

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 in accurately understanding 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 1980s and 1990s (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’, that is, 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

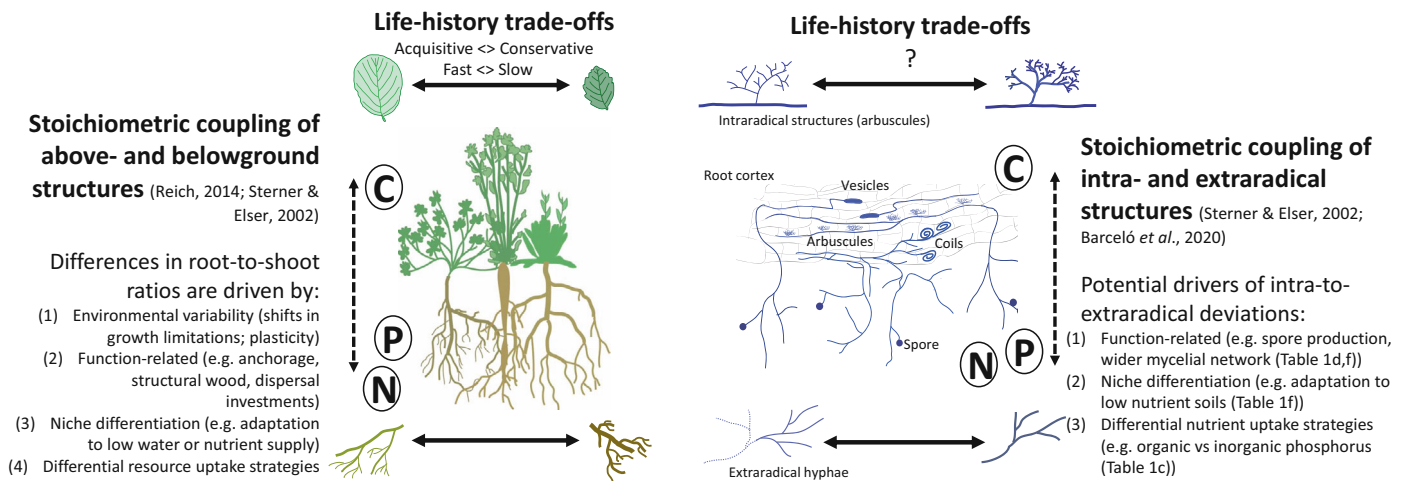


Fig. 1 Similarity in stoichiometric patterns in plant and arbuscular mycorrhizal (AM) fungi and its implication for life-history trade-offs. Solid arrows refer to 'horizontal' life-history trade-offs as discussed in plants separately for above- and belowground structures, conceptually transferred to 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).

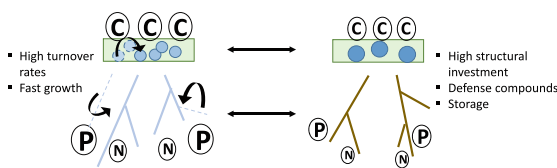
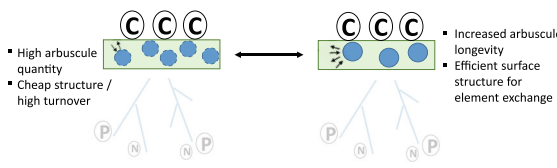
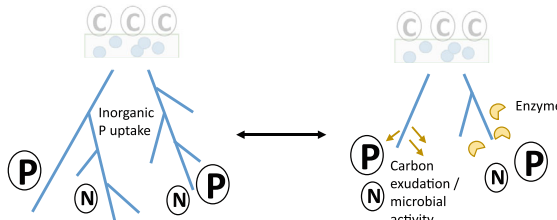
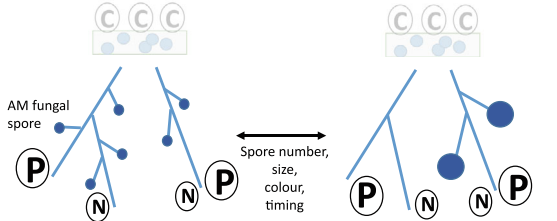
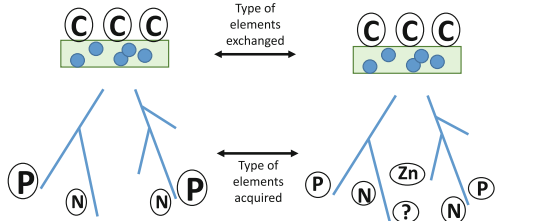
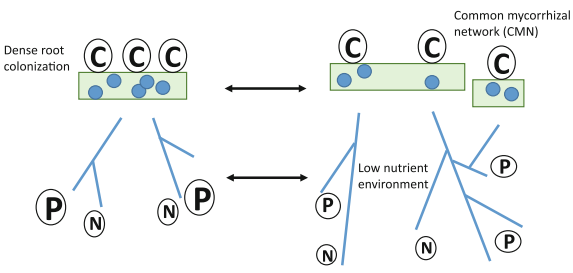
| Proposed AM fungal strategies/trade-offs ^{1,2} | Literature support ³ | Ecological hypotheses |
|---|---|--|
| <p>(a) Short-lived to long-lived hyphal structures</p>  <ul style="list-style-type: none"> High turnover rates Fast growth High structural investment Defense compounds Storage | <p>Persistence 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 Carbon exudation / microbial activity Enzymes | <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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References

- Abbott L. 1982. Comparative anatomy of vesicular–arbuscular mycorrhizas formed on subterranean clover. *Australian Journal of Botany* 30: 485–499.
- Aguilar-Trigueros CA, Hempel S, Powell JR, Cornwell WK, Rillig MC. 2019. Bridging reproductive and microbial ecology: a case study in arbuscular mycorrhizal fungi. *The ISME Journal* 13: 873–884.
- Alberton O, Kuyper TW, Gorissen A. 2005. Taking mycoecentrism seriously: mycorrhizal fungal and plant responses to elevated CO₂. *New Phytologist* 167: 859–868.
- Antunes P, Stürmer S, Bever J, Chagnon P-L, Chaudhary V, Deveautour C, Fahey C, Kokkoris V, Lekberg Y, Powell J *et al.* 2024. Establishing a standardized approach for elucidating glomeromycota life-history traits: advancing consistency in mycorrhizal fungi research. *Authorea* doi: [10.22541/au.171395536.68313579/v1](https://doi.org/10.22541/au.171395536.68313579/v1).
- Awaydul A, Zhu W, Yuan Y, Xiao J, Hu H, Chen X, Koide RT, Cheng L. 2019. Common mycorrhizal networks influence the distribution of mineral nutrients between an invasive plant, *Solidago canadensis*, and a native plant, *Kummerowia striata*. *Mycorrhiza* 29: 29–38.
- Barceló M, van Bodegom PM, Tedersoo L, den Haan N, Veen GF, Ostonen I, Trimbos K, Soudzilovskaia NA. 2020. The abundance of arbuscular mycorrhiza in soils is linked to the total length of roots colonized at ecosystem level. *PLoS ONE* 15: e0237256.
- Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* 12: 13–21.
- Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R, Carmona CP. 2023. Reply to: the importance of trait selection in ecology. *Nature* 618: E31–E34.
- Camenzind T, Hempel S, Homeier J, Horn S, Velescu A, Wilcke W, Rillig MC. 2014. Nitrogen and phosphorus additions impact arbuscular mycorrhizal abundance and molecular diversity in a tropical montane forest. *Global Change Biology* 20: 3646–3659.
- Camenzind T, Philipp Grenz K, Lehmann J, Rillig MC. 2021. Soil fungal mycelia have unexpectedly flexible stoichiometric C:N and C:P ratios. *Ecology Letters* 24: 208–218.

- Chagnon P-L, Bradley RL, Maherali H, Klironomos JN. 2013. A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science* 18: 484–491.
- Chaudhary VB, Holland EP, Charman-Anderson S, Guzman A, Bell-Dereske L, Cheeke TE, Corrales A, Duchicela J, Egan C, Gupta MM *et al.* 2022. What are mycorrhizal traits? *Trends in Ecology & Evolution* 37: 573–581.
- De La Providencia IE, De Souza FA, Fernández F, Delmas NS, Declerck S. 2005. Arbuscular mycorrhizal fungi reveal distinct patterns of anastomosis formation and hyphal healing mechanisms between different phylogenetic groups. *New Phytologist* 165: 261–271.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I *et al.* 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.
- Dodd JC, Boddington CL, Rodriguez A, Gonzalez-Chavez C, Mansur I. 2000. Mycelium of arbuscular mycorrhizal fungi (AMF) from different genera: form, function and detection. *Plant and Soil* 226: 131–151.
- Emery SM, Bell-Dereske L, Stahlheber KA, Gross KL. 2022. Arbuscular mycorrhizal fungal community responses to drought and nitrogen fertilization in switchgrass stands. *Applied Soil Ecology* 169: 104218.
- Fitter AH, Graves JD, Watkins NK, Robinson D, Scrimgeour C. 1998. Carbon transfer between plants and its control in networks of arbuscular mycorrhizas. *Functional Ecology* 12: 406–412.
- Floss DS, Gomez SK, Park H-J, MacLean AM, Müller LM, Bhattarai KK, Lévesque-Tremblay V, Maldonado-Mendoza IE, Harrison MJ. 2017. A transcriptional program for arbuscule degeneration during am symbiosis is regulated by MYB1. *Current Biology* 27: 1206–1212.
- Gao C, Montoya L, Xu L, Madera M, Hollingsworth J, Purdom E, Hutmacher RB, Dahlberg JA, Coleman-Derr D, Lemaux PG *et al.* 2019. Strong succession in arbuscular mycorrhizal fungal communities. *The ISME Journal* 13: 214–226.
- Hammer EC, Arellano-Caicedo C, Mafla-Endara PM, Kiers ET, Shimizu T, Ohlsson P, Aleklett K. 2024. Hyphal exploration strategies and habitat modification of an arbuscular mycorrhizal fungus in microengineered soil chips. *Fungal Ecology* 67: 101302.
- Hammer EC, Pallon J, Wallander H, Olsson PA. 2011. Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability. *FEMS Microbiology Ecology* 76: 236–244.
- Han Y, Feng J, Han M, Zhu B. 2020. Responses of arbuscular mycorrhizal fungi to nitrogen addition: a meta-analysis. *Global Change Biology* 26: 7229–7241.
- Hart M, Reader R. 2002a. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist* 153: 335–344.
- Hart MM, Reader RJ. 2002b. Does percent root length colonization and soil hyphal length reflect the extent of colonization for all AMF? *Mycorrhiza* 12: 297–301.
- Hart MM, Reader RJ, Klironomos JN. 2001. Life-history strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics. *Mycologia* 93: 1186–1194.
- Hawkins HJ, Cargill RIM, Van Nuland ME, Hagen SC, Field KJ, Sheldrake M, Soudzilovskaia NA, Kiers ET. 2023. Mycorrhizal mycelium as a global carbon pool. *Current Biology* 33: R560–R573.
- Hodge A. 2014. Chapter two - Interactions between arbuscular mycorrhizal fungi and organic material substrates. In: Sariaslani S, Gadd GM, eds. *Advances in applied microbiology*. Amsterdam, the Netherlands: Elsevier, 47–99.
- Horsch CCA, Antunes PM, Fahey C, Grandy AS, Kallenbach CM. 2023a. Trait-based assembly of arbuscular mycorrhizal fungal communities determines soil carbon formation and retention. *New Phytologist* 239: 311–324.
- Horsch CCA, Antunes PM, Kallenbach CM. 2023b. Arbuscular mycorrhizal fungal communities with contrasting life-history traits influence host nutrient acquisition. *Mycorrhiza* 33: 1–14.
- Ijdo M, Schtickzelle N, Cranenbrouck S, Declerck S. 2010. Do arbuscular mycorrhizal fungi with contrasting life-history strategies differ in their responses to repeated defoliation? *FEMS Microbiology Ecology* 72: 114–122.
- Johnson NC, Wilson GWT, Wilson JA, Miller RM, Bowker MA. 2015. Mycorrhizal phenotypes and the Law of the Minimum. *New Phytologist* 205: 1473–1484.
- Joner EJ, Johansen A. 2000. Phosphatase activity of external hyphae of two arbuscular mycorrhizal fungi. *Mycological Research* 104: 81–86.
- Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A *et al.* 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333: 880–882.
- Knegt B, Jansa J, Franken O, Engelmoer DJP, Werner GDA, Bücking H, Kiers ET. 2016. Host plant quality mediates competition between arbuscular mycorrhizal fungi. *Fungal Ecology* 20: 233–240.
- Kobae Y. 2019. Live imaging of arbuscular mycorrhizal symbiosis. In: Reinhardt D, Sharma AK, eds. *Methods in rhizosphere biology research*. Singapore: Springer Singapore, 241–253.
- Kutschera L, Lichtenegger E. 2002. *Wurzelatlas mitteleuropäischer Waldbäume und Sträucher*. Graz, Austria: Stocker-Verlag.
- Leigh J, Hodge A, Fitter AH. 2009. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. *New Phytologist* 181: 199–207.
- Lopez-Aguillon R, Mosse B. 1987. Experiments on competitiveness of three endomycorrhizal fungi. *Plant and Soil* 97: 155–170.
- Lutz S, Bodenhausen N, Hess J, Valzano-Held A, Waelchli J, Deslandes-Hérolde G, Schlaeppli K, van der Heijden MGA. 2023. Soil microbiome indicators can predict crop growth response to large-scale inoculation with arbuscular mycorrhizal fungi. *Nature Microbiology* 8: 2277–2289.
- Ma X, Geng Q, Zhang H, Bian C, Chen HYH, Jiang D, Xu X. 2021. Global negative effects of nutrient enrichment on arbuscular mycorrhizal fungi, plant diversity and ecosystem multifunctionality. *New Phytologist* 229: 2957–2969.
- Maherali H, Klironomos JN. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316: 1746–1748.
- Maherali H, Klironomos JN. 2012. Phylogenetic and trait-based assembly of arbuscular mycorrhizal fungal communities. *PLoS ONE* 7: 0036695.
- McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari H-S, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.
- Munkvold L, Kjoller R, Vestberg M, Rosendahl S, Jakobsen I. 2004. High functional diversity within species of arbuscular mycorrhizal fungi. *New Phytologist* 164: 357–364.
- Ohsowski BM, Zaitsoff PD, Öpik M, Hart MM. 2014. Where the wild things are: looking for uncultured Glomeromycota. *New Phytologist* 204: 171–179.
- Olsson O, Olsson PA, Hammer EC. 2014. Phosphorus and carbon availability regulate structural composition and complexity of AM fungal mycelium. *Mycorrhiza* 24: 443–451.
- Olsson PA, van Aarle IM, Allaway WG, Ashford AE, Rouhier H. 2002. Phosphorus effects on metabolic processes in monoxenic arbuscular mycorrhiza cultures. *Plant Physiology* 130: 1162–1171.
- Pearson JN, Jakobsen I. 1993. Symbiotic exchange of carbon and phosphorus between cucumber and three arbuscular mycorrhizal fungi. *New Phytologist* 124: 481–488.
- Perez-Lamarque B, Öpik M, Maliet O, Afonso Silva AC, Selosse M-A, Martos F, Morlon H. 2022. Analysing diversification dynamics using barcoding data: the case of an obligate mycorrhizal symbiont. *Molecular Ecology* 31: 3496–3512.
- Phillips ML, Weber SE, Andrews LV, Aronson EL, Allen MF, Allen EB. 2019. Fungal community assembly in soils and roots under plant invasion and nitrogen deposition. *Fungal Ecology* 40: 107–117.
- Pianka ER. 1970. On r- and K-selection. *The American Naturalist* 104: 592–597.
- Powell JR, Parrent JL, Hart MM, Klironomos JN, Rillig MC, Maherali H. 2009. Phylogenetic trait conservatism and the evolution of functional trade-offs in arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B: Biological Sciences* 276: 4237–4245.
- Qiao X, Guo X, Li A. 2020. Common mycorrhizal networks contribute to overyielding in faba bean/coix intercropping systems. *Agronomy Journal* 112: 2598–2607.
- Qin M, Li L, Miranda JP, Tang Y, Song B, Oosthuizen MK, Wei W. 2022. Experimental duration determines the effect of arbuscular mycorrhizal fungi on plant biomass in pot experiments: a meta-analysis. *Frontiers in Plant Science* 13: 1024874.
- Reich PB. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

- Riley RC, Cavagnaro TR, Brien C, Smith FA, Smith SE, Berger B, Garnett T, Stonor R, Schilling RK, Chen Z-H *et al.* 2019. Resource allocation to growth or luxury consumption drives mycorrhizal responses. *Ecology Letters* 22: 1757–1766.
- Rillig MC, Aguilar-Trigueros CA, Camenzind T, Cavagnaro TR, Degrune F, Hohmann P, Lammel DR, Mansour I, Roy J, van der Heijden MGA *et al.* 2019. Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist* 222: 1171–1175.
- Säle V, Palenzuela J, Azcón-Aguilar C, Sánchez-Castro I, da Silva GA, Seitz B, Sieverding E, van der Heijden MGA, Oehl F. 2021. Ancient lineages of arbuscular mycorrhizal fungi provide little plant benefit. *Mycorrhiza* 31: 559–576.
- Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, de Kroon H, Buckley YM. 2016. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences, USA* 113: 230–235.
- Schütz L, Saharan K, Mäder P, Boller T, Mathimaran N. 2022. Rate of hyphal spread of arbuscular mycorrhizal fungi from pigeon pea to finger millet and their contribution to plant growth and nutrient uptake in experimental microcosms. *Applied Soil Ecology* 169: 104156.
- Smith SE, Read D. 2008. *Mycorrhizal symbiosis*, 3rd edn. London, UK: Academic Press.
- de Souza FA, Dalpé Y, Declerck S, de la Providencia IE, Séjalon-Delmas N. 2005. Life history strategies in gigasporaceae: insight from monoxenic culture. In: Declerck S, Fortin JA, Strullu D-G, eds. *In vitro culture of mycorrhizas*. Berlin, Heidelberg, Germany: Springer Berlin Heidelberg, 73–91.
- Stearns SC. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3: 259–268.
- Sterner RW, Elser JJ. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Oxford, UK: Princeton University Press.
- van't Padje A, Werner GDA, Kiers ET. 2021. Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt 'crashes' and 'booms' of resource availability. *New Phytologist* 229: 2933–2944.
- Thonar C, Schnepf A, Frossard E, Roose T, Jansa J. 2011. Traits related to differences in function among three arbuscular mycorrhizal fungi. *Plant and Soil* 339: 231–245.
- Tilman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.
- Treseder KK, Allen EB, Egerton-Warburton LM, Hart MM, Klironomos JN, Maherali H, Tedersoo L. 2018. Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: a trait-based predictive framework. *Journal of Ecology* 106: 480–489.
- Walder F, Niemann H, Natarajan M, Lehmann MF, Boller T, Wiemken A. 2012. Mycorrhizal networks: common goods of plants shared under unequal terms of trade. *Plant Physiology* 159: 789–797.
- Walder F, van der Heijden MGA. 2015. Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. *Nature Plants* 1: 15159.
- Wang M, Chen J, Lee T-M, Xi J, Veresoglou SD. 2023. Context-dependent plant responses to arbuscular mycorrhiza mainly reflect biotic experimental settings. *New Phytologist* 240: 13–16.
- Wang W, Shi J, Xie Q, Jiang Y, Yu N, Wang E. 2017. Nutrient exchange and regulation in arbuscular mycorrhizal symbiosis. *Molecular Plant* 10: 1147–1158.
- Weber SE, Diez JM, Andrews LV, Goulden ML, Aronson EL, Allen MF. 2019. Responses of arbuscular mycorrhizal fungi to multiple coinciding global change drivers. *Fungal Ecology* 40: 62–71.
- Weigelt A, Mommer L, Andraczek K, Iversen CM, Bergmann J, Bruelheide H, Fan Y, Freschet GT, Guerrero-Ramírez NR, Kattge J *et al.* 2021. An integrated framework of plant form and function: the belowground perspective. *New Phytologist* 232: 42–59.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Yang H, Zhang Q, Koide RT, Hoeksema JD, Tang J, Bian X, Hu S, Chen X. 2017. Taxonomic resolution is a determinant of biodiversity effects in arbuscular mycorrhizal fungal communities. *Journal of Ecology* 105: 219–228.
- Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S, Bhatnagar JM, Busby PE, Christian N, Cornwell WK, Crowther TW *et al.* 2020. Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biological Reviews of the Cambridge Philosophical Society* 95: 409–433.
- Zhang H, Churchill AC, Anderson IC, Igwenagu C, Power SA, Plett JM, Macdonald CA, Pendall E, Carrillo Y, Powell JR. 2023. Ecological stoichiometry and fungal community turnover reveal variation among mycorrhizal partners in their responses to warming and drought. *Molecular Ecology* 32: 229–243.
- Zhang L, Zhou J, George TS, Limpens E, Feng G. 2022. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends in Plant Science* 27: 402–411.
- Zhou J, Kuyper TW, Feng G. 2023. A trade-off between space exploration and mobilization of organic phosphorus through associated microbiomes enables niche differentiation of arbuscular mycorrhizal fungi on the same root. *Science China Life Sciences* 66: 1426–1439.
- Zhou X, Li J, Tang N, Xie H, Fan X, Chen H, Tang M, Xie X. 2021. Genome-wide analysis of nutrient signaling pathways conserved in arbuscular mycorrhizal fungi. *Microorganisms* 9: 1557.

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