# Seed plant families with diverse mycorrhizal states have higher diversification rates

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## Abstract

One crucial innovation in plant evolution was the association with soil fungi during land colonization. Today, this symbiotic interaction is present in most of plants species and can be classified in four types: Arbuscular (AM), Ecto (EM), Orchid (OM) and Ericoid Mycorrhiza (ER). Since the AM ancestral state, some plants lineages have switched partner (EM, OM and ER) or lost the association (no-association: NM). Evolutionary transitions to a novel mycorrhizal state (MS) might allow plant lineages to access new resources, enhancing diversification rates. However, some clades are not restricted to one MS, and this variability might promote diversification. In this study we address the relationship between MS and plant diversification rates of seed plant families. For this, we compiled a database for ~6400 seed plant species and their mycorrhizal partners. We assigned a single MS to each plant family, then calculated the heterogeneity of MS and estimated their diversification rates using the method-of-moments. Families with mixed MS had the highest diversification rates and there was a positive relationship between heterogeneity of MS and diversification rates. These results support the hypothesis that MS plasticity promotes diversification and highlight the importance of the association with soil fungi for the diversification of plants. Keywords: diversification rates, mycorrhizal states, seed plants, key innovation, mycorrhizal diversity

# Introduction

Understanding the basis of the exceptional plant diversity has been a matter of interest for ecologist and evolutionary biologist since Darwin. Great focus has been placed on estimating plants diversification rates and identifying the factors that could influence them (Eriksson & Bremer, 1992; Moore & Donoghe, 2007; O´Meara et al., 2016; Vamosi et al., 2018). The acquisition of novel traits (sometimes referred to as “key innovations”), such as pollination by animals (Eriksson & Bremer, 1992) or physiological seed dormancy (Willis et al., 2014), have been proposed to promote diversification of plant lineages. This “key innovation” perspective suggests that the acquisition of a novel trait might allow a given lineage to exploit the environment in a significantly different way, potentially resulting in an explosive radiation.

One crucial innovation in plants evolution was the association with soil fungi during land colonization (Pirozynski & Malloch, 1975; Selosse & Le Tacon, 1998). Before plant colonization, land was hostile, with extreme drought and temperatures, and barren rocky substrate; hence, the association with terrestrial fungi allowed the algae ancestors of plants to successfully colonize the land (Selosse et al., 2015). This initial symbiotic association was the prelude of modern mycorrhizas (Feijen et al., 2018), the association between fungi and root plants in which plants transfer carbon to fungi and receive nutrients in turn (Smith & Read, 2008). Today, this symbiosis is present in 86% of land plants species (van der Heijden et al., 2015), and based on their structure and function can be classified in four major types: arbuscular mycorrhiza (AM), ectomycorrhiza (EM), orchid mycorrhizal (OM) and ericoid mycorrhizal (ER) (Brundrett, 2002).

Ancestral state reconstruction and the fossil record show that the ancestor of seed plants probably had AM associations (Redecker et al., 2002; Maherali et al., 2016). This is the most frequent mycorrhizal type in plants (74% of extant plant species) and is characterized by an association with Glomeromycete fungi (van der Heijden et al., 2015). Between 100 and 200 million years ago, some lineages switched fungal partners to several lineages of Basidiomycetes, forming what is described as the EM associations (Brundrett, 2002). The acquisition of EM resulted in new root functional capabilities as freezing tolerance (Lehto et al., 2008), which seem related to the dominance of EM angiosperms and gymnosperm in cool forests (Brundrett, 2002). Similarly, Orchidaceae and species within the Ericaceae family recruited new fungal lineages and

formed OM and ER associations respectively. Orchids associate with fungal families Ceratobasidiaceae, Tulasnellaceae and Sebacinaceae, which in addition to nutrient exchange, promote seed germination which cannot germinate without mycorrhizal support (Rasmussen, 2002). Ericoid mycorrhizal associations (ER), on the other hand, involve mainly fungi from Sebacinales and Helotiales and are mostly frequent under acidic and infertile heathland conditions (Perotto et al., 2002; van der Heijden et al., 2015). Finally, some lineages have lost their mycorrhizal associations and became non-mycorrhizal (NM). This transition has frequently occurred through an intermediate state of facultative arbuscular mycorrhiza (AM) plants (Maherali et al., 2016). Some of NM lineages evolved alternative resource-acquisition strategies (Werner et al., 2018) like cluster-roots in Proteaceae (Neumann & Martinoia, 2002) or parasitism in Loranthaceae (Wilson & Calvin, 2006).

Therefore, since the AM ancestral state some plant lineages have followed different mycorrhizal evolutionary pathways: switching partner (EM, OM and ER) or losing the association (Werner et al., 2018). Evolutionary transitions to a novel mycorrhizal state might allow plant lineages to access unexplored ecological resources, facilitating them to colonize environments that were not available before, and possibly enhancing their diversification rates. However, there are lineages in which some species acquire a new mycorrhizal state and at the same time, other species retain the ancestral state (AM) (Brundrett, 2008) increasing the variability of mycorrhizal states, which might in fact promote diversification of these lineages. Both hypotheses have not been evaluated in plants; however the few studies available from the fungal perspective suggest that shifts in mycorrhizal associations might affect diversification of involved partners (Sánchez-García & Matheny, 2017; Sato et al., 2017).

Even though mycorrhizal symbiosis has been pointed out as a key factor in the evolution and diversification of land plants (Brundrett & Tedersoo, 2018a; Feijen et al., 2018) this has not been evaluated before. In this study we address the following questions: (1) Do the lineages that established derived mycorrhizal associations present higher diversification rates than the ones that retain the ancestral mycorrhizal state? This investigates the idea of a key innovation mechanism of diversification; (2) Is there a relationship between mycorrhizal variability and diversification rates among different plant lineages? This would investigate the idea

that evolutionary lability might increase diversification dynamics. To answer these questions, we explored the relationship between the mycorrhizal state and the diversification rates of several seed plant families.

# Materials and Methods

## Mycorrhizal state database

We used the species-level dataset of mycorrhizal status from Maherali et al., (2016), which compiles previous lists and surveys of plant species and their mycorrhizal associations. Then, to increase sample size, we reviewed publications that report mycorrhizal states for single species, species list or local vegetation. Our literature compilation resulted in a database of 6440 plant seed species and their mycorrhizal state (Supporting Information, Notes S1). We used Maherali et al., (2016) classification, and assigned species into one of these categories: arbuscular mycorrhizal (AM), ectomycorrhiza (EM) Orchid mycorrhizal (OM), Ericoid mycorrhizal (ER) and Non-mycorrhizal (NM). Species that were characterized as AMNM by Maherali et al., (2016) - i.e. species observed as AM in some environments and NM in others- were here considered as AM as they correspond to facultative AM species. Also, as Maherali et al., (2016), species that formed both AM and EM, were placed in the EM category to account species that were potentially capable of forming EM symbiosis. The species names were reviewed using the Taxonomic Name Resolution Service (Boyle et al., 2013). Recently, Brundrett & Tedersoo (2018b) pointed out potential mistakes in mycorrhizal type identification on large databases, and how these misdiagnoses might lead to wrong conclusions. For the case of Maherali et al., (2016) database, the authors estimated an error in 1.6% genera and 1.0% species,. Moreover, their approach used to determine these errors (taxonomic approach; Brundrett, 2017) is controversial (Bueno et al., 2018; Bueno et al., 2019; Sun et al., 2019). Nevertheless, to assess the effect of possible undetected errors in the mycorrhizal dataset, we introduced error to the mycorrhizal state by changing mycorrhizal type at random of 20% of plant species (one order of magnitude higher than the error estimated from Brundrett & Tedersoo 2018b) and obtained similar results to those derived from original data (Supporting Information, Table S1).

## Family mycorrhizal state and diversity

We obtained information for species belonging to 259 seed plant families, although the species sampling among families was highly variable. To reduce the chance of wrongly assigning a family mycorrhizal state, we considered those families for which we had either 5% or higher of species sampled or at least 8 species sampled. This is justified because although many families are species-rich, they also seem to be quite consistent with respect to mycorrhizal association (Brundrett, 2008). This reduced our dataset to 175 families. Each family was assigned a unique mycorrhizal state (AM, EM, NM, ER or OM) when more than 60% of species sampled belonged to this mycorrhizal state. If no single state were present in more than 60% of species, the family was assigned a "mixed" state, to indicate no dominance of any mycorrhizal association. Other thresholds for the assignment of family mycorrhizal state were tested and the pattern was similar (50%, 80% and 100%, Table S2 and Fig. S1). To investigate the effect of mycorrhizal diversity in the diversification dynamics we estimated the "Mycorrhizal diversity index", which is calculated by estimating the heterogeneity of the mycorrhizal states in each family using the shannon diversity index.

## Diversification rates

First, to explore the underlying diversification model behind plant seed diversification, we assessed the correlation between age and richness among seed plant families. Thus, following Sanchez-Reyes et al (2017), we evaluated the correlation between stem age and richness, including all seed plant families available (i.e. without removing families lacking information on mycorrhizal states) and correcting for phylogenetic structure and not. Stem group ages of the families were obtained from the dated molecular phylogeny of seed plants of Zanne et al., (2014) and the number of species of each family was obtained from The Plant List (theplantlist.org). No correlation was found between stem group age and richness, considering and witouh considering phylogenetic structure ($R^2$ = -0.001341; $R^2$ = -0.00139, respectively; supp material Fig), suggesting that diversification rates vary among clades (Sanchez-Reyes et al., 2017). Given that diversification rates varied among seed plant families, we continue with the further analyses. Diversification rates for each seed plant family were estimated using the method-of-moments from Magallón & Sanderson

(2001). Because the relative contribution of extinction is unknown we used distinct scenarios to characterize the relative extinction rates ($\epsilon$), one with no extinction, $\epsilon$ = 0.0, one with medium extinction, $\epsilon$ = 0.5, and another with high extinction, $\epsilon$ = 0.9. We estimated diversification rates using stem group age obtained from the phylogeny of seed plants, and similar results were obtained using crown group age (Supplementary material Table S3 and S4 XX). We are aware of more sophisticated and direct methods (e.g. BAMM; Rabosky, 2014) to investigate the association between trait states and diversification dynamics, but the plant phylogeny is massively under-sampled at the species level, and we clearly do not have mycorrhizal information for most species. Therefore, we decided to use simpler and less data hungry methods, and to discuss our results in the light of the methods limitations.Phylogenetic signal.

The seed plant phylogeny (Zanne et al., 2014) was pruned to obtain a family level phylogeny, with one species per family as tips. From this pruned phylogeny we calculated the phylogenetic signal of mycorrhizal traits and diversification rates. For the continuous variables - mycorrhizal diversity index and diversification rates - we calculated phylogenetic signal using Pagel's Lambda (Pagel, 1999) using the function phylosig in the package phytools in R (Revell, 2012). For the categorical variable, mycorrhizal state, we estimated the phylogenetic signal using the D parameter (Fritz & Purvis, 2010) with the function phylo.d in caper package in R (Orme et al., 2013).

## Statistical analysis

As some (but not all) of the mycorrhizal traits and diversification rates showed significant phylogenetic signal (Table S5), we evaluated the effect of mycorrhizal associations on diversification rates by both considering and not the phylogenetic structure in the residuals. We tested for potential differences in diversification rates between plant families with different mycorrhizal types using both ANOVA and a phylogenetic ANOVA using the function phylanova from phytools in R. Each mycorrhizal state was used as group and their diversification rates as response variable. Because the mycorrhizal states OR and ER only had one family each, those were removed from this analysis. To test for the relationship between mycorrhizal heterogeneity and diversification rates we performed a linear model with raw data, and a PGLS regression in the R package caper (Orme et al.,

2013) with diversification rates as response variable and mycorrhizal heterogeneity as explanatory variable. For PGLS models we used the lambda value obtained from the previous phylogenetic signal analysis. To further test if any specific mycorrhizal state promotes diversification, we follow the approach taken by Moen & Wiens (2017) and evaluated the correlation between the proportion of each mycorrhizal state in the family and their diversification rate (Fig S4). To further explore the potential confounding effect and the association between mycorrhizal association and diversification dynamics, we performed PGLS regressions to assess the relationship between mycorrhizal diversity index, age and species richness.

Finally, if shifts in mycorrhizal states (MS) occurred only once within each family (e.g. species within sub-clades within each family all have the same MS), the family level analyses might not properly capture the effects of mycorrhizal shifts on diversification rates. To explore whether mycorrhizal shifts in mixed families might have occurred multiple times, we calculated the proportion of MS within genera of mixed families and mapped them in the phylogeny of each mixed family to check if MS form monophyletic sub-clades (Fig. S5).

# Results

We obtained information about mycorrhizal state of 6441 species that belong to 259 families of seed plants. According to our sampling criteria, we kept 175 families from which 132 were AM (for example, Amaryllidaceae, Asteraceae and Lamiaceae), 17 were EM (as Fagaceae, Nothofagaceae, Betulaceae and Pinaceae), 15 were NM (such as Brassicaceae and Caryophyllaceae) and 9 were mixed (Figure 1). Mixed families contain species that retained the ancestral state (AM) and species that present a different mycorrhizal state (EM or NM). There were two different types of mixed families: four mixed families had AM, EM and NM species, (Myrtaceae, Nyctaginaceae, Polygonaceae and Cyperaceae) while the other five had AM and NM species (Amaranthaceae, Anisophylleaceae Bromeliaceae Juncaceae and Montiaceae) (Table S8).The phylogenetic signal strength differs among mycorrhizal types. While AM and EM are mostly spread randomly across the plant phylogeny, NM and MIX are phylogenetically clustered to some extent (Table S5). Likewise, the phylogenetic signal of diversification rates was significantly different from a random structure in r~$\epsilon$ = 0.0~ and

r~$\epsilon$ = 0.5~ but not in r~$\epsilon$ = 0.9~ (Table S5). There was a significant difference in diversification rates between the mycorrhizal states, irrespective of the extinction scenario (r~$\epsilon$ = 0.0~ F = 8.9, P = 2.5x10-5; r~$\epsilon$ = 0.9~ F = 9.7, P = 1x10-5; Fig. 2), which was observed in the ANOVA and in the phylogenetic ANOVA (Table S6). The a posteriori analysis of the ANOVA showed that diversification of MIX families was significantly higher than that of AM, EM and NM families. The same tendency is observed when correcting for the phylogenetic structure (Table S7). The phylogenetic ANOVA also showed there was no significant difference in diversification rates between the two types of mixed families (r~$\epsilon$ = 0.0~ F = 0.07, P = 0.75; r~$\epsilon$ = 0.9~ F = 0.6, P = 0.36).

The higher values of mycorrhizal diversity index were found in Nyctaginaceae (1.088), Polygonaceae (0.926), Phyllanthaceae and Myrtaceae (0.88 and 0.75 respectively), while the lowest was zero and it was observed in 86 families that have all species in the same mycorrhizal state, like in Pinaceae (EM, n = 140), Araucariaceae (AM, n = 9) and Bignonaceae (AM, n = 20). There was a positive correlation between mycorrhizal diversity index and diversification rates, observed with the linear models and with the PGLS (Figure 3a and 3b). The $R^2$ are surprisingly high, and together with the p-values of the models, are shown in Table 1. The significant relationship is observed under the three different scenarios of extinction (Table 1, only r~$\epsilon$ = 0.0~ and r~$\epsilon$ = 0.9~ are shown in Fig. 3). Mycorrhizal diversity index had no correlation with age and a significant but very low correlation with species richness ($R^2$ = xx and xx respectively; Fig. 3e, 3f). There was no correlation between the proportion of any specific mycorrhizal type in the family and their diversification rate (Fig. S4).

# Discussion

The association with mycorrhizal fungi has been indicated as a key acquisition in the evolution of plants, nevertheless its effect on plants diversification has not been evaluated before. Here we presented the first attempt to assess the relationship between mycorrhizal associations and diversification rates of plants. Due to the under-sampling of seed plants phylogeny and mycorrhizal state database, we used a simple and conservative approach that allows us to tackle this question.

Our results showed that there was no difference on diversification rates between AM, EM and NM families

(Fig. 2). This shows that families that acquired novel mycorrhizal associations (EM and NM) do not have higher diversification rates than families that retained the ancestral state (AM), contrary to what was expected in a scenario of key innovation in mycorrhizal associations as a mechanism of diversification. Thus, regarding to our first question, the lineages that established derived mycorrhizal associations do not differ in their diversification rates from AM families.Contrary, our analyses showed that families with mixed mycorrhizal state have higher diversification rates than AM, EM and NM families (Fig. 2). Mixed strategy included two subtypes of mixed: families with AM and NM species, and families with AM, EM and NM species; both had higher diversification rates and there was no significant difference on rates between them. This shows that regardless of the mycorrhizal states that composed the mixed families, they have the highest diversification rates, suggesting that it is the diversity of mycorrhizal states that promotes diversification rather than a specific mycorrhizal state. This is further supported by the fact that there was no correlation between the proportion of any specific mycorrhizal type in the family and their diversification rate.

In addition, there was a positive and significant correlation between mycorrhizal diversity index and diversification rates, which does not depend on our categorical criteria of mycorrhizal state assignment to families. These associations with diversification rates, are both observed when correcting or not for the phylogenetic structure, suggesting that the relationship is not due to phylogenetic relatedness between families. Also, the patterns are observed under different scenarios of extinction, and even with $\epsilon$ = 0.9, where extinction could have an important role, the relationship is conserved. Given that diversification rates are determined by age and richness of the family, the effect of those variables could have driven the relationship between mycorrhizal heterogeneity and diversification rates. We observed no significant correlation between mycorrhizal heterogeneity and age; and we see a similar pattern with species richness, although the correlation is significant, the $R^2$ is quite low (Fig. 3e, 3f). This supports that mycorrhizal heterogeneity is mainly associated with diversification rates, not with age or richness per se.

Both results, the ANOVA for family mycorrhizal type and correlation between mycorrhizal heterogeneity and diversification, suggest that independent of which mycorrhizal state is involved, a higher heterogeneity of mycorrhizal states in a family might promote diversification rates. We interpret mycorrhizal heterogeneity as

a result from a higher evolutionary lability of the mycorrhizal states within these families, which has been suggested to promote diversification in other biotic interactions (Hardy & Otto, 2014). Each mycorrhizal state provides advantages to plants in certain environments but not in others (Brundrett et al., 2002), thus families that are composed by species with different mycorrhizal states might have been able to switch states in evolutionary time, making them able to evolve a higher diversity of niches which would result in a higher diversification rate. Under this scenario, mycorrhizal diverse families would have had more chances to take advantage of a new ecological opportunity, than families with most species within a single mycorrhizal state. It is interesting to note that mycorrhizal diverse families have not only higher diversification when compared to low diverse families with the ancestral state, but also higher rates than families that have switched from the ancestral state to one novel mycorrhizal state (NM and EM families).

The mycorrhizal diversity index might not capture well the effects of mycorrhizal shifts on diversification rates if shifts occurred only once within each Family. However, we observed that mycorrhizal shifts in mix families occurred multiple times, because the MS do not form monophyletic sub-clades and shifts occur even below the genus level. This clearly suggests that diversification rates are not the result of a single mycorrhizal shift, but a result of high lability of the mycorrhizal types within the mixed families (Fig. S5). These results together suggest that rather than a key innovation scenario, it is the evolutionary variability of mycorrhizal state what promotes diversification rates of plant seed families. Our results also highlight the evolutionary role of specialization at different organization levels: even if species are mycorrhizal specialized within a mixed family, the possibility to switch to different mycorrhizal states might increase the diversification of the family.

Because biodiversity dynamics could be rather complex, with clades either expanding, at equilibrium and even declining in diversity, simple metrics like the average rate of diversification might not be able to separate them (Quental & Marshall, 2010). The use of an average rate as a descriptor of a clade diversification dynamics assumes (or at least equates to) a scenario of expanding diversity (Quental & Marshall, 2010), and it might be especially problematic if lineages have a carrying capacity because the average rate might be diluted as time goes by (Rabosky, 2009). Moreover, with an average rate is not possible to distinguish between speciation and extinction rates or to test directly the effect of one trait on diversification dynamics.

Ideally one would use more complex tests, but that would require a lot more phylogenetic data than what is currently available. Additionally, the ecological data is scarce, and the identification of root associations might be complicated by inconsistent applications of definitions (Brundrett, 2008). Thus, our study points out the need for more accurate ecological knowledge on plants species and their mycorrhizal state. Overall, we used a relatively simple and limited macroevolutionary method and our conclusions arised from a limited ecological and phylogenetic data. These conclusions might be tested in future studies, when more data on mycorrhizal states and more complete phylogenies of plants are available.

Acknowledging the limitations of our study, the results suggest that a higher diversity of mycorrhizal strategies promotes diversification of lineages, possibly related with new ecological opportunities that each mycorrhizal state provides to plants. Our results finally suggest that the associations between soil fungi and plants has been key for plant diversification, not only due to the foundational association that allows plants colonize land (Pirozynski & Malloch, 1975) but also for further diversification of seed plant lineages.

## Acknowledgements

We thank all members of the Lab MeMe in the Institute of BioScience at the University of São Paulo for discussions and suggestions; and Guillermo Bueno for his contribution to the database. T.B.Q. thanks FAPESP for financial support (grants # 2012/04072-3 and #2018/05462-6), G. B. thanks FAPESP for financial support (grant # 2018/04821-2) and M.IM. thanks CONICYT for the doctoral scholarship # 21151009.

## Author Contributions

MIM, TQ and MFP designed the research; MIM collected the data, GB, MIM and TQ analyzed the data, GB made the figures; and all the authors wrote the manuscript.

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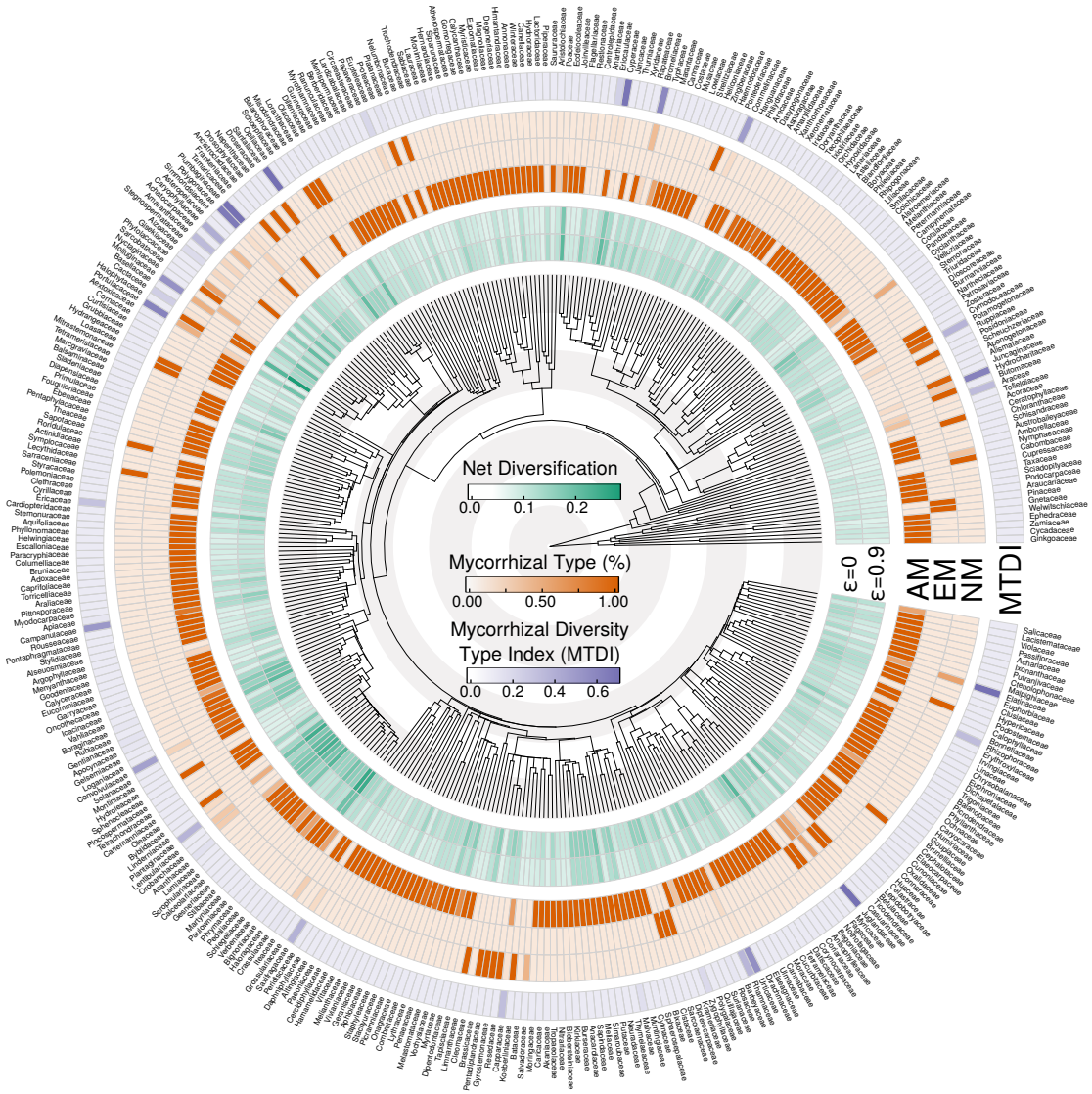


Figure 1: Family-level, time-calibrated phylogeny for the 106 seed plant families included in the analyses. For each family, the proportion of species within each mycorrhizal type is represented in the yellow-to-red boxes, AM: Arbuscular mycorrhiza, EM: Ectomycorrhiza and NM: non-mycorrhizal. The mycorrhizal diversity index (MDI) is represented in the green boxes and the diversification rate (r) is shown in the purple boxes. To illustrate the timescale of the phylogeny, the width of concentric white and gray circles represents 100 million years.

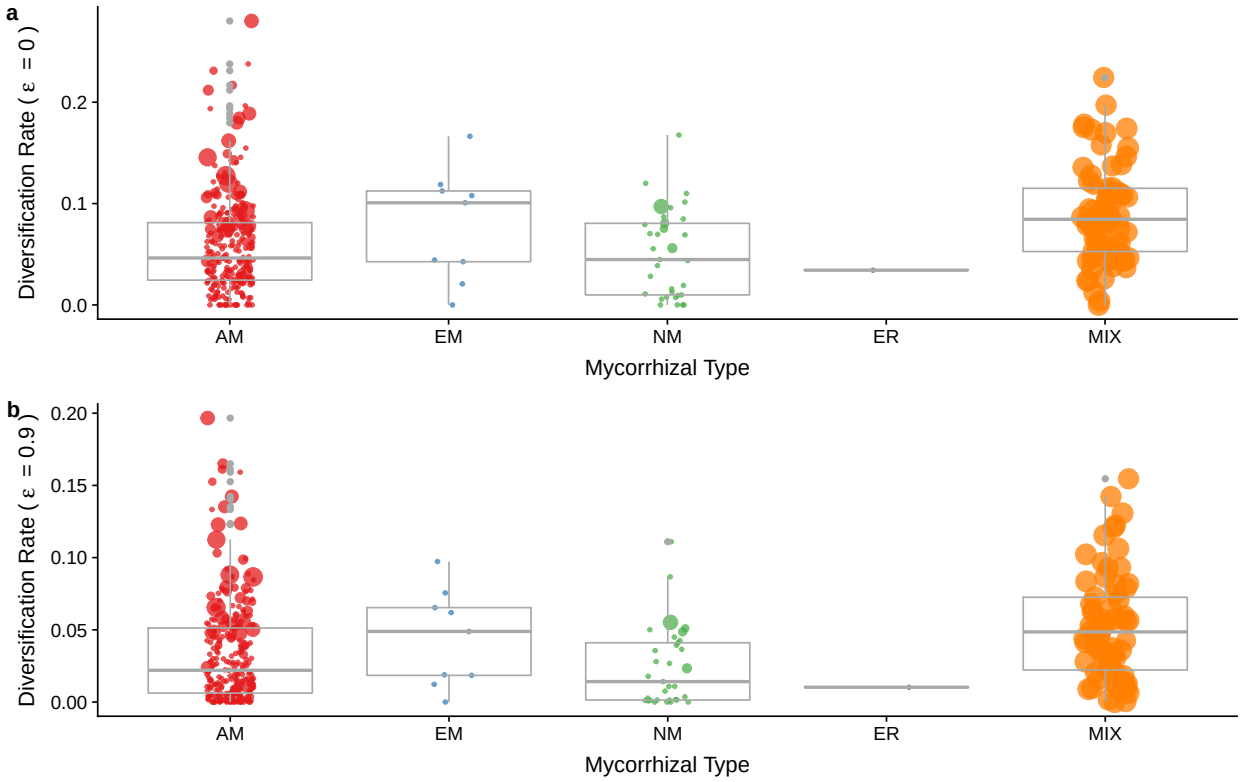


Figure 2: Relationship between mycorrhizal type and diversification rates. a) diversification rate estimated with $\epsilon$ (relative extinction fraction) = 0 and b) diversification rate estimated with $\epsilon$ = 0.9. AM: Arbuscular mycorrhiza, EM: Ectomycorrhiza, NM: non-mycorrhizal and MIX (families with no dominance of any specific mycorrhizal association).

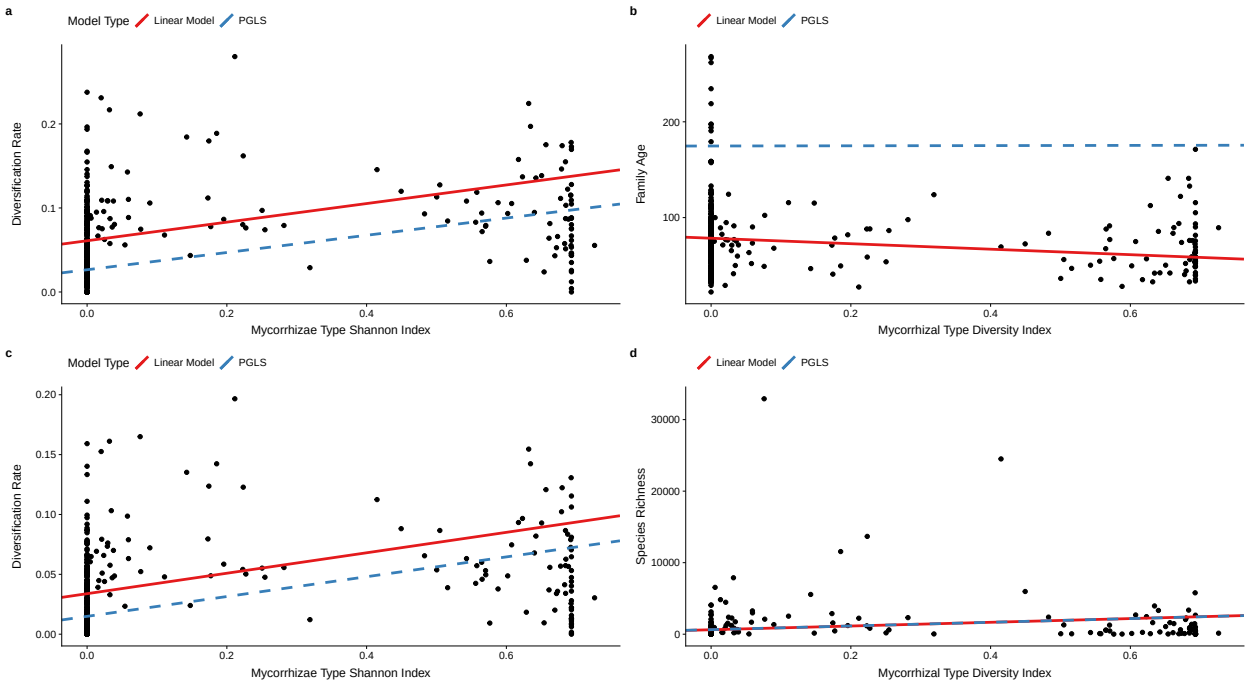


Figure 3: Scatterplots showing the relationship between mycorrhizal diversity index and diversification rates, species richness and age family. The red and blue lines indicate the results of a linear model and a phylogenetic generalized least squares (PGLS) fit, respectively. b) and d) show the correlation between observed values of diversification rate and estimated values obtained from the PGLS (red line represents the perfect fit).