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Mechanisms of coexistence: exploring species sorting and character displacement in woody plants to alleviate belowground competition.

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Data accessibility statement: The data we are using in the paper are all public. We list here the data sources we used and respective repositories:

Global Spectrum of Plant Form and Function Dataset: Díaz et al., 2022 DOI: 10.17871/TRY.81
Wood density information: World Agroforestry 2023 https://www.worldagroforestry.org/output/wood-density-database
Mycorrhizal Status of Plants: Delavaux et al., 2019 DOI: abs/10.1002/ecy.2542
Naturalized Alien Flora database: van Kleunen et al., 2019 DOI:10.1002/ecy.2542
Leaf area dataset: Wright et al. 2017 DOI: 10.1126/science.aal4760

Abstract

Rarely do we observe competitive exclusion within plant communities, even thoughplants compete for a limited pool of resources. Thus, our understanding of themechanisms sustaining plant biodiversity might be limited. In this study, we exploretwo common ecological strategies, species sorting and character displacement, thatpromote coexistence by reducing competition. We assess the degree to which woodyplants may implement these two strategies to lower belowground competition fornutrients which occurs via nutritional (mostly mycorrhizal) mutualisms. First,we compile data on plant traits and the mycorrhizal association state of woodyangiosperms using a global inventory of indigenous flora. Our analysis revealsthat species in locations with high mycorrhizal diversity exhibit distinct meanvalues in leaf area and wood density based on their mycorrhizal type, indicatingspecies sorting. Second, we reanalyse a large dataset on leaf area to demonstratethat in areas with high mycorrhizal diversity, trees maintain divergent leaf areavalues, showcasing character displacement. Character displacement among plantsis considered rare, making our observation significant. In summary, our studyuncovers a rare occurrence of character displacement and identifies a commonmechanism employed by plants to alleviate competition, shedding light on thecomplexities of plant coexistence in diverse ecosystems.

Introduction

Competing species often develop distinct phenotypic traits when they coexist in the same areas (sympatry) compared to when they exist in isolation, a phenomenon known as character displacement. While character displacement has been well-documented in birds (Kirschel *et al.*, 2009), fish (Crampton *et al.*, 2011), insects (Kawano, 2003), and mammals (Dayan & Simberloff, 1998), observations in plants have been limited (reviewed by Beans, 2014)). One reason for the rarity of character displacement in plants might be the spatial and temporal variation in the sets of competitors encountered by individuals of a plant species, offsetting benefits gained from mitigating competition (Connell, 1980). Plants compete for a limited pool of resources, including light, pollinators, and nutrients, mainly nitrogen (N) and phosphorus (P), which often limit growth in terrestrial ecosystems (Güsewell, 2004). Consequently, it remains unclear what triggers character displacement (drivers) in plants and how differences in the plant phenotype manifest (phenotypic responses). For instance, changing the flowering duration overlap of species sharing identical pollinators (e.g., Devaux & Lande, 2009) could act as both a driver and a phenotypic response in pollination strategies. Another potential driver of character displacement in plants could be differentiation in belowground investment strategies over the fungal collaboration gradient (Bergmann *et al.*, 2020). The fungal collaboration gradient, originally proposed for herbaceous plants associating with arbuscular mycorrhizal fungi, ranges from a "do it yourself" strategy to complete dependence on arbuscular mycorrhizal fungi for nutrient acquisition (Bergmann *et al.*, 2020) and could shape to a great degree the ecological stoichiometry (which is captured in the form of the elementome; Peñuelas *et al.*, 2019) of a species. Woody plants engage in various mycorrhizal associations, such as ectomycorrhiza dominant in temperate forests and ericoid mycorrhiza observed in organic soils (Brundrett & Tedersoo, 2018). Evolutionary adaptations that reduce competition may occur due to the frequency with which plant species encounter individuals engaging in different mycorrhizal associations. For woody plants, it is more likely that varying mycorrhizal association types, which significantly affect plant species' nutrient economy (Read & Perez-Moreno, 2003) and fitness, serve as drivers of character displacement. Changes in mycorrhizal association strategies are subtle but could manifest as alterations in mycorrhizal strategies and the resulting changes in the nutrient economy of plant species (Averill *et al.*, 2014) might, hence, manifest themselves (*phenotypic responses*) in the form of one or more commonly measured plant traits (McGill *et al.*, 2006).

In this study, we explored whether mycorrhizal association strategies in woody plants drive changes in their traits. First, we examined how five plant traits varied with mycorrhizal association strategies. Second, we investigated whether the diversity of mycorrhizal associations in the indigenous flora across countries explained variation patterns in those traits. Third, we assessed whether mycorrhizal association strategies led to character displacement in woody plants.

Materials and Methods

Conceptual framework

To address species sorting, we rely on an existing framework in plant biogeography, which authors usually present in the form of correlations between community mean trait values and environmental parameters such as climate or soil properties (e.g. Guerin et al. 2014; Muscarella and Uriarte 2016; Bruelheide et al. 2018; Guerin et al. 2019 but see Warren et al. 2014). Resulting correlations are usually interpreted as evidence that the addressed environmental driver induces community shifts in plants and thereby gives rise to a species sorting (often referred to as environmental filtering; Lepš and de Belo 2023). The approach links interspecific competition with a pattern that we observe at a community level. Ecological theory, thus, predicts unidirectional shifts across community mean trait values over gradients of environmental variables. These correlation tests have been questioned because they occasionally inflate statistical power (Hawkins et al. 2017; Lepš and de Belo 2023). We here used mycorrhizal Shannon diversity as a gradient but address instead the degree to which the community mean traits of groups diverge (mainly arbuscular mycorrhizal associating and non-arbuscular mycorrhizal associating woody plants), instead. In our case we are interested in the statistical interaction term between Shannon diversity index (the gradient) and mycorrhizal type which we couple with visual tests to testify that the weighted means for the different mycorrhizal types indeed diverge (i.e. a significant interaction term could have meant, instead, that the means converged).

To show character displacement, we further develop the approach of Adams and Collyer (2007) which addresses observations across environmental gradients. In our analyses we questioned whether at high mycorrhizal diversity, conspecific responses of multiple plant species in relation to leaf area diverge. We consequently used as a unit of our analysis the plant species instead and compared the slopes of a hypothetical relationship of observations at a species level between leaf area and mycorrhizal diversity. This approach has the advantage that it makes minimal assumptions in relation to the gradient, in specific that at high mycorrhizal diversity, there is more interspecific competition across tress in relation to mycorrhizal association types or nutrient acquisition strategies.

Sources of data and classification of mycorrhizal types

All analyses were carried out to the subset of Angiosperms that were classified as woody species. We obtained data on Leaf Area, tree height, leaf mass per area (LMA), and seed mass trait values from the Global Spectrum of Plant Form and Function Dataset (Díaz *et al.*, 2022), and wood density information from the International Centre for Research on Agroforestry (World Agroforestry 2023). The selection of plant traits for our analysis was a compromise between feasibility of yielding information for divergent sets of plant species and coverage the three documented sets of autocorrelated traits, the leaf economics spectrum, the wood economics spectrum and the root economics spectrum. Lists of indigenous species per location were extracted from The Global Naturalized Alien Flora database, a global inventory (van Kleunen *et al.*, 2019). To assess leaf area variability across plant species' distribution ranges, we utilized the SLA dataset from Wright et al. (2017). Mycorrhizal association type information was retrieved at a plant family level as published in Delavaux et al. (2019). We assigned a fixed mycorrhizal state for a species only if at least 40% of the records in Delavaux et al. (2019) matched a single mycorrhizal association type. All analyses focused on woody species, and mycorrhizal association types were reclassified into arbuscular mycorrhiza, non-arbuscular mycorrhiza, mixes (arbuscular mycorrhizal and other mycorrhizal types), and non-mycorrhizal (Fig. 1). Trees not forming any mycorrhiza were excluded from further consideration due to their limited presence in most analyses.

Estimates of mycorrhizal diversity and correction of plant trait data

We calculated mycorrhizal diversity using the Shannon diversity H' index, representing the number of unique species associating with each mycorrhizal association type. We did not consider richness because in most sites we observed all three classes of mycorrhiza, arbuscular, mixed and non-mycorrhizal plant hosts and richness would have been invariably three. Geometric means, obtained by averaging log-transformed trait values, were used to calculate the average trait value per mycorrhizal association type. This step was conducted for locations with a minimum of 21 woody plant species records and at least two mycorrhizal types represented with trait values. Seed mass, LMA, plant height, leaf area, and wood density were log-transformed due to their log-normal distributions. For character displacement tests using data from Wright et al. (2017), the analysis was limited to 354 species observed in a minimum of three different locations. Locations were defined based on a global map with a resolution of 5^{o} latitude and 5^{o} longitude, ensuring that each species was reported in at least three different grid cells. We averaged mycorrhizal diversity data across these locations, considering records with a standard deviation of mycorrhizal diversity above 0.25. Linear regression models with log-transformed leaf area as the response variable and mycorrhizal diversity as the predictor were used to assess the relationship.

Statistical Analyses

To address unequal sample sizes, most tests were standardized using subsets of 1000 random observations (e.g., Fig. 1). Non-parametric Spearman's rho tests were preferred for correlations to account for potential violations of parametric test assumptions and to control for outliers. Statistical analyses were carried out on R v 4.2.2 (R core team 2022). To address species sorting we used as a unit for our analysis locations in the Global Naturalized Alien Flora with at minimum 20 species with mycorrhizal type information. We carried out an analysis of variance with the weighted per mycorrhizal type mean of a trait as response variable and mycorrhizal type as well as mycorrhizal diversity index as predictors. We considered that an analysis presented evidence for species sorting if the interaction term of the two predictors was significant and the visualization of the responses across mycorrhizal type supported that the weighted means of the three mycorrhizal types diverged with mycorrhizal diversity. To address character displacement, we first projected observations on leaf area from Wright et al. (2007) as well as estimates on mycorrhizal diversity to a 5° by 5° global map via averaging records per grid cell. We then fitted linear models per plant species (i.e. across conspecifics) containing at least 3 observations, with leaf area as response and mycorrhizal diversity as a predictor and extracted the slope of it. We finally carried out an analysis of variance to establish whether the slopes (i.e. responses of conspecifics to mycorrhizal diversity) differed across the three mycorrhizal types we considered in our study.

Sensitivity Analyses

To assess the robustness of our species sorting analyses, we experimented with different thresholds: (1) varying the number of species in the species pool for a location (ranging from 5 to 40 species) and (2) adjusting the stringency of mycorrhizal type records for family classification (ranging from 0.05% to 70%). For species sorting, we tested five inclusion thresholds based on mycorrhizal diversity variability (standard deviations: 0.1, 0.2, 0.25, 0.35, 0.4), resulting in the consideration of 100, 61, 61, 47, and 37 records out of a total of 354, respectively (Test S4.1). We further tested the extend to which our results were reproducibility across different regions through separately analysing records from Europe + Africa, Americas, Australasia and Central Asia. Finally, we assessed the degree to which we could observe comparable interaction terms if we replaced mycorrhizal diversity with two bioclimatic variables which we extracted from WorldClim, mean annual temperature (bio1) and mean annual precipitation (bio12).

Results

Mycorrhizal types foster distinct plant traits but differences are constrained in phylogeny

We conducted extensive analyses to explore the relationship between trait information from the Global Spectrum of Plant Form and Function Dataset (Díaz *et al.*, 2022) and wood density information (World Agroforestry 2023) with mycorrhizal association types, assessed at a plant family level (Delavaux *et al.*, 2019). In each case, we performed 1000 ANOVA tests, each with 1000 random observations with complete information. Our classification of woody plant mycorrhizal associations into four classes (AM; mixed (AM and nonAM); nonAM; non-mycorrhizal) resulted in significant F values above 3.8 at a P=0.01 threshold (Fig. 1b-d; Test S1). However, when we applied phylogenetic comparative corrections using phylogenetic generalized least squares (iterated the tests ten times in each case with 1000 random complete observations) in which we used maximum likelihood estimates for the parameters Pagel's λ and delta but none of the relationships remained significantt (Fig. 1a; Test S1.2).

Global Shannon diversity statistics on mycorrhizal types

We paired mycorrhizal association type information with species lists from The Global Naturalized Alien Flora database which is a global inventory (van Kleunen *et al.*, 2019). We only considered sites with records for at least 21 plant species with mycorrhizal information. The mean Shannon diversity of mycorrhizal types across these sites was 0.67 (standard deviation: 0.16, range: 0.35 – 1.08; Fig. 2b; Tests S2.1-S2.5). Mycorrhizal type diversity did not vary significantly with latitude (rho=0.02, P=0.75, Fig. 2c). We observed higher diversity in mycorrhizal types in sites with many observations and noted declines in sites with many exclusively-AM-associating plants, along with increases in sites with many non-AM-associating and facultatively-AM-associating species (rho=0.40, P<0.001; rho=-0.21, P=0.007; rho=0.39, P<0.001, respectively; Fig. 2d).

Species sorting reduces competition across mycorrhizal types at high mycorrhizal diversity areas

We matched sites from the Global Naturalized Alien Flora database with mean trait values per species and calculated the weighted mean trait value per mycorrhizal type, we found that leaf area and wood density met the criteria for species sorting, exhibiting significant interaction effects between mycorrhiza and mycorrhizal H’ index. Leaf area and wood density demonstrated heterogeneity of slopes for mycorrhiza over the mycorrhizal H’ index, showing diverging responses for AM-associating and nonAM-associating plants (Fig. 3). While seed mass exhibited a trend for heterogeneity of slopes, the two extreme mycorrhizal types converged over the H’ index gradient (Fig S1; Test S3.5).

Woody angiosperms undergo a character displacement in relation to mycorrhiza

We pooled observations on leaf area per plant species from Wright et al. (2017) and mycorrhizal diversity information per site from van Kleunen(2019) at a grain of 5^o x 5^o latitude and longitude. We worked with the subset of 354 plant species for which we have trait information for a minimum of three locations. Regression models with specific leaf area as a response variable and mycorrhizal diversity as a predictor revealed differences across the four association types (F=3.3, P=0.049). Non-AM-associating plants exhibited higher leaf area values in areas of high mycorrhizal diversity, whereas mixed species showed declines (Fig. 4; Test S4.1).

Sensitivity analyses

Species sorting relationships on leaf area were robust to the species inclusion thresholds from 10 species to about 30 species (Fig. S2a). The respective relationships for wood density were less robust to the inclusion thresholds used (Fig. 2b). Both Leaf area and wood density relationships remained stable across alternative classification thresholds for mycorrhiza (Fig. S3). Analyses on character displacement were non-significant when we considered entries with little variance in diversity (i.e. standard deviation = 0.1) but remained significant for the entire range of alternative variance thresholds we used (i.e. standard deviations ranging between 0.2 and 0.4 – Test S4.1). We could replicate our finding that leaf area was driving a species sorting across the subsets of the data describing Americas, Europe-Africa and Australasia. We also found support that our observations on wood density were reproducibly across the subsets of observations addressing the Americas and Europe-Africa. The three cases where we did not find support for our hypothesis on species sorting (Central Asia on leaf area and Australasia and Central Asia on wood density contained small numbers of observations (n = 18, 15, 3, respectively) and were underpowered. Bioclimatic variables explained a fair share of variance in relation to leaf area (F=52.6 – P<0.001 for bio1 and F=4.6, P=0.03 for bio12) but were less powerful in relation to wood density. The interaction terms, however, in these tests ended up being much smaller (<2%) than the largest main effects manifesting the absence of actual interactive effects (i.e. the bioclimatic variables were not driving a species sorting).

Discussion

We provide compelling evidence that woody plants employ two complementary ecological strategies to reduce competition among individuals engaging in diverse mycorrhizal associations. Firstly, they undergo species sorting, where woody plant species in regions with a high diversity of mycorrhizal types exhibit greater phenotypic differences in plant traits compared to regions dominated by a single mycorrhizal type. Secondly, woody plants demonstrate character displacement in response to increased mycorrhizal diversity, leading to observable intraspecific differences in traits such as leaf area between regions with high and low mycorrhizal diversity. To our knowledge, this study presents a rare case of character displacement in angiosperms.

A consistent finding from our analyses on species sorting (Fig. 3) and character displacement (Fig. 4) was that most alterations observed in response to competition among mycorrhizal types could be attributed to a single group: non-AM-associating trees. It is crucial to note that in our analysis, ectomycorrhizal-dominated systems, prevalent in temperate forests, were classified as habitats with high mycorrhizal diversity (Fig. 2a, c). One possible interpretation is that non-AM-associating woody plant species tend to thrive and converge toward specific trait values observed in habitats with high mycorrhizal diversity when favorable environmental conditions prevail. However, we find this scenario unlikely. If this were the case, a strong latitudinal gradient in mycorrhizal diversity would have been expected to capture changes in climatic conditions, but our data did not support this (Fig. 2c). The observed patterns are very likely driven by competition, as supported by several studies demonstrating mycorrhizal competition's significant role in shaping plant communities in woody systems (e.g., Grünfeld *et al.*, 2020; Guy *et al.*, 2022). Although our analysis did not account for the relative abundance of different mycorrhizal types, it is well-established that ectomycorrhizal systems exhibit considerable mycorrhizal diversity and understorey vegetation typically associates with arbuscular mycorrhiza (Veresoglou *et al.*, 2018).

Could these two mechanisms, as reported here, induce ecologically significant changes in competition intensity and significance? Classic inoculation experiments have shown that mycorrhizal colonization can lead to substantial changes in plant species' biomass production (e.g., Grime *et al.*, 1988; Van Der Heijden *et al.*, 1998; Maherali & Klironomos, 2007). Studies addressing plant pairwise interactions have also indicated the potential impact of mycorrhizal associations. Our past research revealed that herbaceous communities containing species highly dependent on arbuscular mycorrhiza exhibited smaller niche differences than those that did not, and mycorrhizal-dependent plant species maintained higher competition coefficients (Veresoglou *et al.*, 2018). Wagg and Mckenzie-Gopsill (2023) demonstrated that mycorrhizal fungi reduced niche differences among herbaceous plant species. Furthermore, Van Nuland et al. (2023) showed that mycorrhizal association types could determine the outcome of pairwise competition in plant species associating with both AM-fungi and ectomycorrhizal fungi. Overall, these studies indicate that interspecific plant competition mediated by mycorrhiza is robust enough to determine coexistence. However, the mechanisms by which woody plants sense competition for mycorrhiza remain unclear. Gruntman et al. (2017)suggested that plants possess a diverse range of alternative growth strategies, optimizing them to maximize their payoff, which might be responsible for the character displacement observed in our analysis. Bridging aboveground and belowground interactions remains a frontier in community and ecosystem ecology (Wardle *et al.*, 2004), and our study contributes to addressing this gap.

It is essential to consider the habitats where we expect these competition mitigation strategies to facilitate plant coexistence. Many ecosystems are predominantly dominated by a single mycorrhizal type. For instance, most herbaceous communities associate with arbuscular mycorrhiza, while temperate forests are almost exclusively dominated by ectomycorrhizal trees (but see Veresoglou *et al.*, 2018). Transitional habitats, like dune slacks, host both AM-associating and ectomycorrhizal-associating plant hosts simultaneously (Smith and Read 2008).

Subtropical forests (Deng *et al.*, 2023) and various ecosystems in Australia, such as West Australia (Brundrett, 2017), support both AMF-associating and ECM-associating woody hosts. These ecosystems, which account for a significant portion of terrestrial land area, exhibit simultaneous presence of different mycorrhizal association types and are depicted remarkably in Figure 2a. We believe our observations on mycorrhizal diversity are generalizable to these systems, paving the way for future studies to confirm this assertion.

In summary, our study provides compelling evidence that mycorrhizal mutualism triggers adaptations in woody angiosperms, that could reduce interspecific plant competition. Moreover, we contend that these phenotypic changes are ecologically significant. By addressing these inconspicuous ecological patterns and linking them to core ecological concepts, we have contributed to the understanding of an ecological process once considered rare in the plant kingdom, character displacement, across angiosperms.

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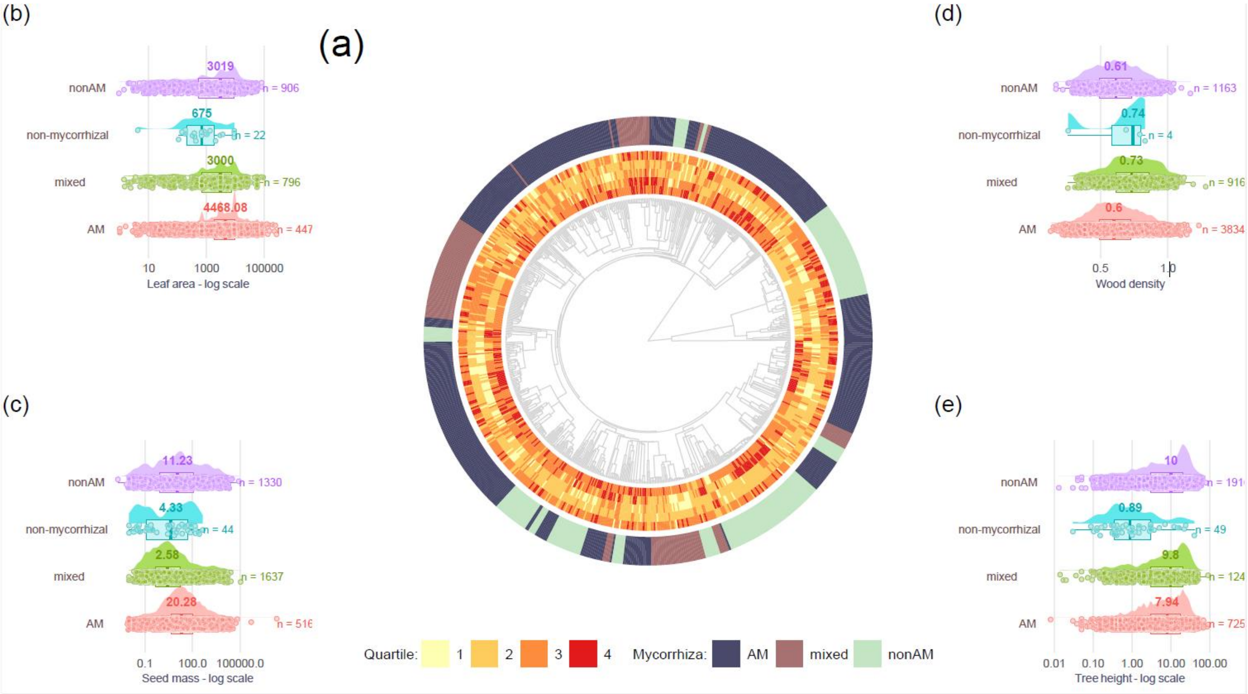
Legends to figures

Fig. 1 (a) Phylogenetic relationships of the plant species in our dataset in relation to the three (we excluded non-mycorrhizal plants) mycorrhizal types (outer circle) we identified. We report on (inside to outside) leaf area, seed mass, wood density, leaf mass per area and tree height trait values in the form of the quartiles of the values (yellow – 1st quartile to red – 4th quartile); (b – e) distribution information of leaf area, seed mass, wood density and tree height, respectively, in relation to the mycorrhizal types to which the species belonged. Notice the considerable variation in relation to the plant traits associating with distinct mycorrhizal types but variation is mainly due to phylogenetic relationships.

Fig 2 (a) Global map highlighting the mycorrhizal diversity H' index statistics across our dataset. We summarize the distribution of H' index values in (b) whereas in (c) we address latitudinal variation in the statistics. Finally, in (d) we present summary statistics on how the richness of the three main mycorrhizal types varied across the H' index gradient. Notice the absence of clear latitudinal patterns in mycorrhizal diversity.

Fig. 3 Leaf area (a) and wood density (b) statistics over the mycorrhizal H' index gradient. We averaged information per location in relation to the three main mycorrhizal types and observed in both cases a heterogeneity of slopes which combined to the fact that the responses of AM and nonAM mycorrhizal types diverged present evidence for a species sorting across the mycorrhizal gradient. The take home message of the figure, that can be generalized at minimum for AM and nonAM trees, is that the weighted means of the traits we evaluate diverge when mycorrhizal diversity increases, which supports the idea of a species sorting.

Fig. 4. Boxplots of the slope (*y axis*) of the relationship with leaf area as a response and mycorrhizal H index as predictor across the three main mycorrhizal types (*x axis*). While the leaf area of AM and nonAM woody plants increases across the mycorrhizal diversity gradient, that of plant species with mixed mycorrhizal association strategies decreases giving rise to a character displacement. For this analysis we only considered cases when the standard deviation of the H' index information exceeded 0.25 but the relationships were robust to changing this threshold (Test S4.1). The take home message of this figure is that while tree species that associate exclusively with AM or do not establish AM associations increase their leaf area in sites of high mycorrhizal diversity, the species that show mixed association patterns present lower leaf area which should reduce the intensity of interspecific competition with the former two groups of species. Because we observe those responses that alleviate competition at sites with a high mycorrhizal diversity and thus extensive interspecific competition in relation to mycorrhiza, we think that we are demonstrating a case of a character displacement.



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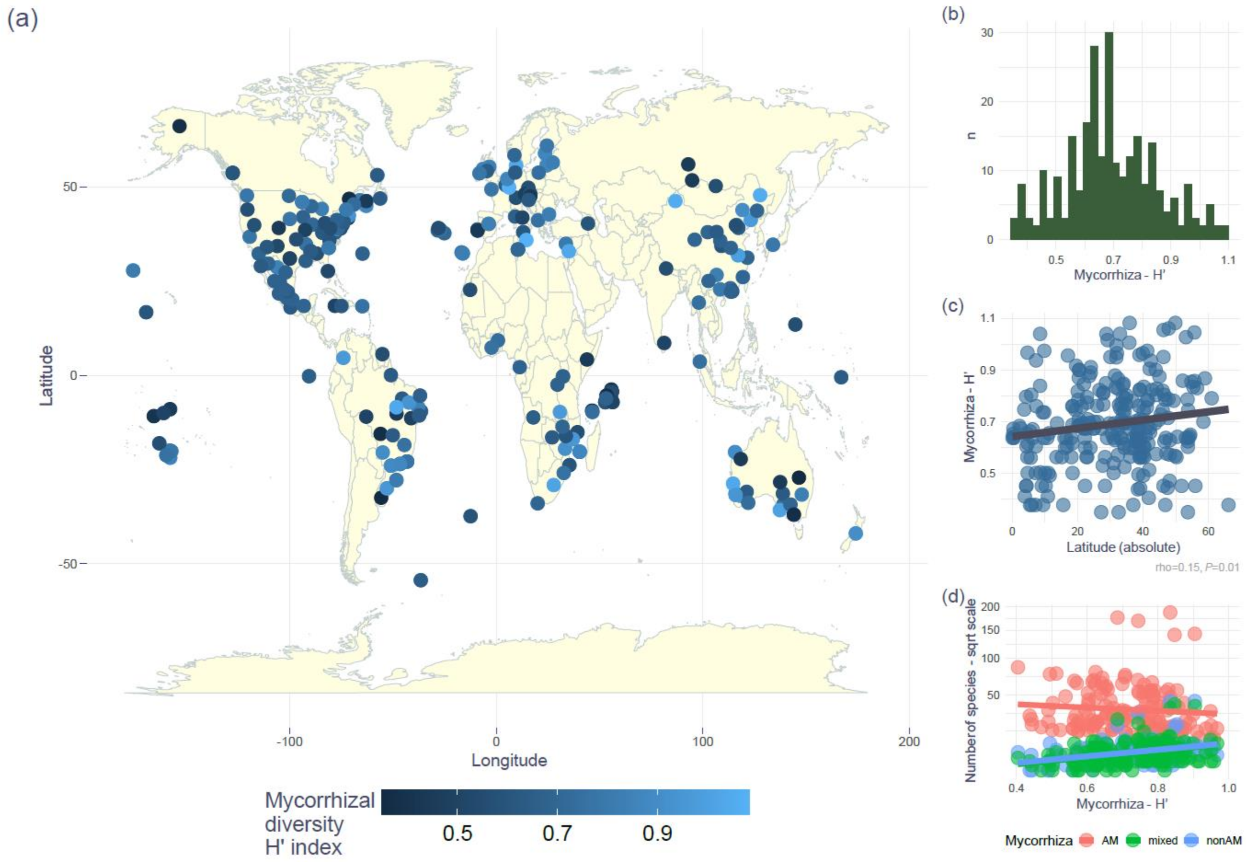

Fig 2 (a) Global map highlighting the mycorrhizal diversity H" index statistics across our dataset. We summarize the distribution of H" index values in (b) whereas in (c) we address latitudinal variation in the statistics. Finally, in (d) we present summary statistics on how the relative abundance of the three main mycorrhizal types varied across the H' index gradient. Notice the absence of clear latitudinal patterns in mycorrhizal diversity.

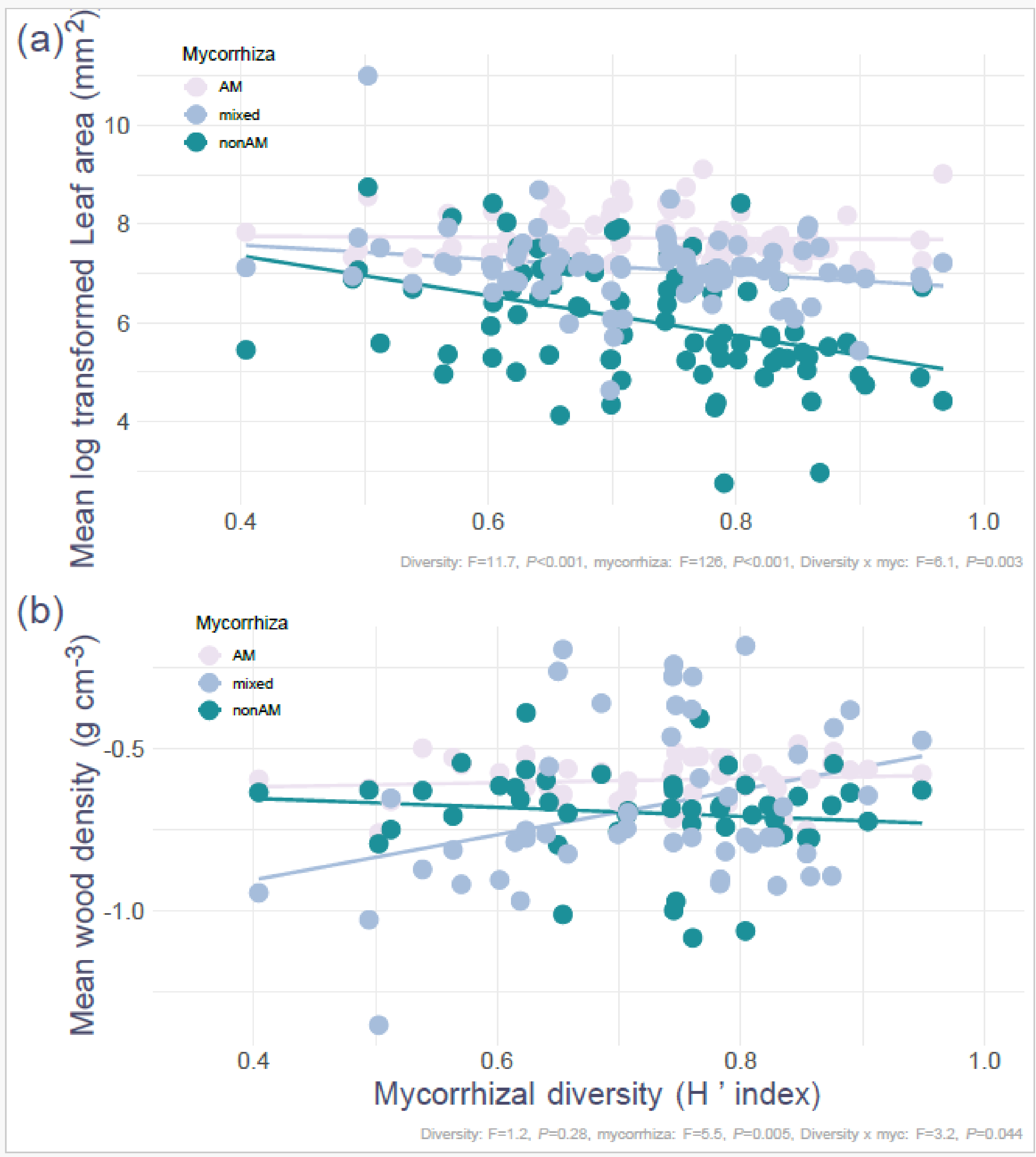

Fig. 3 Leaf area (a) and wood density (b) statistics over the mycorrhizal H' index gradient. We averaged information per location in relation to the three main mycorrhizal types and observed in both cases a heterogeneity of slopes which combined to the fact that the responses of AM and nonAM mycorrhizal types diverged present evidence for a species sorting across the mycorrhizal gradient.

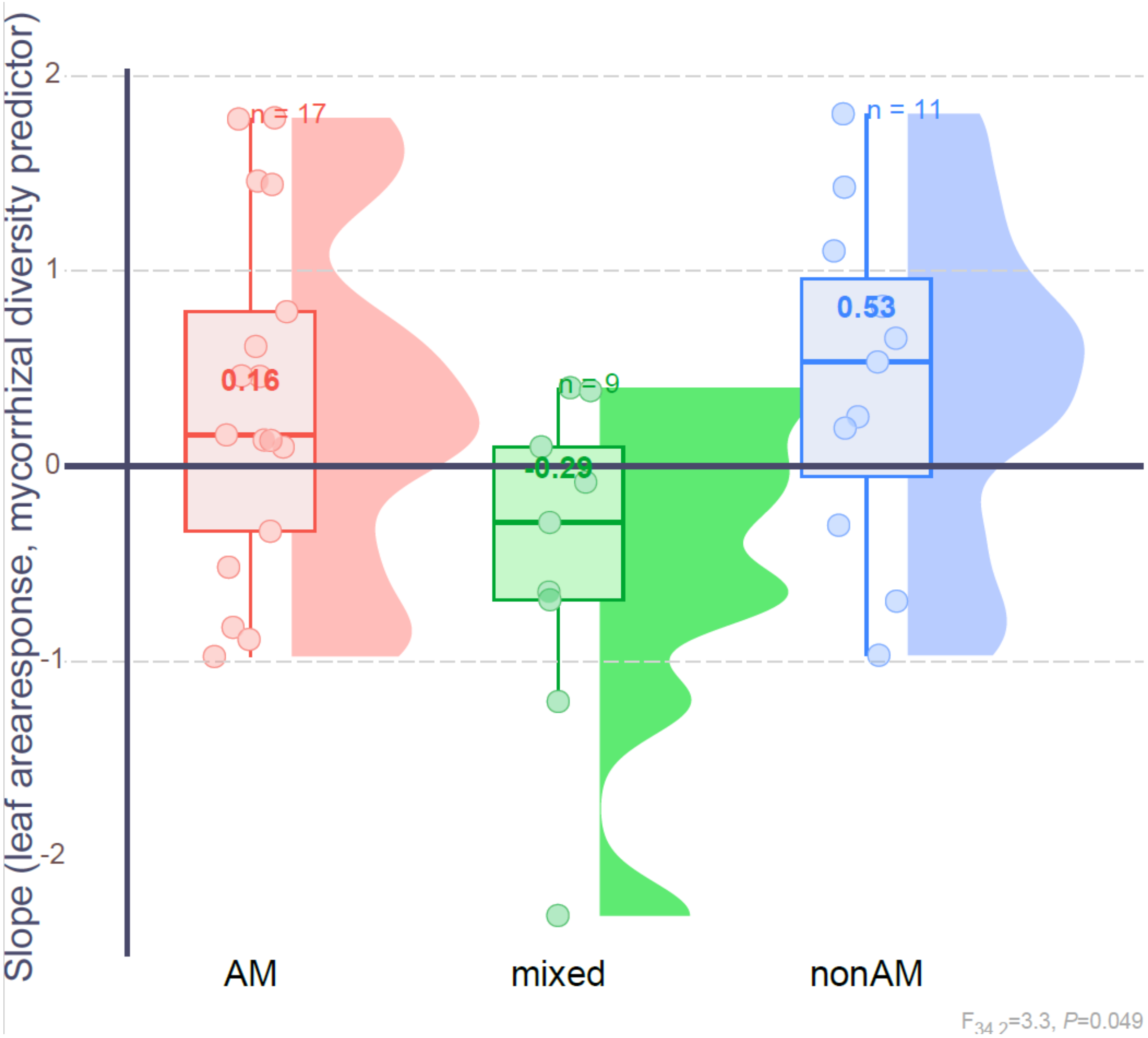

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Fig. S1 Leaf mass per area (a) Plant height (b) and seed mass (c) statistics over the mycorrhizal H' index gradient. We averaged information per location in relation to the three main mycorrhizal types and observed no heterogeneity of slopes for those traits which presents evidence against a species sorting across the mycorrhizal gradient.

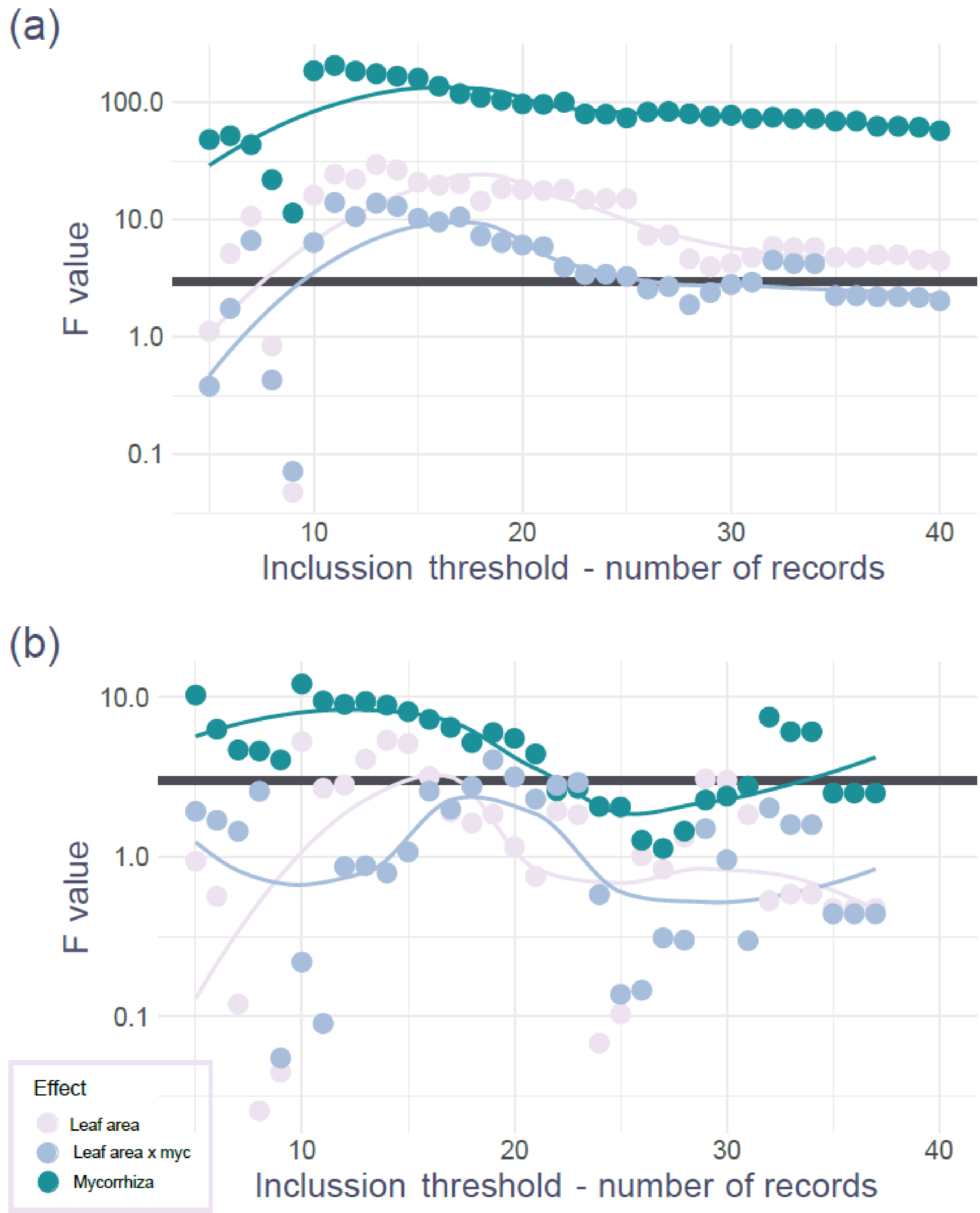
(a)
100.0
10.0
1.0
0.1
F value
10
20
30
40
Inclussion threshold - number of records
(b)
10.0
1.0
0.1
F value
10
20
30
40
Inclussion threshold - number of records
Effect
Leaf area
Leaf area x myc
Mycorrhiza

Fig. S2 Sensitivity analysis of the number of unique species observed per location to get included in the analysis (*x axis*) and the F values for the three main effects of the test (*y axis*) for (a) leaf area and (b) wood density. Unlike the relationship for leaf density, which was idiosyncratic, leaf-area relationships were robust to the inclusion threshold we used. The thick horizontal lines in both captions highlight the F value of three which can be considered as a significance threshold at $P < 0.05$ for the effect sizes.

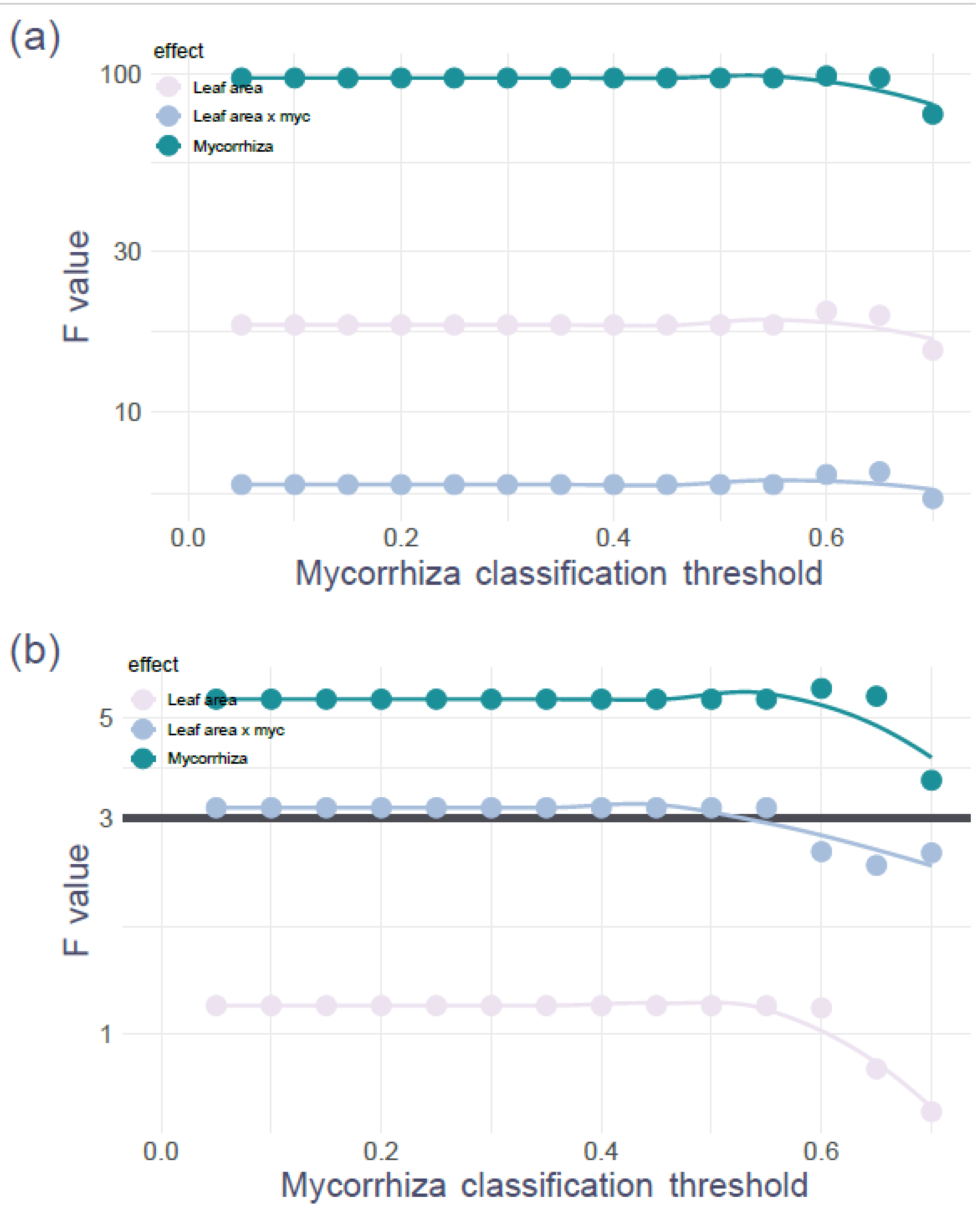

Fig. S3 Sensitivity analysis of the minimum classification threshold to accept the classification of a plant family as associating with a given mycorrhizal type (*x axis*) and the F values for the three main effects of the test (*y axis*) for (a) leaf area and (b) wood density. Relationships were robust to the mycorrhiza classification threshold we used. The thick horizontal lines in both captions highlight the F value of three which can be considered as a significance threshold at $P < 0.05$ for the effect sizes. We were particularly interested in the instances when the interaction term was significant.