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Published Version

Parise, A. G. ORCID: https://orcid.org/0000-0002-2500-6455, Marín, C. ORCID: https://orcid.org/0000-0002-2529-8929, Tamagnini, F. ORCID: https://orcid.org/0000-0002-8741-5094, Tibbett, M. ORCID: https://orcid.org/0000-0003-0143-2190 and Pickles, B. J. ORCID: https://orcid.org/0000-0002-9809-6455 (2025) How mycorrhizal fungi could extend plant cognitive processes. Symbiosis. ISSN 0334-5114 doi: 10.1007/s13199-025-01065-y Available at https://centaur.reading.ac.uk/123628/

Published version at: https://doi.org/10.1007/s13199-025-01065-y
To link to this article DOI: http://dx.doi.org/10.1007/s13199-025-01065-y

Publisher: Springer

Symbiosis
https://doi.org/10.1007/s13199-025-01065-y

# How mycorrhizal fungi could extend plant cognitive processes

**André Geremia Parise**[1,2] · **César Marín**[3,4] · **Francesco Tamagnini**[5] · **Mark Tibbett**[2] · **Brian John Pickles**[1]

Received: 19 May 2025 / Accepted: 2 July 2025

## Abstract

Traditionally, mycorrhizas are studied for their role in plant health and nutrition through a mutually beneficial exchange of solutes. Recent research has revealed additional roles for mycorrhizas, including shaping plant communities and enhancing stress resistance. However, a critical aspect for the survival of organisms remains largely ignored in the study of mycorrhizal symbioses: cognition. This review explores the possibility that plants benefit from the cognition and behaviour of mycorrhizal fungi to enhance their own survival. We examine four case studies that are suggestive of plants extending their cognition through mycorrhizal associations: i) foraging complementarity between roots and mycorrhizal fungi; ii) recruitment and abandonment of mycorrhizal fungi depending on the host plant nutritional status; iii) expanded perception of the below-ground environment; and iv) shaping the mycorrhizal community to meet survival needs. Whilst extended plant cognition is implied, direct experimental evidence corroborating this hypothesis is needed, and we propose a delimiting criterion with suggestions of experiments to test this hypothesis.

**Keywords** Functional complementarity · Plant cognition · Root foraging · Root traits · Functional team selection · Fungal behaviour

## 1 Introduction

The mycorrhizal symbiosis is one of the most important symbioses in the living world. Plants and fungi developed a partnership so successful that it has lasted over 400 million years (Remy et al. 1994; Bidartondo et al. 2011; Strullu-Derrien et al. 2018) and may have enabled plants to colonise the dry landmasses of the planet, transforming them into prolific habitats for terrestrial lifeforms (Pirozynski and Malloch 1975; Smith and Read 2008). There are several types of mycorrhizas, the four major being arbuscular, ectomycorrhizal, orchid, and ericoid, but the list is growing with the ongoing research on these underground mutualisms (Kariman et al. 2018, 2024; Howard et al. 2022; Furtado et al. 2023; Lutz et al. 2025). Yet, despite their importance, much remains to be discovered about mycorrhizal relationships. For example, the mechanisms by which plants and mycorrhizal fungi communicate to form and secure the symbiotic association are poorly understood (Müller and Harrison 2019; Boyno and Demir 2022).

Early research on how plants benefit from the mycorrhizal symbiosis mainly focused on antibiotics produced by the fungal partner (e.g., Zak 1964; Marx 1966, 1972; Marais and Kotzé 1976) and nutrient exchange between the two partners, specifically carbon transfer to the fungus and plant uptake of phosphate and nitrogen (e.g., Clarkson 1985; Nolan 1991; Koide 1991). Recent research on mycorrhizas has demonstrated the importance of this symbiotic relationship regarding different processes including plant competition, plant-fungal signalling, resistance to stresses, seedling survival, and ecosystem services (e.g., Bingham and Simard 2012; Wagg et al. 2014; Stanescu and Maherali 2017; Yu et al. 2022; Kakouridis et al. 2022). Despite the rich body of

✉ André Geremia Parise
a.parise@pgr.reading.ac.uk; andregparise@gmail.com

[1] School of Biological Sciences, University of Reading, Reading, UK

[2] Department of Sustainable Land Management & Soil Research Centre, School of Agriculture, Policy and Development, University of Reading, Reading, UK

[3] Centro de Investigación e Innovación para el Cambio Climático (CiiCC), Universidad Santo Tomás, Valdivia, Chile

[4] Amsterdam Institute for Life and Environment, Section Ecology & Evolution, Vrije Universiteit Amsterdam, Amsterdam, HV, the Netherlands

[5] School of Pharmacy, University of Reading, Reading, UK

literature on the relationship between plants and mycorrhizal fungi, there are several aspects of these symbioses still to be uncovered. In particular, how mycorrhizas relate to the likely cognition of plants.

## 2 Cognition from brains to biology

Every living organism needs to monitor fluctuations in environmental conditions and rapidly respond to them in order to keep its self-organisation functioning properly (in other words, its homeostasis) (Maturana and Varela 1980). However, it is not adaptive to only react to environmental cues because cues sensed at the present may not reliably indicate future conditions. If an organism were only reactive—that is, capable only of immediate, inflexible responses to stimuli without modulation or anticipation (a common criticism to non-neural cognition), it could not prepare to what is coming next, nor could it improve its current conditions to maximise survival (Okasha 2024). Therefore, organisms need some plasticity to deal with unexpected and unpredictable variations in environmental conditions, especially combining past experiences to improve future responses (Sims 2023). Without the ability to perceive the environment, integrate what is perceived, improve its responses over time, and act with anticipation, it is likely impossible to survive for long. This dynamic relationship between living systems and the environment, paired with the ability to respond to internal processes and to predict, process and to flexibly adapt to ever changing environmental conditions, is what we refer to as *cognition* (Maturana and Varela 1980; Souza et al. 2018; Bechtel and Bich 2021; Lyon et al. 2021). As we will explore below, this working definition contrasts with classical views of cognition, and aligns with biological, rather than purely computational, models to explain this phenomenon.

Cognition is a complex and contentious concept with no universally accepted definition despite over a century of research on it (Bayne et al. 2019). Neisser (1967) defined cognition as referring to “all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used. It is concerned with these processes even when they operate in the absence of relevant stimulation”. A similar definition was adopted over forty years later by Shettleworth (2010) in a very influential book on compared cognition. These views on cognition often implicitly or explicitly exclude non-neural organisms from the realm of the cognitive—largely due to a cognitivist tradition that emerged alongside and was influenced by early developments in symbolic artificial intelligence and computationalism. This tradition characterises cognition as the manipulation of discrete symbolic representations according to formal rules—a view that equates cognition with digital information processing, and mirrors the architecture of early computer systems receiving inputs and providing outputs (Pylyshyn 1986; Miller 2003; Piccini and Scarantino 2011). Such an understanding may obscure alternative models of cognition because it requires a brain to fulfil the role of central processor in this scheme, thereby automatically barring non-neural organisms from being considered cognitive. Despite being influential, this approach to cognition is not unanimous, and less brain-centric alternatives have existed for decades and are gaining traction recently (Gibson 1966; Bateson 1972; Maturana and Varela 1980; Souza et al. 2018; Bechtel and Bich 2021).

Today, it is clear that the brain does not work as a computer processing inputs and providing outputs (Dreyfus 1992; Brette 2019; Buszáki 2019; Richards and Lillicrap 2022). Rather, the brain is an active element in our cognitive system, actively seeking stimuli and creating information in interaction with our bodies and the environment (Buszáki 2019). Alternative approaches to the cognitivist programme recognise that cognition emerges from the functioning of the whole body in interaction with the environment, and ground cognition in biology rather than philosophy, where cognitive science has its roots (Buszáki 2019). Cognition is thus understood as the dynamic process of an organism interacting with the environment and modifying its behaviour to keep its self-organised structure functioning properly (Maturana and Varela 1980; Souza et al. 2018; Lyon et al. 2021). It enables biological systems to flexibly cope with environmental fluctuation depending on both external and internal (i.e., physiological) circumstances, giving rise to complex and adaptive behaviour, eventually leading to the most complex forms of cognition that we are presently aware of, including human intelligence. The focus, then, is not on subjective experiences and how the brain processes information, but rather, on the process that organisms enact to flexibly adjust their homeostasis and behaviour to meet existential needs such as nutrition, growth, and reproduction. Within this framework, it is perfectly possible for organisms without neurons, like plants, fungi, and bacteria, to be regarded as cognitive systems.

The idea that non-neural organisms can be cognitive is not new. In fact, it can be traced back to the origins of psychology itself. Alfred Binet, the inventor of the IQ test, wrote a whole monograph on “*The psychic life of micro-organisms*” (Binet 1891), where he described several aspects of protist behaviour. He was not the only one to do so (Verworn 1889; Jennings 1904). Charles Darwin and his son Francis studied the movement of shoot and roots in several plant species, and famously compared the behaviour of roots in particular to that of “one of the lower animals” (Darwin and Darwin 1880). According to the authors, the ability of root tips to respond to the environment and direct the movement of the adjoining root makes them functionally comparable to the anterior body part of organisms like worms when they are foraging in the soil (Darwin and Darwin 1880). Despite these pioneering works, the study of non-neural forms of cognition was never mainstream in science. Nevertheless, in the last couple of decades, there has been a 'renaissance' of these kinds of studies, and knowledge on the cognitive capacities of organisms like bacteria (Shapiro 2007; Bechtel and Bich 2021), slime moulds (Latty and Beekman 2011; Boussard et al. 2021), fungi (Aleklett and Boddy 2021; Fukasawa et al. 2020, 2024; Marín and Suárez 2024), and plants (Trewavas 2003, 2016; Brenner et al. 2006; Gagliano 2015; Souza et al. 2018; Calvo et al. 2020) has undergone a significant development and increasing acceptance.

Lyon et al. (2021) developed the concept of "basal cognition", the most basal form of cognition that is observed in every living organism, and from which all taxa in the tree of life are considered to have evolved their own form of cognition according to the complexity of their bodies and sensorial and enactive apparatuses. Basal cognition comprises sub-phenomena like memory, communication, problem-solving, anticipation, and sensing/perception, among others. The reader is invited to refer to Lyon et al. (2021) for the full list with an explanation of what these sub-phenomena are. This all-inclusive approach to cognition, embraced by many authors (e.g., Cazalis et al. 2017; Bechtel and Bich 2021; Lyon et al. 2021; Shapiro 2021) is the one we adopt here.

Specifically, we adopt the "4E model" of cognition, which considers cognition as an Embodied, Embedded, Enacted, and often Extended process (Calvo Garzón 2007); Dawson 2014; Newen et al. 2018). The first three *E*s are relatively straightforward: cognition requires a body (it is Embodied), it is inextricable from the environment (it is Embedded), and it expresses itself through actions in the world (it is Enacted). The fourth E, Extended cognition, is the most controversial idea: that cognition can happen partly outside an organism's body (Clark and Chalmers 1998; Clark 2008; Menary 2010). Despite evidence for this form of cognition in mammals, arthropods, and even non-neural organisms, testing this empirically is challenging (Parise et al. 2023). Kaplan (2012) proposed using Craver's (2007a,b) mutual manipulability criterion to solve this issue. This criterion predicts matched inter-level interventions (Craver 2007a, b; Craver et al. 2021) between the cognitive system (organism) and the object, such that manipulation of the organism causes an alteration of the object, and manipulation of the object causes an alteration in the (cognitive) functioning of the organism. Extended cognition may partly explain how organisms with minimal or no brains perform complex cognitive behaviours. For example, Japyassú and Laland (2017) proposed that a putative extension of spider cognitive process to their spiderwebs could explain the highly complex behaviours of some spiders (considering the size of their brains), and Sims and Kiverstein (2022) argued that secreted slime may be an external element of the memory of slime moulds. Parise et al. (2020) argued that plants could extend their cognition as well, and that extended cognition may be more common in nature than previously imagined (Parise et al. 2023).

Given the discussion on a contemporary understanding of cognition above, we aim to explore the cognition of plants and fungi, and the idea that plants may benefit from the behaviour of mycorrhizal fungi through a process called extended cognition (Clark and Chalmers 1998; Parise et al. 2020). We propose that, due to the close link between plants and mycorrhizal fungi, their cognitive abilities may overlap somewhat, with the fungi becoming part of the system by which plants perceive and act in the world. We analyse four case studies to strengthen our hypothesis, and conclude that extended plant cognition (EPC) through mycorrhizas is a plausible hypothesis, but requires original studies designed to test it specifically and confirm whether it happens in nature and how it mechanistically works.

## 3 Cognition in plants and fungi

Conceptualising plants as cognitive systems has been controversial, sparking much debate since this hypothesis started to feature in mainstream journals (Flannery 2002; Trewavas 2002, 2003, 2004; Firn 2004; Adams 2018; Chamovitz 2018; Segundo-Ortin and Calvo 2019; Calvo et al. 2020). We do not address this debate here but note that the controversy comes mostly from the clash of two radically different epistemological traditions: one that sees cognition as necessarily tied to a brain or central nervous system, and another that sees cognition as a requirement for every living organism, as discussed in the previous section.

Regardless of the definitions adopted, it is undeniable that plants present behaviours usually considered cognitive such as learning and memory (Thellier and Lüttge 2013; Gagliano et al. 2014; Crisp et al. 2016; Galviz et al. 2020), communication between plants and between plants and other organisms (Oldroyd 2013; Karban 2015; Ninkovic et al. 2020; Falik et al. 2023), decision-making (Runyon et al. 2006; Dener et al. 2016; Gagliano et al. 2017; Gruntman et al. 2017; Née et al. 2017; Wang et al. 2023), and speed-accuracy trade-offs (Ceccarini et al. 2020). Plant anticipatory behaviours are particularly relevant because they cannot be fully explained as mere reactions to environmental stimuli. In these cases, plants respond to likely future conditions based on past experiences and present stimuli (Novoplansky 1991; Shemesh et al. 2010; Latzel and Münzbergová 2018; Guerra et al. 2019). With no brains, the cognitive process of plants (and fungi) could be based on the plastic network structure of their bodies—for example on chemical and electrical signalling (de Toledo et al. 2019; Debono and Souza 2019; Adamatzky et al. 2022), on epigenetic regulation

(Crisp et al. 2016; Latzel et al. 2016), and on reinforcement and interplay of metabolic pathways (Thellier and Lüttge 2013; Souza et al. 2018).

Fungi, for their part, have a network architecture that presumably allows processing of information (Adamatzky et al. 2022). Their behaviours and cognition are much less studied than that of plants, but this gap in the knowledge has begun to be addressed quite recently (Fukasawa et al. 2020; Aleklett and Boddy 2021; Aleklett et al. 2021; Marín and Suárez 2024). Other fungal studies indirectly show some cognitive abilities like the capacity to integrate environmental information to make decisions (Brown Jr et al. 1999; Hornby et al. 2001; Shareck and Belhumeur 2011; Sudbery 2011), memory (Caudron and Barral 2013; Ben Meriem et al. 2019; Fukasawa et al. 2020), and employing foraging strategies (Fukasawa and Ishii 2023). The likely involvement of electrical signalling in these processes is suggested by the production of electrical signals in response to environmental factors (Olsson and Hansson 1995), which can be sophisticated enough to guide the steering of a robot in response to light stimulation through a fungus-machine interface (Mishra et al. 2024). These studies give a glimpse of what fungi are capable of. However, further research in fungal cognitive ecology is needed to understand how this phenomenon operates, and which is the extent of their cognitive capabilities.

According to the extended plant cognition (EPC) hypothesis, the cognition of fungi could be complementing that of plants (Parise and Marder 2023). The EPC hypothesis proposes that, since plants possess a rich sensorial apparatus, but no brain nor neurons, extending their cognitive process to the environment could partly explain their complex cognitive behaviours (Parise et al. 2020), i.e., the ones they implement to meet existential needs such as root foraging, fighting herbivores, and communicating. Plants shape their environment both physically (i.e., through root morphology) and chemically through substances released by their organs, and such modifications may encode information, increase their sensory abilities, and be responsible for external information processing (e.g., Falik et al. 2005; Karban et al. 2014; Wheeldon et al. 2021; Vismans et al. 2022). Plants potentially extend their cognition through at least four different channels: volatile organic compounds (VOCs), root exudates, rhizosphere microbiota, and mycorrhizal associations (Parise and Marder 2023).

In the following sections, we examine the possibility of mycorrhizal fungi being part of their host's cognitive system. This is intriguing because fungi are not simply objects in the environment but living organisms with cognitive systems of their own. In this case, our rationale is that: 1) plants are cognitive systems; 2) fungi are cognitive systems; 3) plants and fungi establish mycorrhizas whereby, under certain conditions, they functionally become a single unit; therefore, 4) fungi are part of plant (extended) cognitive systems. Considering fungi as part of plant cognitive systems could change our perspective on this symbiosis, and adds an extra layer to the importance of soil health for plant development and resilience.

## 4 Extended plant cognition through mycorrhizal fungi

Mycorrhizal fungi establish a tight connection with plants through arbuscules in arbuscular mycorrhizas (AM)—where the fungus penetrate the root cells to establish a surface contact shaped like an arbuscle—, a Hartig net in ectomycorrhizas (ECM)—when the fungus grows hyphae around the cortical cells of the roots to establish contact, although sometimes this structure is absent (see Furtado et al. 2023)—, or other interfaces. Mycorrhizas often exhibit an impressive contact surface between the cell membranes of both partners, where they exchange nutrients, peptides, miRNAs and hormones (Smith and Read 2008; Müller and Harrison 2019). In a study on *Lotus tenuis* roots, Mendoza and Pagani (1997) found six AM entry points per mm, with 400 cm of colonised roots on average suggesting at least 24,000 fungus-plant interfaces per plant even before considering the intimate fungus-plant interactions of arbuscules. In a study of the colonisation of *Allium cepa* by *Glomus mosseae*, every cm of root had 40.7 mm$^2$ of plant-fungal contact (Cox and Tinker 1976). Similarly, in *Medicago truncultata*, 1 cm of root colonised by *Glomus intraradices* had 1–200 + arbuscules and 1–40 vesicles (Salzer et al. 1999). One plant may have millions of such connections, making it difficult to separate plants and AM fungi. This leads us to ask: i) beyond solutes, do plants and fungi signal each other about environmental conditions and their physiological statuses?, ii) does this symbiosis essentially fuse plant and fungal cognition together?, iii) do plants extend their cognition to mycorrhizal fungi? We think that a likely answer to all these questions is *yes*, and will try to address them in the following sections. Of course, these inquiries are valid only to the plants that form mycorrhizas. Whereas extended cognition may help plants improve survival, it is likely to be time- and context-dependent, and it is conceivable that plants are not always extending their cognition to mycorrhizal fungi. Likewise, not extending cognition does not necessarily impose fitness disadvantages to non-mycorrhizal plants—they can survive just as well—but overall, natural selection favours mycorrhizal plants in most environments (Maherali et al. 2016).

To explore our hypothesis that plants extend their cognition through association with mycorrhizal fungi, we examine case studies that could be considered plausible evidence. Unfortunately, since none of these studies were designed to test extended cognition, we cannot fully apply the mutual manipulability criterion outlined above, and our interpretation is necessarily limited. However, this does not invalidate the idea, especially considering that, overall, the behaviour of plants is significantly impaired without mycorrhizas, which already partially fulfils the mutual manipulability criterion. We nevertheless emphasise caution and note that future studies exploring this relationship should be specifically designed to meet the mutual manipulability criterion.

### 4.1 Case study 1: foraging complementarity between roots and mycorrhizal fungi

Nutrients are patchy and transient in soil, requiring plants to adjust their root growth dynamically and rapidly to forage efficiently and secure nutrient sources (Giehl and von Wirén 2004; Rajaniemi 2007). Plant roots are not particularly efficient in foraging (van Vuuren et al. 1996), but mycorrhizal fungi help plants immensely in this endeavour. For example, colonisation by AM fungi can increase plant N uptake by 3- to 12-fold (Hestrin et al. 2019). Mycorrhizal associations are so critical that plants may invest 20–30% of assimilated carbon into them (Ek 1997; Leake et al. 2004; Ji and Bever 2016). Most mycorrhizal fungi, especially AM, cannot survive without a plant partner (Smith and Read 2008), making this association obligate for many fungi.

Mycorrhizal fungi dramatically increase the extent and absorbing area of the plant-fungal system, facilitating contact with soil pores and particles and increasing its ability to forage for nutrients and water. Following the reasoning proposed by Leake et al. (2004), approximately 16.66 m of mycorrhizal hyphae provide the same surface area as 0.1 m of root. Yet, just 1 g of soil can harbour 200–600 m of ECM hyphae, and 2–8 m of AM hyphae (Leake et al. 2004). Read (1999) calculated the carbon cost to the host per unit of absorptive area and found that mycorrhizal hyphae were 10 times cheaper than root hairs, and 100 times cheaper than roots. In pot cultures of *Pinus taeda* colonised by *Pisolithus tinctorius*, mycelium accounted for 75% of the absorbing area, but only 5% of the plant-fungal belowground biomass (Rousseau et al. 1994). Essentially, mycorrhizal hyphae are cheaper, go farther, and can be rearranged more easily and rapidly without significant cost to the plant *compared* to roots. This makes them great candidates for being part of the foraging apparatus of plants and they can be more important than root proliferation in foraging (Tibbett 2000; Eissenstat et al. 2015). Foraging is not only about absorbing nutrients. It also requires finding resources and employing strategies to secure them (Cahill Jr et al. 2010). Foraging behaviour arguably requires cognition because it involves abilities such as decision-making and anticipation (Kelly 1990; 1992; Koch et al. 2004; Runyon et al. 2006; Grüter and Ratnieks 2011; Calhoun et al. 2014; Dener et al. 2016; Sandhu et al. 2018; Billard et al. 2020; Fukasawa and Ishii 2023). Hence, mycorrhizal fungi, being part of the foraging structure of plants, could also be part of the cognitive structure that foraging represents.

Plant species have different absorbing root thicknesses, which impact the precision of foraging. Studies with different tree species have demonstrated that foraging precision typically decreases with increasing root thickness, especially in ECM species (Liu et al. 2015; Chen et al. 2016; Cheng et al. 2016). However, fungal partners can help thick root plants to compensate for lack of foraging precision (Eissenstat et al. 2015; Cheng et al. 2016). This is particularly effective in ECM symbioses because many ECM fungi can extend their hyphae great distances in the soil (Agerer 2001). Hence, trees may delegate their foraging to fungi, especially in the case of ECM trees with thick roots. Since organic nutrients are patchy and ephemeral, thick-rooted trees cannot afford proliferating too many roots to secure these resources and may use mycorrhizal fungi to do the job for them.

Rosling et al. (2004) studied foraging preferences of *Hebeloma crustuliniforme* and *Piloderma fallax* associated with *Pinus sylvestris*. Plants and fungi developed well in microcosms when cultivated in pure *Sphagnum* peat, with the plants spreading their roots uniformly. However, when inoculated seedlings were cultivated in vertically divided microcosms, one half peat and the other a mineral soil, both fungi and roots preferred mineral soil, allocating $^{14}$C-label and roots in these substrates (Fig. 1). Fungi may have detected the mineral soil as a better source of nutrients, and sent these nutrients to the plant, which preferentially allocated carbon to fungi in contact with the mineral soil. Hyphal growth and synthesis of enzymes and exudates requires carbon, but in turn makes more nutrients available to the plant. This feedback might stimulate further hyphal growth and guide the roots to follow the hyphal front to the richest area of resources. Ultimately, the plant benefits from more efficient foraging and root placement. Although predictors of plant success and improved fitness such as plant growth and nutrient uptake were not examined by Rosling et al. (2004), root behaviour appears to have been induced by the behaviour of hyphae, which is an interesting example of fungi potentially being part of the perception and action process of plants.

Mycorrhizas can also buffer potentially toxic effects of nutrient excess. In a study with *Eucalyptus marginata* and *Acacia celastrifolia*, both native to soils poor in phosphate (P), Tibbett et al. (2022) demonstrated that P-fertilisation beyond a certain threshold is toxic to *E. marginata*. However, in inoculated plants, AM fungi significantly restrict the amount of P incorporated into plant biomass, an effect not observed in the P-tolerant *A. celastrifolia*. This implies that AM mycorrhizas are required for ensuring the homeostasis of the whole plant-fungal system in a challenging

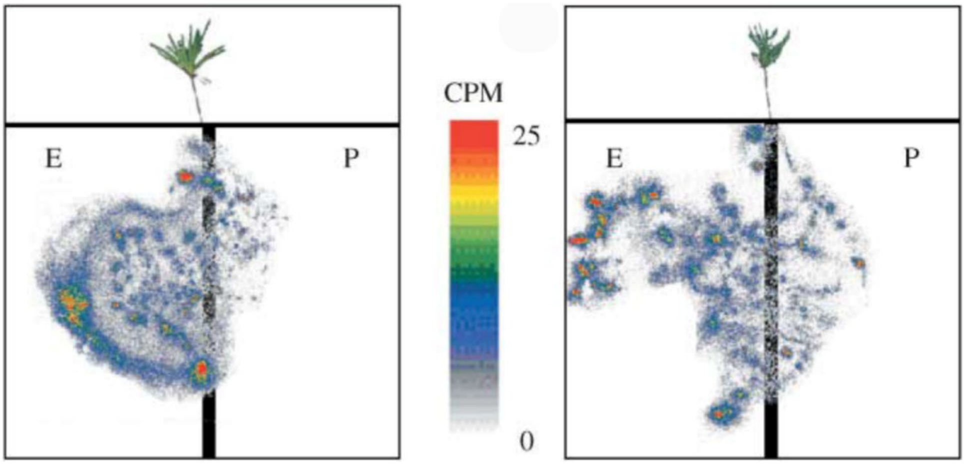

**Fig. 1** Figure from Rosling et al. (2004) showing ectomycorrhizal *Pinus sylvestris* cultivated in microcosms with *Hebeloma crustuliniforme* (left) or *Piloderma fallax* (right). The microcosms were vertically divided, and the left side contained mineral soil (E) and the right side, peat (P). Electronic autoradiography of labelled $^{14}$C shows the C allocation of both hyphae and roots, here represented as counts per minute (CPM). There is a clear preference of both partners for the mineral soil, despite the fact that they can grow well in peat only. The mechanisms behind this uneven choice of substrate could point to extended cognitive mechanisms where plants use mycorrhizal roots to find the best nutrient patches and distribute their roots more effectively. Reproduced from Rosling et al. (2004) with permission

environment, where AM fungi regulate P-intake to maintain plant health. Such a process requires plant-fungus communication, with the plant using the fungal partner to solve a problem it cannot tackle alone. Hence, fungi appear to be an integral part of the system that perceives the environment and solves problems, implying extended cognition, although more studies are necessary to confirm the mechanisms behind the behaviour observed.

### 4.2 Case study 2: plants recruit and abandon mycorrhizal fungi depending on their nutritional status

It is widely known that soil fertilisation or high inorganic nutrient availability inhibits mycorrhizal formation in both ECM (Jones et al. 1990; Nilsson and Wallander 2003; Sun et al. 2010; Corrales et al. 2017) and AM systems (Thingstrup et al. 1998; Ryan et al. 2000; Covacevich et al. 2008; Konvalinková et al. 2017; Zhang et al. 2016; Yazici et al. 2021). Mycorrhizal fungi respond differently to the type of nutrient (organic or inorganic) added to the soil (Allison et al. 2008; Avolio et al. 2009; Corrales et al. 2017; DeForest and Snell 2020), but this response can be mediated by the host (Avolio et al. 2009) and/or the fungal species (Corrales et al. 2017).

Nevertheless, plants seem to be very much in control of the symbiosis. Their roots attract mycorrhizal hyphae by secreting the signalling molecules strigolactones and flavonoids in the soil, which stimulate spore germination, hyphal growth, and branching, helping fungi to find the roots (Akiyama et al. 2005; Yoneyama et al. 2012; Decker et al. 2017; Tian et al. 2021). Strigolactone synthesis is influenced by nutrient starvation (Foo et al. 2013a; Decker et al. 2017). Yet, despite having an important stimulating role, strigolactones do not simply regulate the symbiosis through a linear chain of events (Foo et al. 2013a). This suggests that communication between plants and fungi is more complex than cause-consequence mechanisms and may involve feedback loops. Conversely, when plants experience high phosphate availability, they suppress or decrease mycorrhizal colonisation (Jones et al. 1990; Nilsson and Wallander 2003; Covacevich et al. 2008; Foo et al. 2013a; Eissenstat et al. 2015; Liu et al. 2015; Konvalinková et al. 2017; Zhang et al. 2016; Yazici et al. 2021; Bennett and Groten 2022), indicating that plants can control mycorrhizal colonisation depending on their nutritional needs. The proposed mechanism for suppressing AM colonisation is limiting the supply of carbohydrates, perhaps with the involvement of plant hormones like gibberellic and salicylic acids (Foo et al. 2013b; Yu et al. 2014).

The mechanisms that govern this dynamic are not fully understood. Some researchers invoke biological markets where trade of carbon-for-nutrients is regulated by sanctions and rewards (Kiers et al. 2011; Wyatt et al. 2014; Hortal et al. 2017; Noë and Kiers 2018). Others, in turn, suggest that if plants cannot use all the C assimilated through photosynthesis, the surplus of C is sent to fungi, either as a mere surplus disposal (Corrêa et al. 2012; Prescott et al. 2020) or following a stoichiometry of resources, particularly C, P, and N (Johnson 2010). The debate, however, is not yet settled, and both hypotheses need more empirical evidence (Bunn et al., 2024). Nevertheless, the available evidence suggests that plants have some kind of control over the symbiosis which is based in their own physiological status.

Plant nutrient acquisition strategies depend on internal assessment of nutrient status and comparison with environmental nutrient availability. This trade-off can result in suppression of mutualistic partners under high nutrient conditions, or recruitment of mutualists to acquire nutrients when experiencing starvation (Johnson et al. 2010, 2014). Mycorrhizal associations can be facultative in many plants (Moora 2014; Meng et al. 2023), meaning such plants may employ mycorrhizas as a problem-solving strategy. Mycorrhizal fungi are sometimes described as extensions of the roots (Cheng et al. 2016; Bunn et al. 2024), but beyond an extension of plant nutritional apparatus, mycorrhizal fungi may also be part of plant cognitive systems as an essential element of the plants' problem-solving apparatus. Studies are needed to verify how the nutritional status of plants influences the behaviour of mycorrhizal symbiont partners when foraging in the soil, or the types of mycorrhizal fungi that plants will associate with.

### 4.3 Case study 3: plant communication through mycorrhizal networks

Connection between two or more plants via the mycelium of at least one mycorrhizal fungus creates what is called common mycorrhizal networks (CMN). These networks may or may not involve direct hyphal contact between two or more roots (Rillig et al., 2024) and can facilitate the exchange of solutes, water, and infochemicals between plant roots. In particular, the possibility of roots sharing information through these networks was demonstrated in two laboratory-based experiments (Song et al. 2010; Babikova et al. 2013).

Song et al. (2010) cultivated tomato plants in compartments separated by membranes that either allowed mycelium to connect the roots or not. Donor plants were infected with the leaf pathogen *Alternaria solani* and all plants were enclosed in plastic bags, preventing aboveground communication through VOCs. After 65 h, receiver plants separated from infected donors by mycelium-permissive membranes presented higher activity of defence-related enzymes (peroxidase, polyphenol oxidase, chitinase, β−1,3-glucanase, phenylalanine ammonia-lyase, and lipoxygenase) and higher expression of defence-related genes (Song et al. 2010). Finally, when receiver plants were infected with *A. solani*, those connected to previously infected donor plants exhibited significantly higher disease resistance.

Using *Vicia faba* plants, Babikova et al. (2013) planted four receiver plants around a donor that would be infested with aphids. One receiver could interact with the donor through both roots and hyphae, a second only by hyphae, a third could initially interact through hyphae with connection severed prior to donor infestation, and a fourth receiver was grown in a mesh core that blocked donor interaction by roots and hyphae. Each plant was isolated aboveground to avoid VOC communication. Following donor infestation, the production of defence-related VOCs was analysed in all plants. Receiver plants that could interact via roots and/or hyphae after donor infestation presented the best results when it came to repelling aphids and attracting parasitoid wasps, with the VOC methyl salicylate being a key component modulating the response of both insect species (Babikova et al. 2013).

Both studies potentially show transmission of information between plants (i.e., communication). Unfortunately, to our knowledge, these are the only reliable studies addressing signalling between plants directly through a continuous CMN, and there is currently no published evidence that this phenomenon happens in the field. However, at least in these experimental settings a putative extended cognition through CMN might have happened.

When plants associate with a mycelium, there are two ways in which they could extend their cognition. The first is by linking roots of the same plant. Due to the dendritic architecture of roots and branches, communication between spatially close apexes can be slow if they are physiologically distant. Mycorrhizal hyphae could provide a shortcut belowground in a manner analogous to VOCs aboveground (Frost et al., 2007; Heil and Karban 2010); Parise and Marder 2023). If true, mycorrhizal hyphae would perform a similar role in plant cognition to internal channels of communication, perhaps using hormones, electrical signals, and/or hydraulic cues. Functionally, for the plant there would be no difference between the cognitive processes resulting from communication through plant tissue or fungal tissue, implying that plant cognition is extended through mycorrhizas (Parise and Marder 2023). The second is by linking roots of different plants. This could potentially open channels of communication with other plants belowground, expanding their sensorial world. Hence, through mycorrhizal hyphae, plants may gain perception of each other's existence. This alternative expands the array of possible interactions, cognitive or otherwise, of plants with a perceptually wider environment.

Song et al. (2010) and Babikova et al. (2013) studies can be analysed in two layers. The first layer suggests communication between plants through mycorrhizal hyphae, even if only in a laboratory setting, and likely via transmission of signalling molecules indicating pathogen or herbivory attack. Thanks to these conduits allowing reliable information transfer, plants prepared themselves for a future stress by upregulating defence-related genes, increasing the activity of defence enzymes, and changing VOC composition. The second layer is that plants increase their perception of other plants and their physiological status through mycorrhizal hyphae. It could well be the case that plants have other means for perceiving distant plants, some of them not yet characterised (Gagliano et al. 2012; del Stabile et al. 2022). Nevertheless, the parameters analysed in the studies of Song et al. (2010) and Babikova et al. (2013) suggest that the receiver plants could not be informed about the donor plant's physiological status without connection to the CMN. The evidence provided by Song et al. (2010) and Babikova et al. (2013) are a case in favour of plant-plant communication through CMN, but in the future, it will be important to verify whether this happens on the field, particularly, since the occurrence and importance of CMN in situ has been soundly questioned (Karst et al. 2023). However, they show another mechanism by which EPC could be operating at least in laboratory conditions.

### 4.4 Case study 4: plants shape the mycorrhizal communities according to their needs

We have seen earlier that plants can strengthen or reduce their mutualistic behaviour based on internal (e.g., nutrient stoichiometry) and external (e.g., nutrient availability) conditions. There is also evidence that plants can actively select the most beneficial fungi from the pool of species and strains available in the environment (Bever 2015; Chagnon et al. 2015; Werner and Kiers 2015; Bogar et al. 2019). However, recent research has suggested that through time (often, within an individual's lifetime), plants can alter the community of mycorrhizas associated with them (Frew and Aguilar-Trigueros 2024) to adapt to local environments. They could do so by preferentially allocating more resources to the more advantageous fungi depending on the context (Ji and Bever 2016), thus building a community over time that helps them survive in specific environments. This is particularly important in stressful environments, but not so much in benign conditions. For example, by studying *Bouteloua gracilis*, a grass native to North America, Remke et al. (2020) found that the sympatric communities of AM fungi support their hosts better than allopatric communities during drought stress. These results were later confirmed in a three years-long field experiment (Remke et al. 2022), where the origin of mycorrhizal inoculum was the best predictor of plant biomass, specific leaf area, and seed production in plants transplanted to drier and warmer environments. In another field study, Janoušková et al. (2023) analysed the composition of AM fungi associated with transplanted *B. gracilis*, demonstrating that the initial inoculum is the primary determinant of the fungal community, with edaphic and climatic factors playing a secondary role. While this highlights the importance of abiotic conditions, the findings also suggest an active role of the plant in shaping its associated fungal community to optimise performance in diverse environments.

Together, these studies are quite interesting to the EPC hypothesis because they seem to clearly follow the mutual manipulability criterion outlined in Sect. 2. When challenged with a novel, often stressful environment (a top-down manipulation), plants relied on the mycorrhizal communities they shaped for solving the problems imposed by the environment (a cognitive task). If the inoculum is experimentally changed (bottom-up manipulation), this significantly impairs plant performance, at least until the plant has the chance to rebuild its community. This seems to satisfy the mutual manipulability criterion by establishing relations of constitutive relevance of the fungi to the cognitive process of plants.

## 5 Cognition in plants, fungi, and beyond

Plants rely on mycorrhizas to accomplish processes important to their survival such as nutrition, foraging, problem-solving, and perhaps communication, pointing to the intriguing and unexplored possibility that plants extend their cognition to mycorrhizal fungi. Furthermore, if plants indeed extend their cognition to mycorrhizas, the fitness benefits are evident: it may allow plants to perceive nutrient patches or harmful substances in the soil from a distance, inform plants of where to invest more root growth and make foraging decisions, provide awareness of the space available for root growth, facilitate communication, and shortcut physiological constraints due to the modular architecture of the roots, among others. However, compelling phenomena may not be proof of extended cognition, but simple causal background conditions (Kaplan 2012). Well-constructed experiments can develop our understanding of whether extended cognition through mycorrhizas occurs and where the dynamic boundaries of plant cognition might be. Future research will likely have one or another epistemological flaw because philosophical proposals are not easy to transfer directly to empirical experiments. In effect, 'perfect' mycorrhizal experiments that capture the complexity of these symbioses are nearly impossible to achieve (Egger and Hibbett 2004; Jones and Smith 2004). However, we anticipate that a robust empirical framework corroborating (or refuting) extended plant cognition will emerge from the body of studies asking similar questions; much like the way neuroscience determined the neural components underlying human cognition (Kaplan 2012). Ideally, these studies will employ empirical criteria like Craver's (2007a,b) mutual manipulability to establish these relations. For example, by controlling the plant's ability to deliver carbon (Kiers et al. 2011) or the fungus' capacity to provide nutrients (Whiteside et al. 2019), manipulations of both levels could be achieved. See Table 1 for some suggestions on how to test EPC via mycorrhizas using the mutual manipulability criterion. Results from such experiments could have implications

**Table 1** Suggestion of possible methods that, combined, could be used to test extended plant cognition through mycorrhizas

Experiment: Grow plants in conditions that require mycorrhizas to solve problems

| Top-down manipulations | Bottom-up manipulations |
|---|---|
| Prevent plants from being colonised (mutation, blocking) | Use different species of fungi for solving the same problem |
| Prevent plants from delivering carbon to the fungi | Prevent fungi from delivering nutrients to the plant |
| Blocking plant communication with the fungi (e.g., strigolactones) | Alter the fungal community available to the plant |
| Prevent plants from access certain compartments in the substrate | Prevent communication from the fungus to the plant |
| | Use competitors, fungicides, or substances repellent to the fungus but not to the plant |

in agricultural, forestry, and restoration practices focused on mycorrhizal fungi, because management practices that diminish EPC via mycorrhizas might negatively impact plant growth, yield, and/or ecosystem functioning.

Immanuel Kant famously said that experience without concepts is blind, while concepts without experience are empty. With this, he was denouncing—indirectly—scientific advances not based on a solid metaphysic foundation, while also denouncing dogmatic metaphysics which at the time was often not based on empirical data or support (Kant 1998). The EPC via mycorrhizas framework proposed here allows to simultaneously adjust established concepts (like extended cognition more broadly) based on new findings, while at the same time suggesting new experiments and methods to validate such concepts (Table 1). Thus, EPC is different from 'regular' extended cognition, as other examples of extended cognition do not involve the recruitment of other organisms for it (Menary 2010). This requires to theoretically re-evaluate extended cognition and the 4E model when more than one agent (or millions in this case) are interacting simultaneously.

The main idea is to put plants in a condition that requires mycorrhizas to solve a problem or complete a task, and do both bottom-up and top-down manipulations to establish mycorrhizal fungi as constitutively relevant for the completion of that task (see Craver 2007a,b; Kaplan 2012; Japyassú and Laland 2017; Craver et al. 2021). Presumably, plants without mycorrhizas or with disrupted communication with the fungi would perform worse than those with pristine mycorrhizas.

An issue in some cases of extended plant cognition is the problem of "cognitive ownership" (Smart 2022). Who 'owns' the cognitive process when it is extended? When the cognitive agent is manipulating inanimate objects, like a person using a calculator, a spider weaving a web, or a plant releasing VOCs in the air, this is obvious. A human is not the extended element of the cognition of a calculator. But things become blurry when two cognitive agents interact. We suggest that either plants extend their cognition to fungi or both become a single cognitive entity, rather than whole plants becoming an extended element of fungal cognition. In fact, beyond a limited ability to mobilise nutrients in the network and connect with different hosts, the evidence does not suggest that fungi extend their cognition to plants or manipulate them in the way plants do to fungi. Plants seem to have much more control over the symbiosis. They can even survive without mycorrhizal fungi, whereas the opposite is not possible. After all, plants ultimately are the primary producers in the relationship; they hold the 'keys of the treasure' (carbohydrates and lipids), and use it to their benefit. They can recruit and abandon fungi according to their needs, and even parasitise the fungi—even without producing carbohydrates themselves, as seen in the case of mycoheterotrophs (Merckx 2013). Plants seem to shape the mycorrhizal community according to their needs, and use it to solve problems, find nutrients, and perhaps, communicate. Plants are the focal point of this extended cognitive system, and without plants, it would disappear. If fungi extend their cognition to plants, the magnitude of this extension is likely to be more localised, for example, around the roots the fungi are colonising. This is an interesting question worth pursuing when more data becomes available.

When studying the presumed cognitive association between plants and mycorrhizal fungi, shifts in environmental conditions and temporal dynamics must be considered. Like the cognitive process, the interactions between plants and its microbiota is flexible, plastic, and context-dependent. EPC through mycorrhizas can be transient, depending on the context and physiological, developmental, and phenological status of fungi and plants. As can be extracted from our case studies, it could be particularly critical for seedlings, herbaceous plants, and plants in early stages of development, for they have limited resources and ability to synthesise carbohydrates. Using fungi to help guiding foraging and root placement seems advantageous not only for the plant but for the fungi that would benefit from the success of its host. However, nothing prevents mature plants from benefitting from EPC as well, especially locally at the roots level.

Plants and symbiotic fungi often collaborate in mutualistic interactions but, like in any holobiont, the relationship between host and symbionts can shift to a parasitism depending on environmental and biotic context (Johnson et al. 1997; Suárez and Stencel 2020; Harrower and Gilbert 2021). Some questions for the future are: are plants extending their cognitive process to mycorrhizal fungi all the time, or only in specific moments when the symbiosis is working as a mutualism? Under which environmental and biotic conditions does the presumed EPC reach its optimal dynamics? What happens when the mycorrhizal symbiosis drifts toward the parasitism end of the mutualism-parasitism continuum?

Another question for the future, if extended cognition through mycorrhizas is confirmed, is: how does the communication between plants and fungi happen to allow this exchange of information? Hormones, small RNAs, and mycorrhiza-induced small secreted proteins (MiSSPs) are obvious candidates, but calcium, reactive oxygen species (ROS) and electrical signalling are also likely to contribute (Kapoor and Singh 2017; Thomas and Cooper 2022). Overall, what happens at the root-fungus interface is still largely unknown and needs to be better studied (Martin et al. 2016).

The hypothesis of extended plant cognition closely aligns with contemporary hypotheses about holobionts that take a holistic approach to study organisms not as separate individuals, but as clusters of several organisms productively interacting among themselves (Vandenkoornhuyse et al. 2015). It resonates, for example, with the Functional Team Selection framework (Johnson and Marín 2025), a framework to study plant adaptation that does not overlook the role of the microbial community for plant adaptation and survival. Who adapts to the environment is not the plant *and* the microbial community, but the plant *with* the microbial community. EPC further contributes to these views by adding the often neglected cognitive component to these holobionts, helping these "teams" to solve problems, recall past stresses, forage efficiently, and choose the best ways to adapt to new conditions. This perspective is worthwhile, as it will at the very least stimulate scientific questions and original approaches to the study of mycorrhizal symbioses that were never tried before.

Finally, plants are rarely alone in the environment. They are embedded in a rich assemblage of many species and individuals, all of them potentially exchanging nutrients, resources, allelopathic compounds, and information. They may be interconnected in an underground mycorrhizal network with one or many fungal individuals which are in turn connected to one or many other plants, and this is very different from reductionist experiments that investigate single plants and associated mycorrhizal fungi in laboratory settings (Giovannetti et al. 2004; Beiler et al. 2010; Tedersoo et al. 2020). Hence, whereas it might be possible to delineate the boundaries of the plant's cognitive system in laboratory conditions, the reality in the field may prove to be very different.

**Acknowledgements** The authors are grateful to Gustavo Maia Souza, Sofia Gripenberg, and Martin Lukac for reading the manuscript and providing valuable feedback, and to Monica Gagliano for discussions on extended plant cognition. AGP, BJP, MT, and FT are supported by a grant from the V. Kann Rasmussen Foundation. AGP is supported by a University of Reading International PhD Studentship. CM thanks the ANID – Chile projects SIA No. SA77210019 (2021) and Fondecyt Regular Project No. 1240186 (2024).

**Data Availability** There is no additional data associated with this article.

## Declarations

**Competing interest** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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