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Processes underlying the effect of mycorrhizal symbiosis on plant-plant interactions

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ABSTRACT

Mycorrhizal symbiosis has important implications for the diversity and productivity of plant communities. However, our mechanistic understanding of its influence on the outcome of plant-plant interactions is still expanding. In this review we propose a framework that might be useful to efficiently approach the effects of mycorrhizal fungi (MF) on plant-plant interactions. We propose several scenarios that can theoretically result in different outcomes of plant-plant interactions based on the combination of two processes: the diversity of resources provided by MF taxa to their host (resource dissimilarity) and contrasting ways of distributing those resources (resource distribution). Then, we illustrate our arguments with different ecological contexts where certain combinations of these two processes are prone to occur. The proposed framework suggests testable hypotheses that can contribute to elucidate relevant processes underlying the effects of mycorrhizal symbiosis on plant-plant interactions.

1. Introduction

The mycorrhizal symbiosis can have a considerable influence on the structure of plant communities (Grime et al., 1987; van der Heijden et al., 1998a,b; Yang et al., 2014). This symbiosis can affect important ecological processes such as plant succession (Janos, 1980; Montesinos-Navarro et al., 2015; García de León et al., 2016; Koziol and Bever, 2016), the ability of invasive species to colonize new habitats and outcompete local species (Nuñez et al., 2009; Stinson et al., 2006; Vogelsang and Bever, 2009; Marler et al., 1999), and the response of plant communities to habitat fragmentation, perturbations and changes in land-use (Medve, 1984; Smith et al., 1999; Menzel et al., 2016; Maltz et al., 2017). Accumulated experimental and observational evidence suggests that plant coexistence can be enhanced by the diversity of resources that mycorrhizal fungi (MF) provide to plants, both nutritional (e.g, N, P, C) and non-nutritional (e.g, defences against pathogens), and the different ways of exchanging them (Koide, 2000; Bever et al., 2010; Gorzelak et al., 2015). However, how these two processes interact to promote or reduce plant coexistence is still unknown. Contextualizing the different components of the plant-mycorrhizal fungi (MF) interactions, and whether certain combinations of them might result in different outcomes of plant-plant interactions might contribute to efficiently guide our research efforts on this topic.

In mycorrhizal symbiosis, it is commonly considered that the mycorrhizal fungus takes up nutrients from the soil and exchange them for phytosynthetically fixed carbon from the plant. However, important components of this symbiosis can get more complex under realistic conditions because: (a) multiple species of mycorrhizal fungi and plants can interact simultaneously (Fig. 1; Interspecific interactions); (b) the roots of two plants can be linked together through the hyphae of a shared mycorrhizal fungus, constituting a common mycorrhizal network (CMN) (Selosse et al., 2006), while simultaneously the two plants can also harbor other non-shared mycorrhizal fungi in their respective root systems (Fig. 1; Presence of shared and non-shared MF); (c) fungal taxa with contrasting traits can provide different benefits to their host plants (i.e. acquisition of different resources, or protection against

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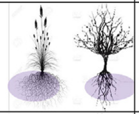
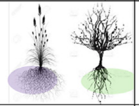
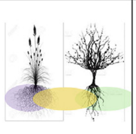
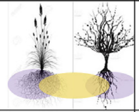
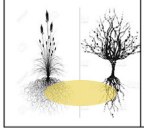
Interspecific interactions (multiple species of mycorrhizal fungi and plants)	Presence of		Provision of contrasting resources by non-shared MF	Fungal taxonomic groups likely to provide contrasting resources to their host plants (Resource dissimilarity)	Pathways of resource distribution between mycorrhizal fungi and plants (Resource distribution)	Asymmetry in resource distribution (Asymmetry)
	A common mycorrhizal network (CMN) (shared MF)	Mycorrhizal fungi that do not connect the plants (Non-shared MF)				
	No	Yes	No		**Plant-fungal resource exchange**: the exchange of mineral nutrients for reduced carbon between mycorrhizal fungi and plants	**Asymmetry in fungal competition for the same resource:** Differences in the rates of resource acquisition between fungal taxa competing for the same soil resource can enhance fitness differences between their host plants.
	No	Yes	Yes	**Different mycorrhizal functional types**: e.g. Ecto- and arbuscular mycorrhizae can differ in the predominant nutrient provided to their hosts (e.g. N *vs* P) **Different mycorrhizae families**: e.g. Gigasporaceae and Glomeraceae can differ in the resources provided to the plant, thus the former are efficient in nutrient acquisition and the later in plant protection against pathogens **Different isolates of the same species**: e.g. Isolates of *Rhizophagus irregulare* differ in their efficiency to contribute to the host plant P and N nutrition		
	Yes	Yes	Yes		**Resource allocation to plants by CMN:** the resources taken up from the soil are distributed to each host plant by the CMN **Interplant resource transfer through CMN**: the resources provided to a host plant come from another host plant, moving from the donor to the receiver through the CMN	**Neutral asymmetry in interplant resource transfer through CMN:** Complementary resources provided to the hosts by their respective non-shared MF can be transferred between plants through CMN. Independently of the flux from one plant to the other, an asymmetric exchange of complementary resources between plants will have no effect on plant fitness differences
	Yes	Yes	No			**Asymmetry in resource allocation to plants by CMN:** Asymmetric allocation of resources through CMN between plants can result in plant fitness differences **Asymmetry in interplant resource transfer through CMN:** A different amount of resource flux from one plant to the other can result in plant fitness differences.
	Yes	No				

Fig. 1. Glossary with definitions of different terms used in the main text grouped under three key processes: Resource distribution, provision of contrasting resources (i.e. resource dissimilarity) and asymmetry in resource distribution. Within rows, each ellipsis indicates a different fungal species, and plant species are represented by different drawings. Ellipses that overlap the roots of the two plants indicate a common mycorrhizal network (i.e. a fungus shared between the two plants that connects their roots), when the ellipsis overlaps a single plant root system the fungus is only present in that plant species. The color of the ellipses represents the resource provided by the mycorrhizal fungi to the host plant. The same color indicates that the different fungus provide the same resource to their respective host plant. Each definition is located grouping those rows in which it could take place.

pathogens). These differences can occur across fungal species, genera, families or functional types of mycorrhiza (arbuscular mycorrhizal fungi (AMF) *vs* ectomycorrhizal fungi (EMF)) (Aerts, 2003; Powell et al., 2009) (Fig. 1; Resource dissimilarity). Therefore, when a single fungal taxon forms a CMN, its traits will define the type of resources provided to the hosts, which will be those provided to both plants. Meanwhile, those mycorrhizal fungi that are non-shared between plants can differ in the resources provided to their respective host; (d) the resources provided by CMN to its host plant can come from different sources, either directly from the soil, or from another host (Meng et al., 2015; He et al., 2004) (Fig. 1; Resource distribution); finally, (e) the mycorrhizal symbiosis can affect the coexistence of plant species by enhancing or reducing the plant fitness differences due to an asymmetry in any of the previously described pathways of resource distribution (Bever et al., 2010) (Fig. 1; Asymmetry).

Mycorrhizal symbiosis mediated by AMF has been traditionally considered to have a low specificity (Klironomos, 2000), influenced by the fact that around two-thirds of land plant (300000 species) are associated with a relatively small number of described AMF (Smith and Read, 1997; Fitter and Moyersoen, 1996). Controlled experiments showing the potential of AMF to colonize different hosts have also contributed to this idea, although the contrasting responses of different hosts to the same AMF have been usually disregarded (Klironomos, 2000). However, new advances suggest that plant-AMF might show a higher host preference than originally thought. Firstly, molecular tools have revealed a clearly higher richness of AMF than previously described; although the definition of operational taxonomic units is still controversial (Rosendahl, 2008; Öpik et al., 2013). Secondly, studies focusing on plant-AMF associations at the community level have shown non-random patterns of plant-AMF interactions, suggesting certain host preference under field conditions (Helgason et al., 2002; Vandenkoornhuyse et al., 2003; Gollotte et al., 2004; Montesinos-Navarro et al., 2012b). Meanwhile, in the case of plant-EMF interactions, host specificity is probably more widespread based on molecular evidence (Tedersoo et al., 2008), showing for instance a differential expression of fungal and plant genes when they are exposed to compatible and incompatible partners (Liao et al., 2014). Host preference in plant-MF associations can influence two different processes by which MF can shape the outcome of plant-plant interactions. On one hand, a low plant-MF specificity can enhance the chance of harboring some MF that are present in both plants, enabling the formation of CMN, and potentially affecting plant-plant interactions by resource exchange through CMN (Selosse et al., 2006; Simard et al., 2012). On the other hand, high plant-MF specificity can enhance the predominance of non-shared MF between plant species, which can also contribute to plant coexistence through a different process. Phylogenetically, and thus functionally diverse MF can provide complementary benefits to plants, enhancing resource partitioning between them (Maherali and Klironomos, 2007). In this sense, the association of plant species harboring a distinct MF community can increase the diversity of MF in the shared rhizosphere, enhancing plant coexistence (Montesinos-Navarro et al., 2012a). The two processes are not mutually exclusive, as interacting plants could harbor both CMN and non-shared MF (Rasmussen et al., 2018). Thus, contrasting effects might emerge from the combinations of the two processes.

Here, we propose a framework that integrates two main processes by which mycorrhizal symbiosis may influence the outcome of plant-

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plant interactions, identifying hypotheses about the theoretical outcomes of such interactions under different scenarios. Finally, we identify ecological contexts in which each scenario is prone to occur.

2. Framework proposal

The outcome of plant-plant interactions can be antagonistic, mutualistic or neutral (Callaway, 2007), and we propose that these possible outcomes can be theoretically predicted based on two components of the plant-MF interaction: the predominance of certain pathways of resource distribution (i.e. interplant resource transfer through CMN) and the contrasting resources potentially provided by the MF (Fig. 2). Interplant resource transfer can occur through a CMN, which can lead to positive plant-plant interactions when the resources transferred are dissimilar (i.e. plants differ in their access to different resources, and resources are transferred from the resource-rich to resource-poor plant following source sink gradients, so exchanging those resources that the other plant is missing). However, when a CMN is absent and the interacting plants are only associated with non-shared MF, the fungi can provide dissimilar resources to their respective host, but the lack of exchange between plants will prevent the plants from benefiting from the exchange of dissimilar resources, resulting in a neutral plant-plant interaction, as plants could coexist due to resource partitioning. Finally, negative plant-plant interactions will emerge when the dissimilarity of the resources provided by fungi is low, and there is asymmetry in either: interplant resource transfer through a CMN, and/or non-shared MF competition for the same resources (Fig. 3). Therefore, a CMN and non-shared MF can shape the outcome of plant-plant interactions in different ways, but a better understanding of these processes requires detailed information on the specificity of plant-MF interactions.

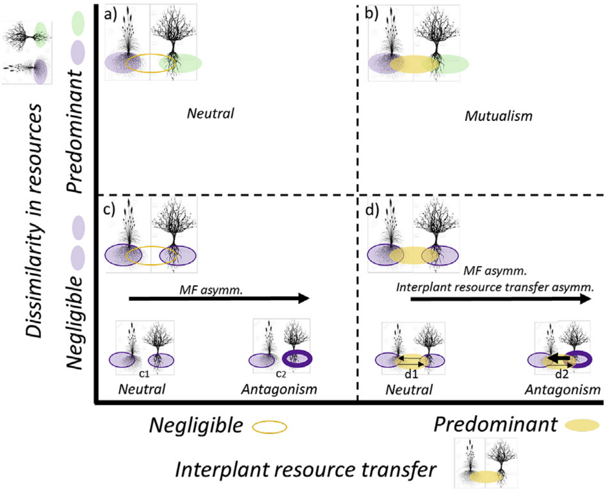

Fig. 2. Conceptual framework. The outcome of plant-plant interactions, (i.e. mutualistic, neutral and antagonistic), is proposed to depend on: the contribution of mycorrhizal fungi (MF) to interplant resource transfer through a CMN, and the dissimilarity in the resources provided to their hosts. The former is driven by the CMN (i.e. MF shared among the interacting plants) (yellow ellipses overlapping the roots of the two plants), and the latter by non-shared MF (non-overlapping ellipses in each plant). Non-shared MF can provide the same resources (ellipses in the same color: purple), or dissimilar resources (ellipses in different colors: purple and green). For each combination of the two factors (scenarios) we theorized that a plant-plant interaction will be (a) neutral: when non-shared MF provide complementary resources to interacting plants, enhancing resource partitioning; (b) mutualism: when interplant transfer of complementary resources through CMN occur, resulting in benefits for both plants independently of the amount of each resource transferred; or can shift from neutral to antagonism (c–d), when the dissimilarity in the resources provided by the non-shared MF is negligible. In the case of a negligible interplant resource transfer through CMN (c), the outcome of the plant-plant interaction will shift from neutral (c1) to negative (c2) depending on the asymmetry in fungal competition for the same resource of the MF present in each host (inequality in the thickness of the ellipses). A similar shift can occur when an interplant resource transfer through a CMN predominates (d), but in this case, an asymmetry in interplant resource transfer through a CMN (inequality in the thickness of the arrows) will also contribute to the shift from a neutral (d1) to a negative (d2) outcome.

3. Resource distribution

Interactions between plants can be affected by the ways in which the mycorrhizal symbiosis can influence the acquisition and distribution of resources. Mycorrhizal fungi can acquire resources from the soil and re-distribute them between the plants connected through a CMN, enhancing either coexistence or competitive exclusion between the plants (Bever et al., 2010). Plants can also enhance (Simard and Durall, 2004; Selosse et al., 2006), or reduce (Becklin et al., 2012) the symbiotic fungi of neighbor plants, thus potentially conditioning the outcomes of plant-plant interactions. Moreover, the resources provided by a MF to its host plant can be released later through root exudates to the rhizosphere shared with other plants, indirectly influencing the performance of neighbor plants.

In addition, there is experimental evidence showing that MF can also play a role in interplant resource transfer through a CMN, which has been assessed using physical barriers (meshes) which ensure that plants roots are only connected through a MF. Using elements with unusual isotopic composition as tracers, a donor plant is labeled by foliar absorption of the tracer, which is afterwards quantified in the receiver plant. Interplant resource transfer has been shown for both AMF (Yao et al., 2003; Cheng and Baumgartner, 2004; Wilson et al., 2006; Meding and Zasoski, 2008; Jalonen et al., 2009; Li et al., 2009; Meng et al., 2015; Teste et al., 2015) and EMF (Egerton-Warburton et al., 2007). However, in some experimental studies the reported amount of resources transferred to the receiver plant can be relatively low, when a short period of time from the application of the tracer to the measurement in the receiver has been allowed, and when just a few pulses of tracer have been applied to the donor. Therefore, we are still uncertain about the magnitude of interplant resource transfer through a CMN, and further research is required to assess the ecological significance of this process.

CMN can be established within and across plant species, either because the same MF simultaneously colonizes several plants, or due to hyphal fusions (i.e. anastomosis) of MF from different plants. Inter-specific plant connections mediated by MF can occur between plants from different species, genera and families (Selosse et al., 2006), creating a large network interconnecting plants within a community. *In vivo* experiments showed that 44–49% of the hyphal contacts between two contiguous mycorrhizal networks of *Glomus mosseae* led to anastomosis (Giovannetti et al., 2004), supporting also the potentially large extension of the network. Although further research is required, anastomosis seems to occur only within the same isolate of a given MF species (Giovannetti et al., 1999, 2003). Therefore, if anastomosis is unlikely to occur across MF species, it will be unlikely that plant species harboring different MF taxa will be connected through a CMN. Nevertheless, these studies have been conducted under laboratory conditions, and it is largely unknown whether these patterns are maintained in natural communities.

The main studied mechanism by which MF can enhance plant fitness is the provisioning of nutrients such as nitrogen (N), phosphorus (P), and carbon (C) to their hosts, and other resources such as water. Interplant N transfer has been widely studied in agroecosystems, specially from a N-fixing legume to forbs (Chalk et al., 2014), and a CMN have been also shown to enhance this transfer

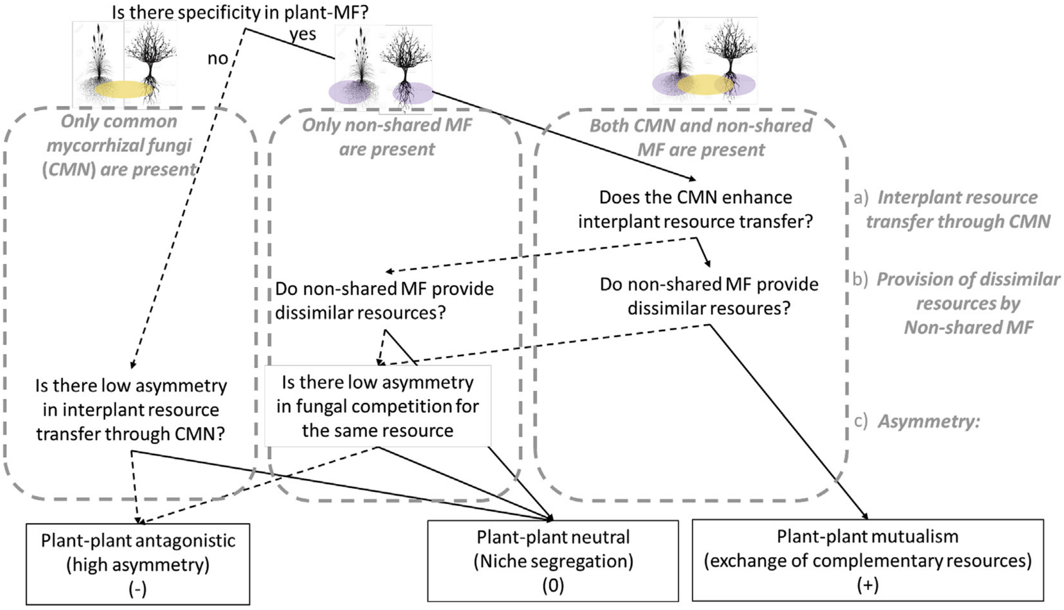

Fig. 3. Main questions which further exploration might contribute to improve our mechanistic understanding of the effects of mycorrhizal symbiosis on plant-plant interactions based on the proposed framework. Questions are grouped in three topics: (a) interplant resource transfer through CMN, (b) dissimilarity in the resources provided by mycorrhizal fungi to their host plants, and (c) asymmetric effects in either of the two processes. Each sentence represents a statement to be tested, and arrows indicate the subsequent question to be approached if the answer of the test was yes (continuous lines) or no (dashed lines).

(He et al., 2009), both under controlled conditions (Bethlenfalvay et al., 1991; Cheng and Baumgartner, 2004; Li et al., 2009; Jalonen et al., 2009) and in natural communities (He et al., 2006). The role of a CMN in interplant N transfer has been shown for both AMF (Cheng and Baumgartner, 2004; Meding and Zasoski, 2008; Jalonen et al., 2009; Li et al., 2009; Meng et al., 2015; Teste et al., 2015) and EMF (He et al., 2004), resulting in a moderate amount of N transferred (i.e. the N content received can range from 0.03 to 25% in the previous references). In natural communities of semiarid environments where plant communities are governed by facilitation, N transfer mediated by fungi has been reported between plants involved in long-lasting facilitative interactions (Montesinos-Navarro et al., 2016a), potentially contributing to plant coexistence under stressful conditions. Interplant P transfer through a CMN can also be mediated specially by AMF (Heap and Newman, 1980; Newman and Eason, 1993; Yao et al., 2003; Wilson et al., 2006), like other elements such as arsenic, cesium and rubidium (Meding and Zasoski, 2008). Meanwhile, interplant water transfer through a CMN has been mainly studied mediated by EMF (Egerton-Warburton et al., 2007; Plamboeck et al., 2007; Schoonmaker et al., 2007). In the case of C, the interplant transfer through a CMN is more controversial. Firstly, the role of AMF has been little studied, but there is evidence supporting that C remains in the fungal tissues (Fitter et al., 1998; Pfeffer et al., 2004). However, regarding EMF, other studies show that EMF can mediate interplant carbon transfer through a CMN, reporting the transfer from the donor plant to the above ground biomass of the receiver plant (Philip et al., 2010; Song et al., 2015; Klein et al., 2016). For instance, in temperate forests, substantial multi-year allocation of C assimilated by 40-m-tall spruce has been reported to be allocated to the sapwood of neighboring beech, larch, and pine, assisted by common ectomycorrhizal networks (Klein et al., 2016). Both inter and intraspecific interplant C transfer have also been reported between mature trees in boreal forests and shaded tree saplings connected through a CMN (Simard et al., 1997; Philip et al., 2010).

The amount of transfer and its uni- or bidirectional nature is influenced by fertilization and the interaction with N-fixing symbionts of the plants involved, indicating an influence of interplant source-sink gradients in this process (Simard et al., 1997; Simard and Durall, 2004). In this sense, recent studies show an increase in N transfer between distantly related plant species, due to a phylogenetic conservatism of N content across plant species, which results in steeper N gradients among distant relatives (Montesinos-Navarro et al., 2017).

Moreover, it is increasingly recognized that MF can also provide a suite of non-nutritional benefits to plants, such as increasing their disease resistance, or inducing plant chemical defenses against herbivores and pathogens (Delavaux et al., 2017), and MF have been suggested to contribute the interplant transfer of all these benefits (Gorzelak et al., 2015). CMN have been shown to transfer chemical signals between plants mediating the activation of defense-related genes when healthy plants are connected to pathogen-infected and herbivores-attacked tomato plants (Song et al., 2010, 2014). Furthermore, healthy *Vicia faba* plants connected through a CMN to aphid-attacked plants produce volatile organic compounds that are repellent to the aphids but attractive to a parasitoid wasp, which is a natural enemy of the aphid; similarly to the plants actually infected by aphids (Babikova et al., 2013).

CMN can also induce negative plant-plant interactions. On one hand, a CMN can transport chemicals that are harmful for the neighbor plants. Thus, allelochemicals can move through a CMN from focal to target plants, accumulating these substances at levels that could not be reached by diffusion through soil (Barto et al., 2011), although, a meta-analysis showed that this factor has an ambiguous effect on plant fitness across studies (Delavaux et al., 2017). On the other hand, the transport of beneficial resources provided by a CMN might be unevenly distributed between the interacting plants, resulting in asymmetric processes (Fig. 1).

However, the assessment of potential asymmetries within the mycorrhizal symbiosis might not necessarily be related to the total amount of resources provided and received by each partner. Instead, the plant-fungal resource exchange falls within a mutualism-parasitism continuum governed by the cost/benefit ratio for the fungi and the plant involved (Johnson et al., 1997).

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Thus, identifying what constitutes a fair trade for each partner requires a proper assessment of the net benefit for each mutualist in terms of their efficiency, requirements and contribution to the symbiosis (Koide and Elliott, 1989; Kiers et al., 2011). This balance within the mycorrhizal symbiosis could in turn influence plant-plant interactions, although much less information is available in this regard. In addition, MF can to distribute resources asymmetrically between plants by allocating more nutrients to large or healthy plants because of their superior ability to provide fixed-carbon to them (Kytöviita et al., 2003; Merrild et al., 2013; Weremijewicz et al., 2016), influencing the outcome of plant-plant interactions. In other cases, certain plants might be more prone to provide than to receive certain resources than others. For instance, nodulated-legumes tend to provide N (He et al., 2004), or non-shaded *Betula papyrifera* provide C (Simard et al., 1997), while other plant species tend to receive those resources. However, it is the response of each plant species to this asymmetric distribution of resources what will finally result in a given plant-plant interaction outcome. For example, under controlled conditions, Walder et al. (2012) showed that in microcosms where two plant species were connected through a CMN, the plant which invested less carbon into the mycorrhizal symbiosis received more than 90% of the N and P provided by the CMN. Meanwhile, the neighbor plant that invested massive amounts of carbon had little in return. Interestingly, this asymmetric trade barely affected the growth of the later, and the biomass production in interspecific cultures surpassed the mean of the two monocultures (Walder et al., 2012). Thus, despite the strong asymmetry in the nutrient trade, a CMN may contribute to interplant facilitation when the response of the plant species to the investment in nutrients counter balances the asymmetric trade.

Finally, different hypotheses have been proposed about the mechanisms driving the direction of resource exchange from MF to plants. Some examples are nutrient transfer following source sink gradients, which have been generally invoked for C and N transfer (Francis and Read, 1984; Finlay and Read, 1986; Simard et al., 1997; Simard and Durall, 2004; Montesinos-Navarro et al., 2017), plant C investment in the most cooperative fungi (Kiers et al., 2011), although evidence of transfer irrespective of C inputs can also occur (Walder et al., 2012), and water transfer based on water potential (Kikuchi et al., 2016). Nevertheless, more research is required in this regard as the mechanistic understanding of these processes is still largely unknown.

4. Dissimilarity in the resources provided by mycorrhizal fungi

Nutrient-plant-mycorrhizal interactions can also influence plant coexistence (Jiang et al., 2017). Fungal species can differ in the amount of nutrients provided to different hosts (Ravnskov and Jakobsen, 1995; Klironomos, 2000), or in their effects on hosts' tolerance to environmental stresses such as drought (Michelsen and Rosendahl, 1990), shaping in turn the outcome of plant-plant interactions.

When the resources provided to each host are the same, the MF associated with each host can compete asymmetrically for those resources. Negative interactions between fungal taxa have been documented (Lopez-Aguillon and Mosse, 1987; Maherali and Klironomos, 2012; Maynard et al., 2017). In turn, MF can also alter the outcome of plant-plant interactions by inverting the competitive ability of the interacting plants when the symbiosis is present (Marler et al., 1999; Callaway et al., 2001), or on the contrary, they can also contribute to plant coexistence when they suppress the growth of strong plant competitors or dominant plant species (Zhang et al., 2014; Wagg et al., 2011; Stanescu and Maherali, 2017). Furthermore, both the reduction of MF using a fungicide (Moora and Zobel, 1996) and the physical disruption of a CMN (Weremijewicz et al., 2018) can decrease interspecific competition while amplifying intraspecific competition, thus enhancing plant community diversity. However, plant kin recognition can also benefit relatives through the investment in mycorrhizal fungi promoting the persistence of the mycorrhizal symbiosis (File et al., 2012).

In contrast, when the two communities of MF provide complementary resources to their host plants, plant coexistence can be enhanced by the MF contribution to reduce plant competition. Mycorrhizal fungi can provide different search strategies for resource acquisition. For instance, AMF are more efficient than EMF in acquiring P, while the latter are more prone to provide N uptake benefits (Aerts, 2003). Thus, the competition between plants interacting with different types of MF can be relaxed compared to when they compete in the absence of MF by root resources-acquisition. Furthermore, there is accumulated evidence that supports the idea that an increase in MF richness and diversity can enhance plant performance and coexistence (van der Heijden et al., 1998a,b; Wagg et al., 2011; Hiiesalu et al., 2014). In simulated old-field plant communities, an increase in the diversity of MF from 1 to 14 increased plant community P uptake and biomass (van der Heijden et al., 1998a,b). The authors suggest that a greater hyphal length and MF diversity might more completely exploit the soil for P. However, an increase in MF diversity does not necessarily imply an increase in complementarity between plant species (Wagg et al., 2015). For instance, an increase in MF diversity can also increase the likelihood of including the most favorable host-MF combination, potentially resulting in a similar pattern (van der Heijden et al., 1998a,b; Scheublin et al., 2007; Wagg et al., 2011; Shi et al., 2016).

MF can differ in the nature of the benefit provided to their host. Fungal species of Gigasporaceae tend to produce extraradical hyphae while their root colonization is limited, while the opposite is true for species of Glomeraceae which highly colonize the host roots but produce little biomass in soil (Hart and Reader, 2002; Varela-Cervero et al., 2016). These differences have led to the hypothesis that Glomeraceae might be more efficient protecting roots from pathogen infections, while Gigasporaceae might enhance nutrient and water uptake (Newsham et al., 1995; Maherali and Klironomos, 2007; Powell et al., 2009), although, for instance, *Gigaspora margarita* imposes large C requirement on the host plant and provides negligible P uptake benefits compared to Glomus species (Lendenmann et al., 2011). MF can also differ in the proportion of nutrients provided, with some MF providing more N and others more P. Therefore, plants that associate with AMF are expected to have increased access to P, whereas plants associating with ecto- or ericoid mycorrhizal fungi are expected to have increased access to N (Aerts, 2003). Interspecific MF differences have also been reported for other mineral nutrient acquisition, with *Cenococcum geophilum* containing high levels of sulphur, *Clavulina cristata* of calcium and *Glomus* sp. of potassium (Seven and Polle, 2014). Within AMF, isolates can differ in whether they provide both P and N to their hosts, or predominantly only one of the two nutrients, usually P (Mensah et al., 2015).

Functional and ecological similarity can be shaped by patterns of common ancestry, and so the evolutionary relationships among species can be used to assess patterns of trait diversity (Felsenstein, 1985). In MF, there is certain phylogenetic conservatism in traits related to the benefits provided to their host, such as intra-/extra-radical hyphae development that can reduce the host infection by root pathogens (Powell et al., 2009). Therefore, an increase in phylogenetic diversity of mutualistic fungi might result in an increase in the functional diversity provided to their hosts, due to the complementary effects among MF. A high phylogenetic diversity of

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MF results in low phylogenetic diversity of the non-mutualistic fungi colonizing the roots (Montesinos-Navarro et al., 2016b) and an increase in plant community productivity (Maherali and Klironomos, 2007), potentially due to functional complementarity among MF. Plant co-existence might be enhanced between plant species that increase the MF richness in the shared rhizosphere (Montesinos-Navarro et al., 2012a), and can result in a mirroring between plant and MF diversity (Hiiesalu et al., 2014; Montesinos-Navarro et al., 2015). Across several communities, plant facilitative interactions between distant relatives are more likely to persist (Valiente-Banuet and Verdú, 2008), and a tendency of phylogenetically distant plants to harbor dissimilar MF communities has been hypothesized, but this hypothesis has not been conclusively supported (Montesinos-Navarro et al., 2012a; Reinhart and Anacker, 2014; Veresoglou and Rillig, 2014; Chen et al., 2017).

5. Hypotheses (plant-plant interactions scenarios)

We propose several scenarios that can theoretically result in different outcomes of plant-plant interactions, and illustrate them with the ecological contexts where each scenario is prone to occur. Four combinations are possible, based on the predominance (or negligibility) of interplant resource transfer through a CMN and the dissimilarity in the resources provided by non-shared MF.

A predominance of the provision of dissimilar resources can be combined with:

(a) A negligible interplant resource transfer through a CMN (Fig. 2 a). In this scenario, plants will tend to interact with non-shared MF, which will provide complementary resources to their host plants. The resultant outcome would be plant coexistence due to resource partitioning, but without any benefit derived from the interplant transfer of those complementary resources (i.e. a neutral plant-plant interaction). This situation is likely to occur in plant-plant interactions where one plant species is exclusively associated with EMF and the other with AMF. In shrublands, where dwarf shrubs (commonly associated to EMF) coexist with Poaceae (usually associated to AMF), different nutrient-acquisition strategies between MF types can lead to this situation. Across 23 subarctic vascular plant species, ectomycorrhizal plants tended to use the organic N in fresh litter, while arbuscular mycorrhizal plants were more likely to use the inorganic N (Michelsen et al., 1996). In addition, plants associated with AMF have increased access to P, whereas plants associating with EMF have increased access to N (Aerts, 2003). Either of these two processes can result in lower competition between plant species associated to AMF and EMF respectively.

However, our theoretical prediction of a neutral plant-plant interaction can be modified by plant species traits. For instance, antagonistic plant-plant interactions might also emerge when the traits of the ectomycorrhizal plant species reduce the mycorrhizal symbiosis of the plants interacting with AMF. This has been shown by willow species with a dense canopy. They can reduce the light intercepted by their associated forbs due to shading effects, and the carbon limitation of the forb can affect its cost-to-benefit ratio of the maintenance of the AMF (Becklin et al., 2012).

(b) A predominant interplant resource transfer through CMN (Fig. 2 b). This scenario is similar to the previous one, but now both plant species can benefit from the transfer of complementary resources through a CMN. Independently on the amount of resources transferred, any amount of a complementary resource might result in positive effects for both plants, enhancing mutualistic plant-plant interactions. This scenario will be likely between plant species where each of them harbor both EMF and AMF. This will enable a high dissimilarity in the resources provided, while enhancing the probability of establishment of a CMN potentially enhancing interplant resource transfer through it. Interactions between plant species within the families Oleaceae, Rubiaceae, Nyctaginaceae, Polygonaceae or Myrtaceae, which harbor the two types of mycorrhizas (Wang and Qiu, 2006), might be prone to result in positive plant-plant interactions.

However, mycorrhizal symbiosis is context-dependent, and therefore so are its effects on plant-plant interactions. For instance the performance of MF can be decoupled from their host plant in environments with high nutrient loading, where nutrients availability can alter the cost and benefits which each partner incurs from interacting (Shantz et al., 2016). In this case, the positive plant-plant interactions resulting from associating with a CMN and non-shared MF might be weaker.

When the dissimilarity in the resources provided is negligible (i.e. non-shared MF are acquiring and providing the same resources to their host plants), asymmetric effects will result in a shift from neutral to antagonistic plant-plant interaction. Two different ecological contexts can be associated with the combination of negligible dissimilarity in the resources provided with:

(c) A negligible interplant resource transfer through a CMN (Fig. 2 c). This might be the case in interactions between plant species associated with the same type of MF (i.e. EMF or AMF), and a predominance of fungal species that do not enhance interplant connections. In the case of AMF, this can occur when the dominant MF tend to produce more intra-radical than extra-radical hyphae, such as Glomeraceae (Hart and Reader, 2002; Varela-Cervero et al., 2016), thus reducing the likelihood of forming anastomoses among hyphal networks. A reduction of interplant resource transfer through CMN among ectomycorrhizal plants can be due to the predominance of tree species which interact with a low number of fungal species. This is the case of alder which associates with 50 known EMF (Pritsch et al., 1997), compared to Douglas fir which can be associated to 2000 MF (Molina and Trappe, 1982).

In this scenario, a neutral plant-plant interaction can still emerge when non-shared MF show a low asymmetry in fungal competition for the same resources (Fig. 2 c1). Different competitive abilities between fungal species can be balanced if the persistence of fungal species depends on non-hierarchical competitive relationships, so that no single species outcompetes all the others. Simulation approaches show that these non-hierarchical competitive relationships are more prone to emerge at high fungal species richness (Maynard et al., 2017), and thus neutral plant-plant interactions might be more likely when plants are associated with MF-rich communities. However, in fungal communities with a low fungal richness, hierarchical competitive relationships might be more prone to occur, potentially resulting in antagonistic plant-plant interactions (Fig. 2 c2). In addition, these processes can be influenced by intra-guild competitive and facilitative interactions (Valiente-Banuet and Verdú, 2013; Maynard et al., 2017) which can in turn affect the community structure of the other guild.

(d) A predominant interplant resource transfer through a CMN (Fig. 2 d). This scenario might be likely in plant-plant interactions where plant species interact with the same type of

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MF increasing the likelihood of forming a CMN, and the predominant MF have traits that enhance interplant resource transfer through a CMN. For instance, AMF communities dominated by Gigasporaceae, which tend to produce extraradical hyphae (Hart and Reader, 2002; Varela-Cervero et al., 2016), or species such as *Glomus claroideum* which tend to have anastomoses in its hyphal network (Thonar et al., 2011). In contrast, species of Gigasporaceae that more often produce anastomoses within the same hyphae, might be less likely to form CMN (de la Providencia et al., 2005). In the case of EMF, the likelihood of forming a CMN with neighbor plants can be enhanced when the interacting plant species have a broad range of MF partners, such as Douglas fir (Molina and Trappe, 1982), enhancing the probability of interplant resource transfer through CMN.

In this case, either asymmetries in interplant resource transfer through a CMN and/or in fungal competition for the same resources can result in a shift from a neutral to an antagonistic interaction. A neutral interaction might result when there is a low asymmetry in both processes (Fig. 2 d1). When transfer is driven by source sink gradients (Montesinos-Navarro et al., 2017), a low asymmetry in interplant resource transfer through a CMN is expected in plant communities dominated by closely related plant species, which share similar resource acquisition strategies and thus are not prone to generate steep gradients of nutrients between them. This scenario is likely in highly stressful environments where lineages with similar traits to acquire resources have been selected, such as Cactaceae in deserts or other succulent plants in salt marshes (i.e. some Chenopodiaceae). On the other hand, a high asymmetry in interplant resource transfer through CMN can emerge in plant-plant interactions where plant species generate steeper resources gradients (Fig. 2 d2). This might be the case of plant interactions with hemiparasitic plants, which maintain more negative water potential than their hosts by an elevated transpiration rate and an abnormal behavior of stomata which do not close even in dark or under water stress conditions (Tesitel et al., 2010). This results in a transfer of solutes as a passive mass flow driven by a water potential gradient between the host and the parasite (Tesitel et al., 2010). In the similar case of myco-heterotrophic plants, the asymmetric interplant resource transfer through a CMN (Merckx et al., 2009) is likely to shift plant-plant interactions to an antagonism.

6. Conclusions and new avenues of research

The proposed framework decomposes the influence of MF on plant-plant interactions into two relevant processes. This framework is intended to facilitate its mechanistic understanding by organizing the accumulated knowledge within a general context, although the final outcome of plant-plant interactions will be context-dependent. We propose that the combination of interplant resource transfer through CMN and the dissimilarity in the resources provided by MF can result in different outcomes of plant-plant interactions. Interplant resource transfer occurs through CMN, while contrasting resources might be more likely provided by non-shared MF. When non-shared MF provide the same resources to their hosts, asymmetries in interplant resource transfer through CMN, and in fungal competition for the same resource, can shift the outcome of plant-plant interactions from neutral to antagonistic.

In the development of the proposed framework we identify research topics that could efficiently contribute to a mechanistic understanding of the effects of MF on the outcome of plant-plant interactions. Firstly, further research is required to elucidate the patterns of specificity of plant-MF interactions and to assess their potential underlying mechanisms (Fig. 3). Whole-genome sequencing has allowed the detection of suites of genes shaping specificity within ecto-mycorrhizal associations (Martin et al., 2008, 2010), by affecting mechanisms regulating the exudation of distinct chemical signals into the rhizosphere (Churchland and Grayston, 2014). However, the factors involved in the specificity of plant-AMF associations, occurring in approximately 85% of plant species, are just beginning to be understood (Brachmann and Parniske, 2006; Bonfante and Genre, 2010; Churchland and Grayston, 2014). Exploring whether generalist or specialist MF tend to share certain traits, can be useful for discovering the mechanisms underlying specificity. Secondly, further information about how interplant resource transfer through CMN is regulated, and potential asymmetries on resource distribution (Fig. 3), is essential for understanding the effect of MF on plant communities. Identifying plant traits or plant community properties that can condition asymmetries in interplant resource transfer through CMN, will also provide a more complete understanding of the ecological contexts in which certain plant-plant interaction outcomes are more prone to occur. Further research is also necessary on the fungal traits that can condition the distinctiveness of the benefits provided by MF to their hosts, and how this can affect competition processes among them. In the case of EMF, interesting experiments have shed light into the potential niche differentiation of EMF by studying the activity patterns of different EMF morphotypes exposed to a variety of organic sources (e.g. organic soil, mineral soil, or dead woody debris), measuring several enzymatic reactions involved in decomposition of organic compounds (Buée et al., 2007). There is less information about AMF in this regard, but similar approaches can be useful to cover this gap of knowledge. Finally, although interplant resource transfer through CMN and the functional complementarity in the resources provided by MF have received considerable attention they have been usually approached independently. Studying in the interaction between these two processes simultaneously is necessary for understanding potential synergic effects on plant-plant interactions.

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