Plant facilitation through mycorrhizal symbiosis is stronger between distantly related plant species

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Summary

- The tendency of closely related plant species to share natural enemies has been suggested to limit their co-occurrence and performance, but we lack a deep understanding on how mutualistic interactions such as the mycorrhizal symbiosis affect plant–plant interactions depending on the phylogenetic relatedness of the interacting plants. We hypothesise that the effect of the mycorrhizal symbiosis on plant–plant facilitative interactions depends on the phylogenetic distance between the nurse and facilitated plants.

- A recently published meta-analysis compiled the strength of plant facilitative interactions in the presence or absence (or reduced abundance) of mycorrhizal fungi. We use phylogenetically informed Bayesian linear models to test whether the effect size is influenced by the phylogenetic distance between the plant species involved in each plant facilitative interaction.

- Conspecific facilitative interactions are more strongly enhanced by mycorrhizal fungi than interactions between closely related species. In heterospecific interactions, the effect of the mycorrhizal symbiosis on plant facilitation increases with the phylogenetic distance between the nurse and facilitated plant species.

- Our result showing that the effect of mycorrhizal symbiosis on the facilitation interactions between plants depends on their phylogenetic relatedness provides new mechanisms to understand how facilitation is assembling ecological communities.

Introduction

The mechanisms shaping plant communities have intrigued ecologists since the origins of the discipline (Watt, 1947; Rolhauser & Pucheta, 2017). A greater intensity of negative interactions between close relatives has been traditionally invoked to explain plant community structure (Valiente-Banuet & Verdú, 2013). Janzen (Janzen, 1970) and Connell (Connell, 1971) formally hypothesised that host-specific natural enemies can maintain tree species diversity in tropical forests by reducing the seedling performance near the parent tree (Bagchi *et al.*, 2014). This idea was expanded by Webb *et al.* (2006) shifting from a single conspecific/heterospecific dichotomy to a continuous gradient of phylogenetic relatedness. Since then, there has been an increasing interest on using phylogenetic relatedness to predict the outcome of plant interactions (Verdú *et al.*, 2012). Several authors have tested whether seedling performance is negatively correlated with the phylogenetic relatedness between neighbours (Castillo *et al.*, 2010; Metz *et al.*, 2010; Paine *et al.*, 2012; Lebrija-Trejos *et al.*, 2014), usually appealing to enemy-mediated mechanisms. The probability of sharing an enemy will decrease with the phylogenetic distance between hosts (Parker & Gilbert, 2004; Novotny *et al.*, 2006; Gilbert & Webb, 2007), as closely related species

may share traits that enhance their vulnerability to the same enemies (Mitter *et al.*, 1991; Gómez *et al.*, 2010). Although more rarely considered, positive interactions like plant facilitation and the mycorrhizal symbiosis, have also shown to follow a phylogenetic pattern that can be used to explain plant community structure (Montesinos-Navarro *et al.*, 2012a, 2016a, 2018a).

Mycorrhizal symbiosis can influence facilitative interactions among plants (Callaway *et al.*, 2001; Callaway, 2007; Montesinos-Navarro *et al.*, 2012a), defined as plant–plant interactions in which one plant (facilitated) gets a benefit from growing associated with another, without resulting in any disadvantage for the latter (nurse) (Callaway, 2007). Contrary to enemies-mediated mechanisms shaping plant co-occurrence, the presence of conspecifics or closely related species may counterbalance competition between close relatives by increasing the abundance of shared symbionts in the rhizosphere. However, the expected effect of the mycorrhizal symbiosis on facilitative plant interactions might differ between conspecific and heterospecific plant interactions if species specificity in plant–fungi interactions exists. Although there is no consensus on whether closely related plant species tend to interact with similar mycorrhizal symbionts (Montesinos-Navarro *et al.*, 2012a; Reinhart & Anacker, 2014; Veresoglou & Rillig, 2014; Chen *et al.*, 2017), it is increasingly

recognised that these interactions are more species specific than previously considered (Gollotte *et al.*, 2004; Tedersoo *et al.*, 2008; Montesinos-Navarro *et al.*, 2012b, 2018a). Therefore, facilitative interactions between conspecific plants, unlike those between heterospecific plants, might provide a higher abundance of shared mycorrhizal fungi potentially increasing seedling survival (Dickie *et al.*, 2002; Teste *et al.*, 2009; Booth & Hoeksema, 2010). A particular case of conspecific interaction is facilitation between individuals with different degrees of kinship. Seedlings can preferentially transfer carbon (C) to their full-siblings through shared common mycorrhizal fungi (Pickles *et al.*, 2017), potentially mediated by the recognition of specific root exudates that can allow the detection of offspring's roots (Biedrzycki *et al.*, 2010). At present it is unknown whether kin recognition mechanisms can be also at work in plant–plant interactions.

The effect of the mycorrhizal symbiosis on the outcome of heterospecific facilitation can be influenced by the phylogenetic distance between the nurse and facilitated species through two main factors: (1) mycorrhizal fungi can provide dissimilar resources to distantly related host plants, and (2) mycorrhizal fungi can enhance interplant resource transfer between distant relatives (Montesinos-Navarro *et al.*, 2018a). Major plant lineages differ in their ability for resource acquisition (Cornwell *et al.*, 2014), potentially demanding different resources to their associated fungal community. In addition, distantly related species can create steeper resource gradients that promote nutrient exchange between them (Montesinos-Navarro *et al.*, 2017), in part mediated by shared mycorrhizal fungi that allow nutrient movement from nutrient-rich to nutrient-poor environments (Bethlenfalvay *et al.*, 1991; Frey & Schüepp, 1993). However, a myriad of different mechanisms mediated by mycorrhizae may also affect plant interactions (Montesinos-Navarro *et al.*, 2018a), blurring the expected pattern of enhanced facilitation with phylogenetic distance between plant species. Nevertheless, in nature, there is a pervasive pattern of successful facilitation between distantly related plants (Valiente-Banuet & Verdú, 2007, 2008).

In this study, we used data compiled in a recently published meta-analysis to hypothesise that the effect of the mycorrhizal symbiosis on plant–plant facilitative interactions depends on the phylogenetic distance between the nurse and facilitated plants. We specifically tested whether the effect of mycorrhizal symbiosis on plant facilitation: (1) differs between conspecific and heterospecific interactions; and (2) depends on the phylogenetic distance between the nurse and facilitated species.

Materials and Methods

Database compilation

We used the data from a meta-analysis focused on the effect of the mycorrhizal symbiosis on plant biomass and nutrient content of facilitated plants (Montesinos-Navarro *et al.*, 2018b). This meta-analysis provides a thorough description of the data in terms of distribution of data across ecosystems, mycorrhizal type (arbuscular or ectomycorrhiza), performance variables measured and the full reference of the papers used. The response variable compiled was the performance of the facilitated plant measured in 'control' and 'treated' environments, the 'control' environment being places where mycorrhizal abundance was higher than in its 'treated' pair. Two more papers with relevant data were found and added to the database (Borchers & Perry, 1990; Onguene & Kuyper, 2002). Finally, we discarded cases in which the identity of the nurse species was unknown. The database resulted in 215 cases from 19 studies (Supporting Information Table S1). We also assessed whether the database used can be considered a representative sample of the phylogenetic distances between species in which facilitative interactions have been reported. To do so, we compiled the pairwise interactions reported in two revisions of plant facilitative interactions (Bonanomi *et al.*, 2011; de Toledo Castanho *et al.*, 2015) that included 2127 facilitative interactions between 1650 plant species, and estimated the phylogenetic distances between each pair using the methodology described in the following section. As shown in Fig. S1, the distribution of the phylogenetic distances in our database matched very well that in the overall database of facilitative interactions, indicating that our database is a representative sample of the phylogenetic distances between plants involved in facilitative interactions published in the literature. Future research on facilitation covering under-represented phylogenetic distances will help to support or refute the patterns found here.

Phylogenetic distances between plant species

The phylogenetic relationships among the plant species were generated with the R function S.PHYLOMAKER (Qian & Jin, 2016). It uses the PhytoPhylo backbone megaphylogeny, which is an updated and expanded version of the time-calibrated angiosperm species-level phylogeny (Zanne *et al.*, 2014). The community phylogeny was produced by matching the family names of the plant species in our database with those in the backbone phylogeny, using the R package APE (Paradis *et al.*, 2004). Then, we used a database compiling expert-knowledge in molecular time estimates of divergence among taxa (TimeTree: http://www.timetree.org/) to extract the confidence interval of the age estimate for each node, and used it to calibrate the tree by performing a branch smoothing using the 'chronos' function in the APE package implemented in the software R v.3.2.2 (Paradis *et al.*, 2004; R Core Team, 2015). To account for the uncertainty of age estimates, we iterated the branch smoothing 100 times to generate 100 phylogenies. The branch lengths of those phylogenies were constrained by the confidence interval of each node's age. For each of the 100 phylogenies, the phylogenetic distance between the nurse and facilitated species was obtained using the 'cophenetic' function in the APE package (Paradis *et al.*, 2004).

Effect size

We calculated the facilitated species' performance under controlled or treated conditions to assess the effect size using Hedges' g standardised mean difference (Hedges, 1981), and used large-sample approximation to compute the sampling variances (Viechtbauer, 2015). Hedges' g can be defined as the difference between the mean of the control and treated individuals, divided

by the pooled and weighted standard deviation. This metric quantifies the increment (if positive) or decrement (if negative) in the benefits that the facilitated plant obtained from its nurse in an environment with a higher abundance of mycorrhizal fungi. Hedges' g metric and the sampling variance for each case were calculated using the function ESCAL in the package METAFOR (Viechtbauer, 2015) in R v.3.5.2 (R Core Team, 2015).

Statistical analyses

The estimated I^2 index of heterogeneity (Higgins & Thompson, 2002) reported in Montesinos-Navarro *et al.* (2018b) showed that the effect size's variation cannot be fully explained by measurement error. Therefore, other sources of variation can be explored, and we tested whether the effect size of mycorrhizae on plant facilitative interactions can be explained by the phylogenetic distance between the nurse and the facilitated species. First, we assessed whether the effect of mycorrhizal fungi on plant facilitative interactions was similar in conspecific and heterospecific interactions at different phylogenetic distances. We classified the phylogenetic distances between interacting plant species into: conspecifics (i.e. phylogenetic distance 0 Myr), species within the same clade (monocots, dicots or gymnosperms) (< 300 Myr), species from close clades (one monocot and one dicot) (300–500 Myr), and species from distant clades (one gymnosperm and one angiosperm) (> 500 Myr). Then we fitted a Bayesian linear model with the effect size as the response variable and the categorised phylogenetic distances as the explanatory variable, and post-hoc tests between each pair of relatedness categories to assess differences between them. Second, we tested whether the effect size of mycorrhizae on plant facilitative interactions can be explained by the phylogenetic distance between the nurse and the facilitated species. We considered only heterospecific interactions if conspecific and heterospecific interactions showed different patterns in the previous test. For this, we fitted a phylogenetically informed Bayesian linear model with the effect size as the response variable and the phylogenetic distance between the nurse and the facilitated species as explanatory variable. Previous studies suggested that the phylogenetic patterns observed in plant facilitative interactions were more usually driven by the facilitated than by the nurse species (Verdú *et al.*, 2010, 2012). Therefore, we informed the model with the phylogenetic relationships among facilitated species, and included the original paper and the identity of the facilitated species as random factors. We also tested for the significance of considering the phylogeny of the facilitated plants by repeating the analyses without considering it, and compared the deviance information criterion (DIC) of both models. For each model, we reported the probability that the estimate was higher than 0, expressed in %, and its credibility interval (CI). In each Bayesian model we used a prior with an expected mean value of $mu = 0$ and a (co)variance matrix of $V = I \times 1e + 10$, where I is an identity matrix of appropriate dimension. Models were weighted by the inverse of the sampling variance of each case. The settings were chosen to store at least 1000 MCMC (Markov chain Monte Carlo) iterations with an autocorrelation between successive stored iteration < 0.1. This

was usually reached using 13 000 iterations, thinned every 10 and discarding a burn-in period of 25% of the iterations. To account for the uncertainty in node age estimates, each model was repeated 100 times using, in turn, each of the 100 phylogenies. Then, the 100 MCMC were integrated by concatenating a random sample of estimates across all of them. Bayesian models were performed using the package MCMCGLMM (Hadfield, 2010). Only two records in our database involve a plant–plant interaction with a phylogenetic distance above 500 Myr mediated by arbuscular mycorrhizal fungi. To discard that the phylogenetic patterns could be confounded with the type of mycorrhizal fungi, we also tested for the relationship considering only plant–plant interactions mediated by ectomycorrhizal fungi.

Data availability

The data used in this study is provided as Table S1.

Results

Our database compiled 215 cases published in 19 studies, in which the pairwise interactions of 26 nurse species and 21 facilitated species were reported (Table S1). The phylogenetic distance between the nurse and the facilitated species (i.e. twice the time since the two species diverge from their common ancestor) in the cases of heterospecific facilitation ranged from 29.1 Myr to 669 Myr.

The effect of the mycorrhizal symbiosis on plant facilitation depended on whether the interaction occurred between conspecifics or heterospecifics across different phylogenetic distances between them. The mycorrhizal symbiosis enhanced facilitation between conspecifics (mean = 1.25; 99% CI = 0.85, 1.67), while the effect size between heterospecifics belonging to the same clade (either within monocots, dicots or gymnosperms) had a mean of −0.29, with a low probability of being different from zero 61% CI = −0.60, −0.06). Between heterospecifics from distant clades (a gymnosperm with an angiosperm), the mycorrhizal symbiosis enhanced facilitation even more than between conspecifics (mean = 2.38; 99% CI = 1.55, 3.35). There was not a significant difference between conspecific interactions and those between species from close clades (mean = 0.96; 99% CI = 0.23, 1.60) (Fig. 1). When we considered only interactions mediated by ectomycorrhizal fungi, the same pattern emerged (conspecifics: mean = 1.31; 99% CI = 0.97, 1.61; heterospecifics in the same clade: mean = −0.41; 99% CI = −0.89, −0.02; heterospecifics in distant clades: mean = 2.35; 99% CI = 1.76, 3.01). None of the interactions between plant species from close clades was mediated by ectomycorrhizal fungi.

The effect size tended to be stronger in cases in which heterospecific interacting species were distantly related (Fig. 2). The Bayesian models showed that the effect size of mycorrhizae on plant facilitation significantly increased with the phylogenetic distance between the nurse and the facilitated species (mean effects size = 0.009; 99% CI = 0.005, 0.01). The phylogenetic relationship between the facilitated species did not contribute significantly to improve the model accuracy, shown by the similar

Fig. 1 The effect of mycorrhizal symbiosis on conspecific and heterospecific plant facilitation with different phylogenetic distances between the two plant species involved. Conspecific relationships are presented on the left and heterospecific interactions on the right of the dashed line. Heterospecific interactions are classified as: species within the same clade (either within monocots, dicots or gymnosperms) (< 300 Myr), species from close clades (one monocot and one dicot) (300–500 Myr), and species from distant clades (one gymnosperm and one angiosperm) (> 500 Myr). In the inset, divergence time between species is expressed as millions of years ago (Ma) and orange, blue and white rectangles group pairs of species within clade, from close and distant clades, respectively. The icons represent from top to bottom: gymnosperms, monocots (e.g. Poaceae), and dicots (e.g. Fagaceae). Significant differences in the mean effect size (mean ± SE) between interactions across phylogenetic distances, quantified as Hedges' g standardised mean difference, are represented by different letters. Sample size in brackets. Phylogenetic distance between two species in millions of years (Myr) is twice the time since they diverged from their most common ancestor.
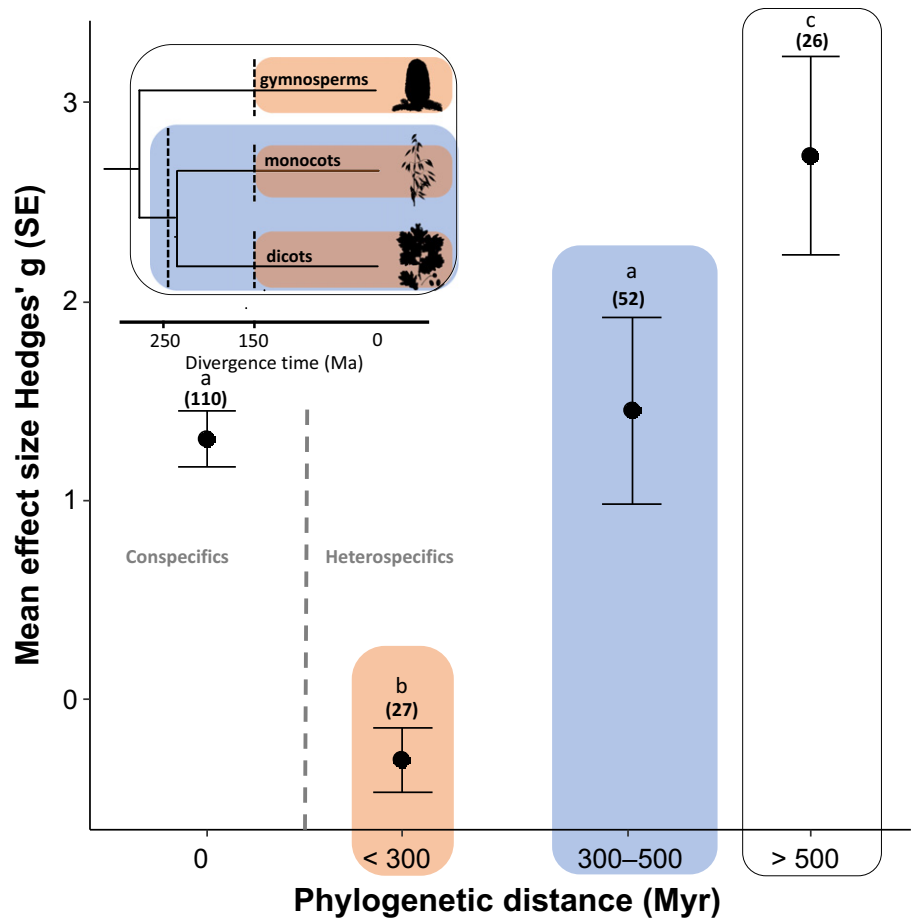
DIC found in the model considering (DIC = 352) and not considering (DIC = 354) the phylogeny. Therefore, there are not specific clades driving the pattern observed. The positive relationship between the phylogenetic distance between the nurse and facilitated species and effect size was also maintained with 86% of probability when only the interactions mediated by ectomycorrhizal fungi were taken into account (mean effects size = 0.004; 86% CI = 0.001, 0.007).

Discussion

Our meta-analysis revealed that the enhancement of plant facilitation by the mycorrhizal symbiosis increased with the phylogenetic distance between the heterospecific interacting plants. Plants facilitated by conspecifics benefit more from a higher abundance of mycorrhizal fungi than plants facilitated by closely related heterospecifics (i.e. both species belonging to the same monocot, dicot or gymnosperm clades). In heterospecific interactions, the benefits gained by the facilitated plant increases when the plant is growing with a distant relative, and this pattern is independent of specific families or clades.

In our database and in plant facilitative interactions in general, the most common gymnosperms belonged to the Pinaceae family (57% of the interactions involving gymnosperms reported in Bonanomi *et al.*, 2011; de Toledo Castanho *et al.*, 2015). This results in a predominance of Pinaceae, when one of the interacting plants is a gymnosperm (i.e. interactions between distant relatives in our database), which are usually associated with ectomycorrhizal fungi. The enhancement of plant facilitation by the mycorrhizal symbiosis between distant relatives might be influenced by the predominance of ectomycorrhizae in these particular interactions. However, this seems unlikely considering that this relationship is maintained when only interactions mediated by ectomycorrhizal fungi are considered across all phylogenetic distances. Unfortunately, facilitative interactions mediated by arbuscular mycorrhizal fungi between distant relatives are less frequent in the literature, this situation prevents testing for the correlation that considers only arbuscular mycorrhizal fungi-mediated interactions. Further research on arbuscular mycorrhizal gymnosperms will allow the comparison of its effect on both close and distant relatives within this clade, due to a wider range of divergence time between species in this clade.

The contrasting pattern between interactions involving conspecifics and closely related plant species suggested that different mechanisms through which the mycorrhizal symbiosis enhances plant facilitation are acting. Several mechanisms that might specifically enhance facilitation between conspecifics but not closely related species are: (1) shared mutualists, (2) shared defenses, and (3) showed kinship selection. Considering that certain specificity in plant–mycorrhizal fungi interactions is

Facilitated species   Nurse species
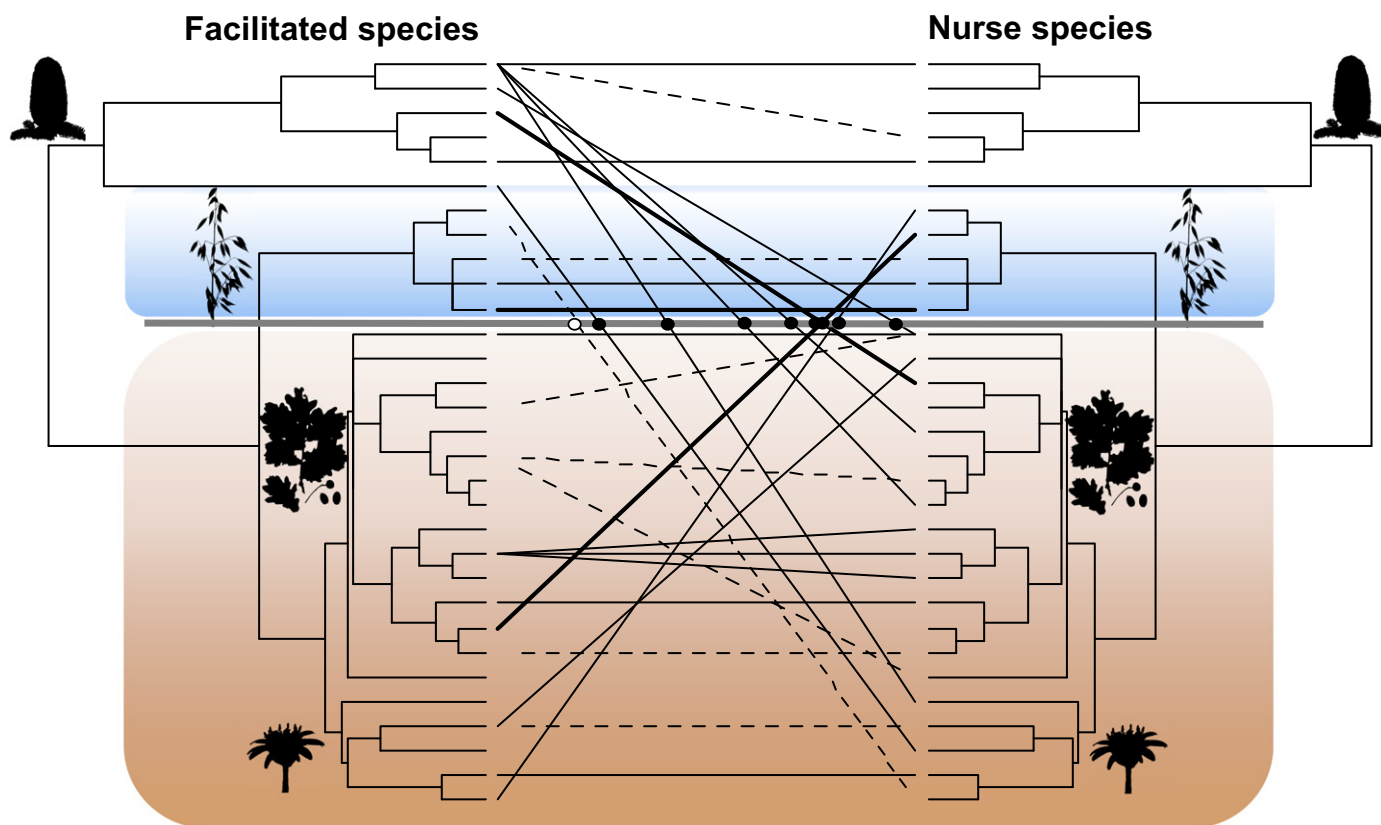
Fig. 2 The effect size of mycorrhizal symbiosis on plant facilitation interactions between plant species with different phylogenetic distance. The phylogenetic trees represent the relationship between all the plant species included in the meta-analysis (full species names are presented in Supporting Information Table S1). Facilitated and nurse plants are presented on the left and right trees, respectively. The icons identify from top to bottom: gymnosperms, monocots (i.e. Poaceae), and two families of dicots (i.e. Fagaceae and Asteraceae). Links between the two phylogenies represent the presence of a given pairwise plant–plant interaction in our data set, and the thickness of the links represent the logarithm of the arithmetic weighted mean of the effect size across all the cases where the specific plant–plant interaction was measured. Solid and dashed lines represent positive (facilitation is enhanced by mycorrhizae) and negative (facilitation is reduced by mycorrhizae) values, respectively. Lines crossing the grey horizontal bar correspond to interactions between distant relatives, as one of the two species involved is a dicot (highlighted in orange), and the other is outside that clade. Black points highlight facilitation between distant relatives enhanced by mycorrhizae (i.e. solid links crossing the grey bar) and white points represent facilitation between distant relatives reduced by mycorrhizae (i.e. dashed links crossing the grey bar). The predominance of black vs white points indicates that mycorrhizae promote facilitation between distant relatives (see the Results section for statistical tests).

increasingly recognised, both in arbuscular and ectomycorrhizal fungi (Gollotte *et al.*, 2004; Tedersoo *et al.*, 2008; Montesinos-Navarro *et al.*, 2012b, 2018a), conspecific plants will provide the same symbionts with which the facilitated plant interacted, therefore increasing the abundance of symbionts in the shared rhizosphere. Another potential mechanism can be influenced by mycorrhizal protection against pathogens: ectomycorrhiza may protect the external layers of the roots with their structures while arbuscular mycorrhizae can trigger systemic defense mechanisms (Pozo & Azcón-Aguilar, 2007; Bennett *et al.*, 2017). Mycorrhizal symbiosis, especially ectomycorrhiza, has been suggested to reduce conspecific competition due to pathogen protection, with closely related plant species having a similar sensitivity to conspecific/heterospecific competition (Bennett *et al.*, 2017). Finally, other mechanisms affecting only conspecific interactions are those related to the facilitation associated with kinship. Seedlings connected through ectomycorrhizal fungi can transfer a threefold amount of ^{13}C to full-siblings than to nonsibling pairs, potentially mediated by root exudates (Pickles *et al.*, 2017).

Plants can also recognise kin neighbours and horizontally reoriented leaf growth to avoid competition mediated by the perception of the vertical red/far-red light and blue light profiles (Crepy & Casal, 2015). Moreover, volatiles have been suggested to allow self-recognition, inducing a higher resistance to herbivory when volatile cues are emitted from genetically identical cuttings; this could be a first step towards kin recognition (Karban & Shiojiri, 2009; Karban *et al.*, 2013). Further research is needed to unravel the relative contribution of each mechanism to explain the positive effects of mycorrhizae on conspecific facilitation.

Regarding heterospecific interactions, our model estimated that the effect size of the mycorrhizal symbiosis on plant facilitation will increase by 0.9 if the phylogenetic distance between the nurse and the facilitated species was 100 Myr greater (estimate of the slope = 0.009 effect size increase per year). To show the biological meaning of this increase in effect size, we will exemplify it using total plant biomass. The mean and averaged standard deviations of the control plants' biomass were 3.2 g and 2.8 g, respectively. An effect size of 0 implied that both control and treated

plants had a similar biomass, therefore 3.2 g. Then, based on a simplified definition of the Hedges' g (effect size = mean control − mean treated/standard deviation) we can calculate the estimated plant biomass of the treated plants if the effect size was 0.9 (i.e. 3.2 − (0.9 × 2.8) = 0.68 g). Therefore, we can state that when mycorrhizal symbiosis is present, the facilitated plant biomass can increase by 78% when growing with a nurse that is 100 Myr more phylogenetically distant to it than the other ((3.2 − 0.68)/ 3.2 × 100) = 78%).

Some mechanisms could result in a mycorrhizae-mediated enhancement of facilitative interactions between distant relatives: (1) nutrient transfer through common mycorrhizal networks; and (2) reduced competition. Common mycorrhizal networks can connect plant roots of different plant species and families (Selosse *et al.*, 2006). These connections can allow the transfer of a wide diversity of compounds between plants, including nutrients such as C, N and P (He *et al.*, 2009; Ren *et al.*, 2013; Song *et al.*, 2015). Nutrient transfers from rich-nutrient to poor-nutrient plants (Bethlenfalvay *et al.*, 1991; Frey & Schüepp, 1993). The foliar content of nutrients such as N and P are likely to be phylogenetically conserved, as several traits involved in nutrient acquisition are strongly phylogenetically conserved (i.e. N_2 fixation through rhizobium symbiosis or clustered roots that improve P uptake) (Stock & Verboom, 2012; Cornwell *et al.*, 2014; Yang *et al.*, 2015). This can result in steep nutrient gradients between distantly related plant species that, in the case for N, has been shown to result in an increase in N transfer among distant relatives (Montesinos-Navarro *et al.*, 2017). Although this transfer can occur through different pathways besides mycorrhizal connections, a high abundance of mycorrhizal fungi in the soil has been shown to promote nutrient transfer between plants involved in facilitative interactions (Montesinos-Navarro *et al.*, 2016b).

Reduced competition between distant relatives is thought to be the most common mechanism that allows plants to coexist (Valiente-Banuet & Verdú, 2007; Castillo *et al.*, 2010; Pausas & Verdú, 2010). A balance between the benefits of reduced competition between distant relatives and a higher abundance of shared mycorrhizal fungi between conspecific can result in the observed pattern of similar benefits for the facilitated plant when they grow with conspecific and with intermediate distant relatives. Interactions with species from close clades might lack the benefits of conspecific interactions, and it is currently under debate whether plant−mycorrhizal fungi interactions are evolutionarily conserved (Montesinos-Navarro *et al.*, 2012a; Reinhart & Anacker, 2014; Veresoglou & Rillig, 2014; Chen *et al.*, 2017). In addition, a contrasting effect of plant–plant interactions along gradients can be due to shifts in the net effects of each component, and partitioning these net effects into each component can contribute to understanding the underlying mechanisms (Michalet *et al.*, 2014). The presence of the mycorrhizal symbiosis (i.e. control cases) could increase the benefits between distant relatives due to poorer performance of the plants without mycorrhizae (i.e. treated) or due to increased performance of the plants with mycorrhizae (i.e. control). Further experiments exposing the same target species across a wide phylogenetic context (i.e.

phylogenetic distances between the nurse and facilitated between 300 and 669 Myr) would be necessary to disentangle the underlying mechanisms.

Other mechanisms linking mycorrhizal symbiosis and plant facilitation might now be revisited under the plant phylogenetic perspective. For example, the well known mechanism in which mycorrhizal fungi promote heterospecific facilitation is the provision of inoculum, including reduced costs of establishing an extensive fungal mycelium (Newman, 1988). Through this mechanism, pioneer plants facilitate later successional plants (Dickie *et al.*, 2004; Nara & Hogetsu, 2004; Nara, 2006), a pattern that usually occur between distantly related species (Verdú *et al.*, 2009).

In short, this meta-analysis reveals that mycorrhizal symbiosis enhances facilitative interactions between conspecifics and also between distant relatives, and proposes some mechanisms consistent with this observation. Our results can contribute to a better understanding of the phylogenetic patterns imprinted by facilitation, an interaction, increasingly recognised as a relevant mechanism structuring plant communities.

Author contributions

AM-N, AV-B and MV planned and designed the research. AM-N compiled and analysed the data, and wrote the first draft of the manuscript. All authors contributed to the last version of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Comparison between the distribution of the phylogenetic distances between plant species used in this study and those reported in facilitation literature.

Table S1 Dataset including the pair-wise plant–plant interactions used in this study, the references from which they were obtained and other plant–plant interactions compiled from facilitation literature to contextualise the dataset.

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