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Viewpoint

Progressing beyond colonization strategies to understand arbuscular mycorrhizal fungal life history

Summary

Knowledge of differential life-history strategies in arbuscular mycorrhizal (AM) fungi is relevant for understanding the ecology of this group and its potential role in sustainable agriculture and carbon sequestration. At present, AM fungal life-history theories often focus on differential investment into intra- vs extraradical structures among AM fungal taxa, and its implications for plant benefits. With this Viewpoint we aim to expand these theories by integrating a mycocentric economics- and resource-based life-history framework. As in plants, AM fungal carbon and nutrient demands are stoichiometrically coupled, though uptake of these elements is spatially decoupled. Consequently, investment in morphological structures for carbon vs nutrient uptake is not in competition. We argue that understanding the ecology and evolution of AM fungal life-history trade-offs requires increased focus on variation among structures foraging for the same element, that is within intra- or extraradical structures (in our view a 'horizontal' axis), not just between them ('vertical' axis). Here, we elaborate on this argument and propose a range of plausible life-history trade-offs that could lead to the evolution of strategies in AM fungi, providing testable hypotheses and creating opportunities to explain AM fungal co-existence, and the context-dependent effects of AM fungi on plant growth and soil carbon dynamics.

Background

There is great interest to accurately understand the ecology of arbuscular mycorrhizal (AM) fungi, a monophyletic group of obligate plant symbionts. Such knowledge has implications beyond ecology as many advocate the potential of AM fungi in agriculture (Rillig *et al.*, 2019) and in carbon sequestration (Hawkins *et al.*, 2023). Though AM fungi are associated with the vast majority of land plants across the globe, species diversity is low: c. 300 currently described AM fungal species, with a total diversity estimate of only a few thousand species (Ohsowski *et al.*, 2014). With such relatively low diversity compared to other fungal clades, the task of understanding the variation in life-history strategies

among AM fungal species and using this understanding to develop management strategies appears achievable. Unfortunately, the biotrophic nature of AM fungi presents a practical challenge in crafting an understanding of the fungus itself and heavily biases interpretation of its ecology towards a plant-centric view (Alberton *et al.*, 2005). As a result, we still lack a predictable framework for the impact of AM fungal species composition on plant benefits and soil carbon dynamics. This is despite extensive morphological analyses of the symbiosis since the 80s and 90s (Smith & Read, 2008) and the rise of molecular methods providing insight into AM fungal community composition under different environmental conditions (Ma *et al.*, 2021).

Since the beginning of this century, categories of life-history strategies in AM fungi have emerged (Hart *et al.*, 2001; Chagnon *et al.*, 2013) and have been applied in various contexts (e.g. Ijdo *et al.*, 2010; Weber *et al.*, 2019; Horsch *et al.*, 2023a). The underlying basis for these categories for AM fungi lies in classical life-history theories derived from plant ecology: 'an organism cannot be, at once, a quick and extensive colonizer' (Hart & Reader, 2002a). This rationale goes back to the ideas of Tilman (1994) and others (Pianka, 1970; Stearns, 1989), in which life-history trade-offs necessitate the development of strategies that confer competitive advantage under certain environmental conditions. The main hitherto described strategies in AM fungi were based on traits measured in experimental field and pot studies, most notably the quantity of intra- vs extraradical structures (% root length colonized and extraradical hyphal length; Hart & Reader, 2002a; Maherali & Klironomos, 2007; Maherali & Klironomos, 2012). These studies found a consistent deviation in the ratio of intra-to-extraradical structures among AM fungal families (based on at least 26 isolates, most of which were derived from a single field site), with differences conserved during AM fungal evolutionary history (Powell *et al.*, 2009). A high level of intra-to-extraradical colonization was interpreted as a strategy of ruderal species that specialize in fast colonization of roots to acquire space and carbon, in contrast species with low intra-to-extraradical colonization are considered better competitors for phosphorus uptake as a result of the exploration of soil by extensive extraradical hyphae (Hart & Reader, 2002a; Chagnon *et al.*, 2013). Matching terms were coined by the research community – *rhizophilic* vs *edaphophilic* groups (Weber *et al.*, 2019) – that categorize these groups at the family level and are used to functionally interpret AM fungal community shifts (Phillips *et al.*, 2019; Wang *et al.*, 2023). This trade-off and derived categorizations are appealing because they are 'plant-centric', and can directly be used to infer functions provided to the plant.

We believe it is time to revisit and develop a more mycocentric perspective in life-history theories of AM fungi, that is focusing on carbon and nutrient demands of the fungus itself (Fitter *et al.*, 1998; Alberton *et al.*, 2005). Such revision meets the ongoing discussion

advocating for the use of trait-based approaches in mycorrhizal research (Chaudhary *et al.*, 2022; Antunes *et al.*, 2024) and understanding dynamics of resource acquisition based on stoichiometric principles (Johnson *et al.*, 2015; Riley *et al.*, 2019). We believe that the focus on whether an AM fungus produces more biomass within roots than in soil (or vice versa) is likely limiting our understanding of what has driven life-history evolution. Intra- and extraradical structures represent two separate structural components of the fungus that forage for the uptake of different resources/elements, that is carbon vs nutrients that are both essential for the fungus. Our central argument is that a true life-history (or economics) trade-off can only be found by comparing morphological structures competing for the same resource (e.g. in plants by comparing leaves of different species that show a gradient to maximize carbon fixation efficiency over the short- or long-term). With this Viewpoint we reconsider how to investigate AM fungal life-history strategies, shifting the focus from the plant-centric view of whether investment is occurring within or outside of roots towards an economics- and resource-based framework following the most parsimonious stoichiometric principles.

Using AM fungal physiology to define life-history strategies

Obligate biotrophic AM fungi can only forage for the carbon provided by roots (hexoses and lipids (Wang *et al.*, 2017)), for which they need to provide proportional amounts of nutrients in return (Bever *et al.*, 2009; Kiers *et al.*, 2011). At the same time, the construction of new fungal biomass relies on parallel carbon and nutrient investments. Importantly though, nutrients and carbon are not accessed by the same parts of the mycelium, instead the uptake of carbon and nutrients is spatially and structurally decoupled in AM fungi. This spatial segregation of necessary resources is in contrast to other fungal guilds, including saprobes and pathogens, but is in fact similar to plants (Fig. 1). Aboveground parts (leaves) forage for carbon, whereas nutrients are acquired by roots. Sterner & Elser (2002) concluded that, despite carbon:nutrient ratios being fixed to a certain degree, this spatial decoupling of resource acquisition is a special stoichiometric characteristic in plants, and we argue the same is true for AM fungi. A further similarity is given by the comparatively simple resource types used by plants and AM fungi – one or two carbon forms and nutrients mainly in inorganic form – compared to the large resource diversity available to other heterotrophic organisms.

Given the analogy of structural and spatial decoupling in resource acquisition with plants, we propose that there is value in similarly differentiating investment by AM fungi along ‘horizontal’ and ‘vertical’ axes (Fig. 1). Plant life-history strategies are primarily based on a ‘horizontal’ axis (leaf and root economics spectra (Wright *et al.*, 2004); fast–slow continuum (Reich, 2014; Salguero-Gómez *et al.*, 2016)). ‘Horizontal’ here refers to trade-offs occurring for structures produced within, not between the above- or belowground environment, respectively. By contrast, variation among and within plant species along the ‘vertical’ axis (root-to-shoot ratios) do not reflect life-history strategies, but relate to shifts in relative resource availability, niche differentiation or other

functional parameters (e.g. water limitation, anchorage, flower investment; Fig. 1). Horizontal axes are better targets to infer life-history evolution of structures that differently achieve the aim of acquiring resources from the same environment.

For AM fungi, the ‘vertical’ axis is an explicitly plant-centric axis, that is differential investment to intra- vs extraradical structures. Variation along this axis is postulated to be associated with a proportionally higher uptake and transfer of nutrients to plants in AM fungal taxa with more extensive extraradical mycelium (Chagnon *et al.*, 2013; Weber *et al.*, 2019). Assuming fungi have relatively fixed stoichiometric carbon: nutrient demands for their own physiological growth (similar to other biota, Sterner & Elser, 2002; although we have these data for very few AM fungi), a proportionally extensive extraradical mycelium along the vertical axis would acquire nutrients in excess of fungal growth demands, which may lead to nutrient efflux to the plant – increased nutrient: carbon exchange ratios. Some evidence suggests high-plant phosphorus uptake rates by extraradical mycelia with high-hyphal densities (Munkvold *et al.*, 2004 (only including *Glomus* isolates); Maherali & Klironomos, 2007). However, further studies did not support the existence of species-specific nutrient: carbon exchange ratios among families associated with high or low intra-to-extraradical structures (Kiers *et al.*, 2011; Walder & van der Heijden, 2015; Yang *et al.*, 2017; Zhou *et al.*, 2021), neither for increased plant benefits from ‘edaphophilic taxa’, i.e., taxa from AM fungal families purported to produce relatively high-extraradical mycelium (Thonar *et al.*, 2011; Säle *et al.*, 2021; Qin *et al.*, 2022). These latter studies observed patterns where edaphophilic taxa produced lower plant benefits; hyphal production was not assessed in two of the studies (Säle *et al.*, 2021; Qin *et al.*, 2022), but in the third (Thonar *et al.*, 2011) the high density of hyphae in the edaphophilic taxon (*Gigaspora margarita*) was clustered near the root and performed poorly in the uptake and transfer of phosphorus.

Carbon: nutrient exchange dynamics in the AM fungal symbiosis appear to follow simple mechanisms: a higher fungal provision of nutrients (primarily evaluated with phosphorus) to the plant leads proportional carbon return (Bever *et al.*, 2009; Hammer *et al.*, 2011; Kiers *et al.*, 2011; van’t Padje *et al.*, 2021). Moreover, evidence also supports that this ratio of nutrient-to-carbon does not correlate with differences in colonization patterns (i.e. while some variation in this ratio has been reported, it is not explained by differences between taxa of families characterized in high or low extraradical investment (e.g. Pearson & Jakobsen, 1993; Kiers *et al.*, 2011)). Molecular processes at the cellular interface of arbuscules also support simple carbon: nutrient reciprocal exchange mechanisms (Floss *et al.*, 2017; Wang *et al.*, 2017). Thus, a view towards the ‘horizontal’ axis (i.e. morphological or functional trade-offs within intra- or extraradical structures (Fig. 1)) broadens our understanding of AM fungal life-history strategies by focusing on how fungi differ (trade-off) in terms of their abilities to efficiently mobilize, take up and transport nutrients towards or across the fungal-root interface regardless of colonization strategy. Perhaps the simplicity of this mechanism (implying reduced possibilities of niche differentiation along this specific horizontal axis) is also supported by the low level of

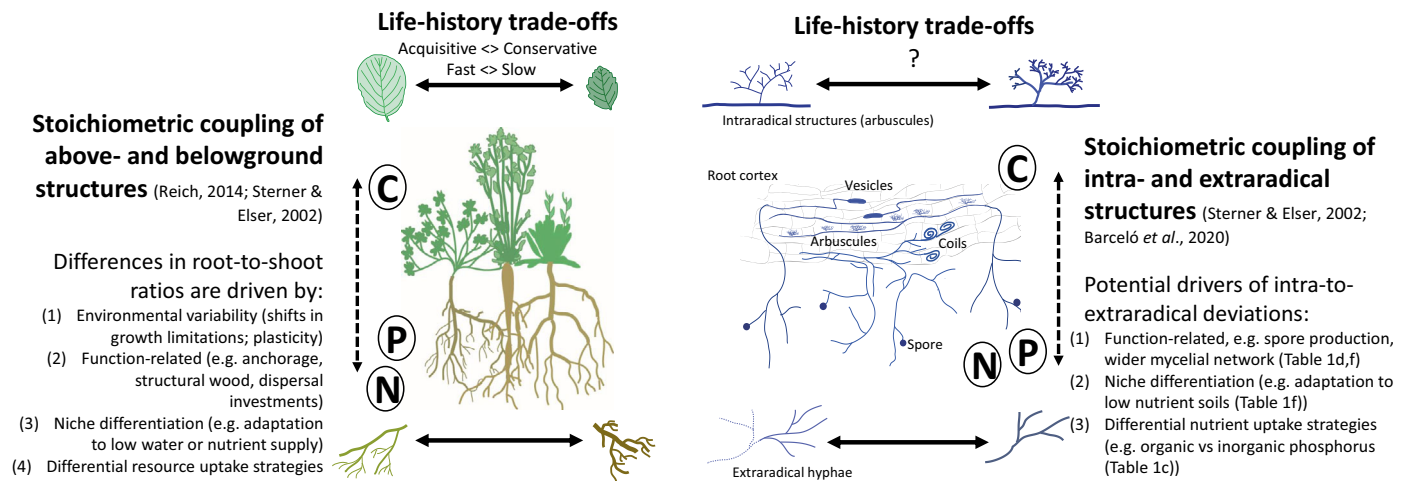


Fig. 1 Similarity in stoichiometric patterns in plant and AM fungi and its implication for life-history trade-offs. Solid arrows refer to 'horizontal' life-history trade-offs as discussed in plants separately for above- and belowground structures, conceptually transferred to AM fungi ('?' indicates that life-history trade-offs in AM fungi are currently unresolved). Dashed arrows indicate the 'vertical' stoichiometric coupling of above- to belowground structures, or intra- and extraradical structures, respectively. Element uptake in the respective compartments is indicated by circles (C, carbon; N, nitrogen; P, phosphorus). Morphological characteristics of intra- and extraradical AM fungal structures defining life-history strategies were drawn following ideas of an economics spectrum, that is fast growth/rapid return vs high investment/slow return as described in Table 1a,b (though other trade-offs are possible and need to be tested; see Table 1). Plant and AM fungal communities illustrated in the centre reflect the coupling of structures in these groups, not the economics spectrum; plant drawings were adapted based on Kutschera & Lichtenegger (2002) (Barceló *et al.*, 2020).

diversification, both in terms of species numbers and host specificity in this ancient symbiosis (Perez-Lamarque *et al.*, 2022). It must be noted that such simple mechanisms may shift within complex common mycorrhizal networks, where a fungus is engaged in symbioses with more than one plant of the same or different species (Walder *et al.*, 2012). The capacity to acquire carbon from multiple hosts is dependent on characteristics of the extraradical mycelium (e.g. the distance from the root that the fungus explores, Thonar *et al.*, 2011) and a trade-off could arise that drives different strategies of resource acquisition (see Table 1).

An additional horizontal axis enables us to develop new life-history theories that may be elaborated in future studies. Here, we start with the most parsimonious assumptions that (1) carbon and nutrient exchange between AM fungi and plants is stoichiometrically coupled, (2) the fungus is not performing a function for the plant but maximizes its own resource use efficiency and (3) the two-compartmental nature – similar to plants – results in stoichiometric coupling of extra- and intraradical structures (rather than these structures representing a trade-off in investment). These simple principles allow for a wide range of possible life-history trade-offs to occur in AM fungi (Table 1). Proposed functional trade-offs are supported and inspired by existing studies on AM fungal morphology and physiology (though studies rarely address functional traits as part of life-history trade-offs, these would need to be tested; Table 1). Important examples include the observation of a potential trade-off between root colonization rates and the longevity of intraradical structures (Table 1a; de Souza *et al.*, 2005), variation in extraradical hyphal extension rates to form common mycorrhizal networks (Table 1f; Schütz *et al.*, 2022), or a trade-off in hyphal space exploration for orthophosphate uptake vs mobilization of organic phosphorus via activation of the associated microbiome (Table 1c; Zhou *et al.*, 2023).

AM fungal life-history strategies in an ecological context

Some of the strategies that could arise from hypothesized trade-offs along the horizontal axis may reveal niche adaptations (Table 1). For example, a species relying on carbon exudation/microbial activity or higher phosphorus enzyme capacities may have growth advantages in organic substrate (Leigh *et al.*, 2009), while species adapted to the uptake of elements other than phosphorus may become dominant under phosphorus-rich conditions (Treseder *et al.*, 2018). Similar to the analogue in plant roots, further differentiation into specialists adapted to aridity, infertility, grazing pressure, varying soil pH or temperatures are likely (Emery *et al.*, 2022). Such niche-related strategies may also provide an explanation for the high context-dependencies in plant mycorrhizal growth responses to AM fungal inoculation under varying environmental conditions (Lutz *et al.*, 2023; Wang *et al.*, 2023).

The primary AM fungal life-history trade-off is presumably a combination of the strategies presented. Inferring again from plant ecology, it is possible that AM fungal species vary in their traits along a major economics spectrum from conservative (slow return of resource investment, late successional) to acquisitive (fast return of resource investment, early successional) taxa (Wright *et al.*, 2004). There is some evidence suggesting species level differentiation into early colonizing, fast growing species compared to later colonizing, slow growing species with higher longevity and more structural investment (de Souza *et al.*, 2005). Such small-scale successional niche differentiation is likely since root carbon is not a uniform resource; roots have varying degrees of activity, leading to differing exchange rates of carbon: nutrient with AM fungal partners (rates = the pace and quantity of elements exchanged under fixed stoichiometric exchange ratios). Variation in activity

Table 1 A selection of proposed life-history trade-offs and possible strategies in AM fungi based on simple stoichiometric principles in which carbon and nutrient exchange between AM fungi and plants is stoichiometrically fixed, including respective support from the literature and derived ecological hypotheses; trade-offs (individual double-headed arrows) are proposed to occur independently for intra- or extraradical structures although correlations among these strategies are likely (Weigelt *et al.*, 2021).

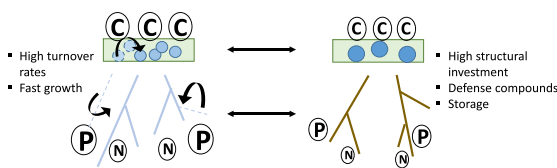
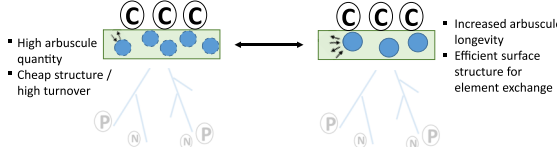
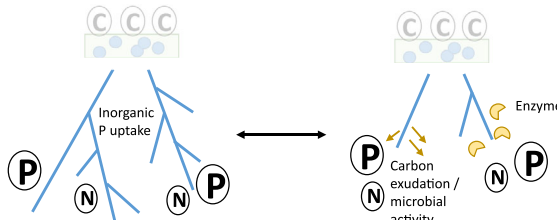
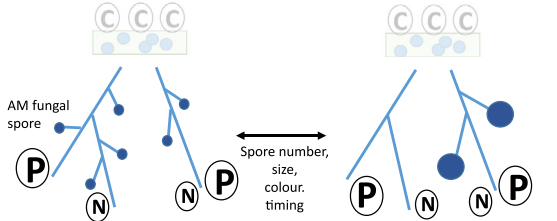
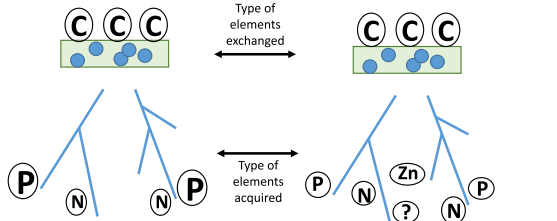
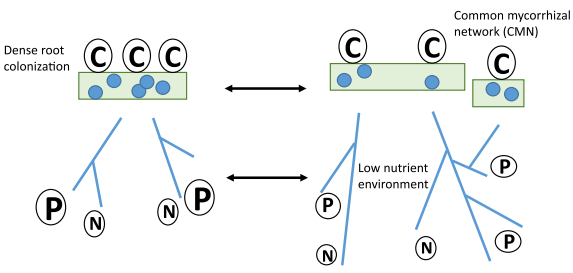






Proposed AM fungal strategies/trade-offs ^{1,2}	Literature support ³	Ecological hypotheses
<p>(a) Short-lived to long-lived hyphal structures</p>  <ul style="list-style-type: none"> High turnover rates Fast growth High structural investment Defense compounds Storage 	<p>Persistence of arbuscules varies among AM fungal lineages (de Souza <i>et al.</i>, 2005)</p> <p>Variation in hyphal thickness among AM fungi (Abbott, 1982; Lopez-Aguillon & Mosse, 1987)</p> <p>Differential ability for hyphal healing/anastomosis between Glomeraceae and Gigasporaceae taxa (De La Providencia <i>et al.</i>, 2005)</p> <p>Hyphal cytoplasm can be recycled within AM structures resulting in efficient mycelial turnover (Hammer <i>et al.</i>, 2024)</p>	<p>Trade-off in a successional context: early/fast vs late/longer-lasting colonization of roots</p> <p>Differential disturbance tolerance/longevity among AM fungal species (affecting responses to fauna grazing, tillage, radiation, heat)</p> <p>Nutrient and carbon exchange rates (not ratio, but quantity of elements exchanged) and plant benefits may vary depending on conditions</p>
<p>(b) Differences in element exchange efficiency</p>  <ul style="list-style-type: none"> High arbuscule quantity Cheap structure / high turnover Increased arbuscule longevity Efficient surface structure for element exchange 	<p>Differential structure of arbuscules in AM fungal taxa (surface-to-volume ratios (Dodd <i>et al.</i>, 2000))</p> <p>Longer persistence of arbuscules in Gigasporaceae (de Souza <i>et al.</i>, 2005)</p>	<p>Competitiveness for root space: early/fast arrival vs longer persistence</p> <p>Element exchange rates per arbuscule may vary, also over time; with potential effects on short- vs long-term plant benefits</p>
<p>(c) Contrasting nutrient (phosphorus) uptake strategies</p>  <ul style="list-style-type: none"> Inorganic P uptake Enzymes Carbon exudation / microbial activity 	<p>Trade-off in hyphal exploration vs stimulation of microbial activity (three strains; Zhou <i>et al.</i>, 2023)</p> <p>Variable phosphatase capacities among taxa (likely cell-wall bound or cytoplasmic location; Joner & Johansen, 2000; Olsson <i>et al.</i>, 2002)</p> <p>AM hyphae may stimulate microbial activity via carbon exudation (Hodge, 2014; Zhang <i>et al.</i>, 2022)</p>	<p>The investment of resources to extraradical enzyme activity or exudates varies among AM fungal species</p> <p>AM fungal species adapt differently to soils varying in organic vs inorganic nutrient supply</p>
<p>(d) Trade-offs in sporulation strategies</p>  <ul style="list-style-type: none"> AM fungal spore Spore number, size, colour, timing 	<p>Primary trade-offs in AM fungal spore production between spore size and numbers (Aguilar-Trigueros <i>et al.</i>, 2019)</p> <p>AM fungal species show different investment to sporulation (Ijdo <i>et al.</i>, 2010)</p> <p>Spore colour/structural investment varies among taxa (Zanne <i>et al.</i>, 2020)</p>	<p>Relevant trade-off in a successional context: early/rapid colonization of new habitats vs investment to survival/longevity</p> <p>Variability in strategies of the presymbiotic life stage of AM fungi (e.g. distance to host plants), dependent on spore resource supply</p>
<p>(e) Specialization to different elements transferred to plants</p>  <ul style="list-style-type: none"> Type of elements exchanged Type of elements acquired 	<p>Zinc (Zn) and N transporters are present in arbuscules (Wang <i>et al.</i>, 2017)</p> <p>Other elements than phosphorus are enriched in AM plants (Horsch <i>et al.</i>, 2023b)</p>	<p>AM fungal species may specialize in phosphorus uptake (traded for plant carbon), but also in other element uptake/exchange strategies</p> <p>Expected niche adaptation of certain AM fungal species to soils characterized by high-phosphorus supply (but nitrogen or other nutrient limitations)</p>

Table 1 (Continued)

Proposed AM fungal strategies/trade-offs ^{1,2}	Literature support ³	Ecological hypotheses
<p>(f) Adaptation to low-resource environments</p> 	<p>Variable hyphal extension rates to establish common mycorrhizal networks (Schütz <i>et al.</i>, 2022)</p> <p>Niche differentiation in AM fungal species along fertility (Camenzind <i>et al.</i>, 2014; Han <i>et al.</i>, 2020)</p> <p>Density of AM fungal colonization of roots and soil varies (Hart & Reader, 2002b; Maherali & Klironomos, 2012)</p>	<p>Niche adaptation to low-nutrient environments will favour species with high-extraradical investment</p> <p>A trade-off may exist in receiving carbon from few root pieces (short extraradical network, low connectivity) vs several roots/plants (wide extraradical mycelial growth/common mycorrhizal network)</p> <p>High-network connectivity demands investment to growth and long-lived hyphae, but provides stable carbon supply</p>

¹  , plant root;  , intraradical AM exchange structure (arbuscules and coils);  , extraradical AM fungal hypha;  , carbon taken up from the plant;   , different nutrients taken up and transferred to the plant.

² Some proposed strategies are relevant to both intra- and extraradical structures; in cases where only one type of structure is relevant, the other type of structure is faded.

³ Literature support includes references suggesting variation in proposed functional traits among AM fungal taxa, as well as physiological mechanisms that may support the existence of these functions.

exists within root systems, during plant development and also among different plant species (McCormack *et al.*, 2015; Weigelt *et al.*, 2021). In turn, this also affects the extent of rhizosphere nutrient depletion zones and nutrient supply for the fungus itself. Following principles of an economics spectrum, we hypothesize that AM fungal species are either specialized to rapid colonization of highly active root zones, or slow growing but competitive in less active parts of the root (Yang *et al.*, 2017). This type of specialization would result in trade-offs among growth rates, hyphal turnover, longevity, storage, structural complexity or sporulation syndromes (Díaz *et al.*, 2016; Salguero-Gómez *et al.*, 2016). Strong successional turnover of AM fungal communities and differential adaptations to varying carbon supply support these ideas (Knecht *et al.*, 2016; Gao *et al.*, 2019). The degeneration of arbuscules under unstable phosphorus supply, initiated by the plant, may further contribute to rapid growth and turnover of fast growing species with short-lived mycelia (Floss *et al.*, 2017; Kobae, 2019).

From a plant perspective, AM fungi with high-exchange rates may be more favourable under optimal conditions, that is more 'cooperative' (Kiers *et al.*, 2011). On the other hand, slow growing plant species or plants exposed to stressful environmental conditions may profit from more stable (long-term) interactions. This complements the current debate about whether acquisitive leaf traits correspond with acquisitive root traits (fast resource acquisition and growth, short lifespans; Weigelt *et al.*, 2021; Bueno *et al.*, 2023). The same question may be asked for root associated AM fungi, as well as for intra- vs extraradical structures (Reich, 2014). Within diverse plant communities, it will be crucial to understand life-history strategies in the context of dynamic plant-AM fungal interactions. The identity of AM fungal taxa influences the balance of carbon: nutrient exchange with different plant individuals and species linked to common mycorrhizal networks (Walder *et al.*, 2012; Awaydul *et al.*, 2019; Qiao

et al., 2020). Despite a lack of host specificity in AM fungi, strategies suggested in Table 1 may explain differential interactions between AM fungal and plant species in a community context, where niche differentiation at dynamic temporal and spatial scales is essential for co-existence (van't Padje *et al.*, 2021).

Future research directions

We believe our proposed framework would offer new insights to resolve four key questions in AM fungal ecology: (1) Why do so many AM fungi co-exist in space, whether in a plot, a single root system or a small volume of soil? Is there an underlying life-history trade-off(s) that promotes co-existence at this scale? (2) Do AM fungi show habitat specialization across environmental gradients and sensitivity to global change? If so, is this due to a fundamental trade-off? (3) How do these trade-offs modify mycorrhizal benefits along resource availability gradients and in response to environmental change, and how can we use this knowledge to manage AM outcomes in an agricultural context? (4) Why has net diversification been so low in this clade compared to other fungi? These questions have not been and will not be answered with our current focus along the 'vertical' axis. To address these we need better data from comparative analyses on hyphal growth rates, hyphal structural investment (e.g. melanin), turnover rates of hyphae and arbuscules, the number of root entry points, arbuscule efficiency (e.g. arbuscule surface area to volume as proposed by Dodd *et al.* (2000)) and investment to foraging structures (Olsson *et al.*, 2014). Spore traits are also essential as spores are resource-demanding structures and, as such, are highly relevant for life history trade-offs (Aguilar-Trigueros *et al.*, 2019). Certainly, it is similarly important to analyse differential nutrient: carbon transfer among AM fungal species and its molecular mechanisms (e.g. the role of 'cheaters'), and how these are affected by physiological mechanisms associated with internal storage or nutrient recycling that reduce the coupling

of carbon: nutrient contents in hyphae (Camenzind *et al.*, 2021; Zhang *et al.*, 2023). We acknowledge the importance to implement such 'plant-centric' functions, like plant nutrient uptake or pathogen protection (Maherali & Klironomos, 2007), into primary life-history strategies of AM fungi combining plant and fungal mycorrhizal traits as proposed by Chaudhary *et al.* (2022).

To conclude, we propose to move beyond the 'vertical' axis of intra-to-extraradical fungal investment to define life-history strategies in AM fungi. We believe a shift towards 'horizontal' comparisons of alike structures across AM taxa provides more promise to understand the ecology and evolution of AM fungi and their relevance to plant fitness and biogeochemical dynamics in soils. We hope that the approach that we have proposed provides a new focus for mechanistic, hypothesis-driven research on this important fungal group.

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Competing interests

None declared.

Author contributions

TC, CAA-T, MKH, SM-M, MCR, WKC and JRP developed the conceptual ideas presented. TC led the writing and literature search. All authors contributed to writing and revising the text.

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