetic groupings (examples given in Table 1), particularly at the family level [57]. Such phylogenetic conservatism indicates that phylogeny would be a viable proxy for predicting the life history strategy of AM fungal species and their relative performance in the field. For example, phylogenetic data were recently used to show that environmental filtering and dispersal limitations are important drivers of AM fungal community assembly [56,80]. However, at this stage, AM fungal phylogeny is still undergoing major revisions [81,82]. Moreover, the Glomeraceae family is a very heterogeneous one, with some *Glomus* species found dominating mature stands [64] or late stages of AM fungal succession [43,52]. Furthermore, considerable functional variability has been found among isolates of the same species in the genus *Glomus* [14,83]. We thus acknowledge that an eventual mapping of life histories onto AM fungal phylogeny will yield a portrait much more complex than what is outlined here. Future work should capitalize on the development of high-throughput sequencing to define a reliable phylogeny for AM fungi (e.g., [84]) and, meanwhile, more effort should be placed to characterize life history traits of AM fungi with known phylogenetic affiliation.

Moving forward

The need for a trait-based approach in AM fungal ecology is not a novel idea in the literature [85–87]. In this opinion article, however, we argue that grounding such a trait-based approach into an established life history classification scheme such as the C-S-R framework can provide more

mechanistic insights about the relationship among AM fungal traits, plants traits, and abiotic environment filters. In addition to its potential for summarizing the ecological niche of AM fungi based on functional traits, a C-S-R framework (or other similar frameworks) may help us to predict preferential associations between plant and AM fungal species in the field, as well as the specificity of response to these associations. Moreover, a trait-based functional grouping may improve our understanding of plant–AM fungal successional dynamics as well as biodiversity patterns in natural communities. However, moving our understanding forward will require that progress be made in at least two research areas.

First, it may be tenuous to compare trait values and life history strategies of AM fungal species based on data from disparate studies because trait variation may be biased by differences in experimental design. We need to develop, therefore, a standard trait database for AM fungi with standardized protocols for plant growth conditions, host choice, stages in ontogenic development, and other factors that influence fungal trait states. Second, we need to refine our understanding of the basic biology of AM fungi to link morphology to functions that are targeted by agents of natural selection such as plant hosts, other biota, and the abiotic environment. For example, members of the Gigasporaceae tend to produce thicker walled hyphae than members of other AM fungal families (e.g., [88]), but it remains unknown whether this trait affects hyphal life span, resistance to fungivores, and the efficiency of nutrient translocation to hosts.

In plant science, the trait-based functional grouping is one of the conceptual advances that spurred the rapid expansion of databases that classify plants on the basis

of their traits, the climatic and soil resource conditions under which they grow, and the interactions between plants and other biota [18,89]. Such databases have facilitated comparative studies that correlate plant functions to their evolutionary history and their ecological consequences [90,91], leading to many insights about the mechanisms that govern the distribution and abundance of plants [92]. We suggest that an analogous database for AM fungi offers similar opportunities for understanding the causes of AM fungal distribution and abundance, and may eventually have important ramifications for applied fields such as agriculture and ecological restoration, where a judicious manipulation of the symbiosis could increase crop yields and the stability of introduced plant communities, respectively.

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