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Contrasting mycorrhizal functionality in abiotic stress tolerance of woody species

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Current understanding of how woody plants respond to abiotic stress and how mycorrhizal interactions mitigate this stress is limited, as research has mostly focused on single stress factors. The diverse range of woody plants and mycorrhizal fungi, and the varying intensity and composition of multiple stress factors in different regions worldwide, have made it difficult to study these highly functional symbiotic interactions from a global perspective. Here, we used a top-down approach that involved partitioning known interactions into functional types, and mapping stress tolerances and interactions into overlapping heatmaps. We used a comprehensive dataset of 621 woody species' tolerance of shade, drought, waterlogging, and cold stress, as well as their mycorrhizal interaction data, to test how stress polytolerance correlates with different functional types of mycorrhiza. We show that single mycorrhizal type associates with shade tolerance, while dual type with cold and waterlogging tolerance. Both arbuscular mycorrhiza and obligate interactions are more abundant in drought stress tolerance conditions, while ectomycorrhiza and facultative interactions are found in more cold and waterlogged stressful conditions. Thus, functionally distinct mycorrhizal interactions form significantly contrasting stress mitigation patterns with woody species, providing insights into both evolutionary and biogeographic patterns related to the development of plant-mycorrhiza interactions.

Mycorrhizal symbiosis is an ancient association between plants and fungi, central to plant evolution and expansion. It is crucially important for both herbaceous and woody plants (trees, bushes, shrubs, lianas), the latter of which constitute nearly half of the total vascular plant diversity[1]. Mycorrhizal fungi form a complex and multifaceted symbiosis with plants, providing beneficial stress-mitigating services to plants. This happens mainly by directly supplying plants with additional resources like water and nutrients, but also indirectly mitigating non-resource stress, e.g. by suppressing pathogens in the soil, and retaining soil water more efficiently in dry conditions[2–4]. Services provided by mycorrhizal fungi can vary depending on their functional affiliations and biogeography[2,5]. Recent literature has begun to address these distinctions, with the emergence of comprehensive studies on the niche of mycorrhizal fungi[6]. In this study we assess various properties of plant-mycorrhizal interactions in woody plants, treating them as traits or properties of plants, who can have either single or dual type interaction; interaction with arbuscular mycorrhiza (AM) and/or ectomycorrhiza (ECM); or whose mycorrhizal interactions are either obligate or facultative.

Plants have traditionally been considered to form symbiosis with a single mycorrhizal type. Each mycorrhiza type hosts a particular combination of biotic partners along with distinguished morphological and functional characteristics[2,7]. However, numerous plants (89 genera from 32 families) are now known to form interactions with both AM and ECM, which are the two dominant types of mycorrhizal associations[8]. AM and ECM interactions provide different benefits for woody plants. ECM interactions, especially in temperate and boreal forests, likely play a more significant role in young soils with N-limiting conditions exhibiting a relatively restricted organic-nutrient economy. In contrast, AM interactions are more prominent in older forests with weathered soils under P-limiting conditions hosting a more open inorganic-nutrient economy[9]. Thus, we could expect that dual mycorrhizal interactions are more common in intermediate conditions, where both interaction types would be beneficial.

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These dual mycorrhizal type plants are predominately woody species (84%), distributed across the world where both mycorrhizal types overlap[8]. In addition to the types of mycorrhizal interaction, this symbiosis can also have different statuses, either as obligate or facultative plant symbionts[2,10,11]. Plants with facultative interactions are expected to better adapt to different environmental stresses and contexts[11,12]. They are also known for having higher invasion success[13] and longer dispersal rates[14], which can be explained by larger niche size of facultative than obligate plant symbionts[15]. Considering the variability of stress mitigating services provided, and the biogeography and the functional properties of both the mycorrhiza fungi and the plants, we can expect the patterns of interactions within this symbiosis to be significantly affected by the properties of both organisms and also their distributions.

Abiotic stress polytolerance is a key shaper of species distribution, particularly for sessile organisms like plants[16–18]. Lifelong aboveground plant structures, that define woody species, are often concurrently up against multiple abiotic stress factors like temperature extremes, water and light availability, which are considered to be the dominant abiotic stress factors[18,19]. Long-term exposure to multiple environmental limitations, inherent of any habitat type, shape woody plants tolerance strategies that are defined by differential contribution of different tolerances to given stress factors to the overall tolerance strategy[20].

However, recent studies have demonstrated that these trade-offs are much less exclusive and strict than postulated so far, leaving significant wiggle room for gaining polytolerance through adaptations[17,18,21]. This was clearly shown in a comprehensive analysis by Puglielli and others[18] who analyzed abiotic polytolerance patterns of 799 Northern hemisphere woody species (constituting ~ 40% of woody diversity of Northern hemisphere). Using principal component analysis (PCA) to determine the dimensions of woody species' abiotic stress tolerance, they found that there is a triangular-shaped abiotic stress tolerance space (STS). In this STS the first dimension reflects a trade-off between drought- and cold/waterlogging tolerance strategies, while the second dimension reflects a shade-tolerance strategy spectrum, from low to high shade tolerance, which is independent of the first dimension. This STS can be used as a coordinate system to link woody plants abiotic tolerance strategies with any ecological dimensions[20,22].

The traditional view on how mycorrhizal symbiosis benefits woody species suggests that while woody plants require mycorrhiza to survive, herbaceous plants need them to thrive[23]. Most research on mycorrhiza has been focused on how this interaction benefits plant performance (e.g. faster growth), however plant survival aspects and non-trophic mycorrhizal benefits are relatively understudied in comparison[24]. Thus, we can expect woody species to have more nuanced adaptive interactions with mycorrhizal fungi. This assumption is reflected in the higher phylogenetic diversity of ectomycorrhizal fungi that are mainly interacting with woody plants[5], while arbuscular mycorrhizal fungi, that is relatively omnipresent in both woody and herbaceous plants, have much lower phylogenetic diversity and endemism rates[25]. However, the interactions between plants and mycorrhizal fungi, and the benefits of these interactions, are much less studied in woody species than in herbaceous plants[4]. This study is the first large-scale assessment of how woody plants´ abiotic stress strategies relate to symbiosis types of mycorrhiza.

What do we know about mycorrhizal mediation of abiotic stress in woody plants? Our current understandings of how plants respond to abiotic stress and how mycorrhiza mitigates this stress are almost exclusively limited to single stressors[4,26]. The main stress factor studied in this context is drought stress – interactions with mycorrhizal fungi are known to improve soil water retention capacity[27]. Hyphae are more efficient than plant´s fine roots in absorbing both water and nutrients from smaller soil pores[2] and directly provide water to plants[28], but see[29]. On one hand, ECM has shown to have larger and more extensive extraradical mycelium, which can reach farther soil water pockets[4,30]. In contrast, AM interactions provide woody species more functions in dealing with drought – enhancing plants´ physiological and biochemical functioning[31,32]. Thus, AM interactions are considered more effective at mitigating drought stress than ECM interactions[4]. Actually, gymnosperm-dominated ecosystems—typically characterized by fewer fine roots than those dominated by angiosperms[33]—may have maintained a reliance on AM interactions rather than ECM associations to cope with drought stress, especially in regions that are predominantly or seasonally dry. This is particularly evident for gymnosperms outside the Pinaceae family.

Very similar mechanisms are assumed to work in the case of tolerating high and low temperatures, as these stress factors manifest also through obstructing water availability in ecosystems[34]. Accumulation of sugars in plant cell walls helps to maintain osmotic balance, but also to avoid carbon starvation in low photosynthetic periods[35]. As colder climatic conditions are known to favor ECM interactions over AM interactions, on both latitudinal[9] and altitudinal gradients[36], most probably due to the saprophytic capabilities of ECM fungi, it can be expected that ECM interactions dominate the peripheral zones of STS, in the cold/waterlogging tolerance end, while AM dominates in peripheral zones of STS with more drought stress and moderate cold levels. In turn, facultatively mycorrhizal plants increase following lower temperatures at higher latitudes[11] and elevations[36]. Therefore, it is expected to be associated with adaptations to cold tolerance, given that mycorrhizal associations may be limited in more extreme cold conditions due to a lower photosynthetically active radiation, which could limit the surplus of C for mycorrhizal associations along with possible limitations on the availability of nutrients for plant growth[37].

The relatively high carbon cost for maintaining mycorrhiza typically leads to reduced root colonization of symbiotic fungi[38]. Although this response is known to vary between plant species and their developmental stage[39], it might dominate in plant species with obligate mycorrhizal interactions that occur in sparser vegetation types; or in particular stages of life, as for example the seedlings of woody species are known to tolerate shade much better than adult individuals of the same species[40]. Mycorrhizal symbiosis seems to regulate or buffer limiting resource uptake in changing light conditions, but there is a lack of mechanistic and quantitative understanding behind these processes[41]; thus, the universality of this assumption is unclear.

Functional diversity of both woody plants and mycorrhizal fungi interacting with them in different regions of the world, makes it difficult to predict the patterns of these interactions from both the adaptational and mitigational point of view as the strength and composition of abiotic stress varies along the environmental gradients[4]. In addition, the possibility of dual mycorrhizal interactions is still debated, and this discussion is heavily related to what constitutes a mycorrhizal interaction – when does a fungal colonization become an interaction[8,15]. We followed suit, as most mycorrhizal studies, including data papers, consider colonization as a confirmation of interaction[8,11]. In this study, we used a top-down approach, where known interactions are partitioned into functional and biogeographical groups, and then interactions are mapped into the STS, thus generating heatmaps drawing large-scale correlative patterns of these associations.

In order to shed light on the patterns of these interactions on a global scale we built a comprehensive dataset of 621 woody species stress tolerance (based on stress tolerance space of shade, drought, waterlogging and cold stress[18]) and their known species-specific mycorrhizal interactions. We grouped the plant species (based on[17,19]) according to their life form (angiosperms vs. gymnosperms), growth form (deciduous angiosperms; evergreen angiosperms; evergreen gymnosperms), and biogeographic affinity (Europe, North America, East Asia). Mycorrhizal traits were assigned based on the identity of symbionts and their mycorrhizal structures observed in plant roots (*sensu*[11]): single vs. dual type; arbuscular vs. ectomycorrhiza; and obligate vs. facultative mycorrhiza. Ericoid and non-mycorrhizal types were omitted due to infrequent occurrence in the dataset.

We expected the following patterns of mycorrhizal interactions in relation to abiotic stress in woody species: (1) dual mycorrhizal type is predominantly associated with woody species tolerating cold and waterlogging stress, as these stress factors indicate overall more severe climatic conditions and shorter vegetation season – therefore symbiotic interactions in these dimensions are more abundant and diverse; (2) similarly, ectomycorrhizal interactions may dominate in the cold and waterlogged periphery of stress tolerance space, while arbuscular mycorrhiza may be more adapted to drought conditions; (3) obligate interactions between mycorrhiza and woody species dominate the STS with the exception of cold conditions, given the multiple possible limitations of cold stress to consistently maintain mycorrhizal associations.

Results and Discussion

Our results confirmed significant contrasting patterns between single vs. dual type (Fig. 1), arbuscular vs. ectomycorrhiza (Fig. 2), obligate vs. facultative mycorrhizal interaction in relation with the abiotic stress tolerance strategies (Fig. 3). In addition to different mycorrhizal interaction patterns among angiosperms and gymnosperms shown in the abovementioned figures, the patterns also differed depending on the biogeographical origin of the woody plant species (Fig S2–S4, Table S1).

Single type interactions were associated with the shade tolerance tips of the STS (Fig. 1a), while dual type interactions with cold and waterlogging (Fig. 1b). Considering that cold and waterlogging stress indicate shorter vegetation season, which means more frequent abiotic stress conditions[17], and cold stress also limits water availability, we expected dual type interactions to predominate in these parts of STS. However, this pattern was mainly driven by angiosperm species (Fig. 1e), while gymnosperms did not extend to that portion of the STS. Further, dual gymnosperms were associated with drought tolerance (Fig. 1f).

One explanation for the differences between single and dual mycorrhizal associations is the varying nature of aboveground and belowground stresses. Belowground, plants encounter a range of stressors—excess water, limited nutrients, or reduced water availability due to lower temperatures—while light is a more specific stress[42]. A single mycorrhizal association may specialize in managing one stress (such as excess light), whereas a dual association can simultaneously address multiple stresses by balancing the benefits of different fungal partners[8]. In turn the higher shade tolerance observed in many single mycorrhizal gymnosperms of the northern hemisphere is the result of a combination of evolutionary history and physiological strategies. Their long-lived, needle-like leaves, efficient low-light photosynthesis, and conservative resource allocation allow them to maintain a positive carbon balance under shaded conditions—a strategy that contrasts with the typically faster but less shade-adapted growth strategy of many angiosperms[43].

In addition, our results reveal divergent trends in interaction duality. Specifically, under conditions of cold and waterlogging stress, angiosperms engage in interactions with both arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi. In contrast, gymnosperms predominantly employ dual interactions to alleviate drought stress, and potentially nutrient deficiency as well.

Our second hypothesis found support as well: AM was clustered in regions with higher drought stress and moderate cold stress (Fig. 2a), while ECM is more common in cold and waterlogged peripheral areas of STS (Fig. 2d). However, it depended significantly on life form—angiosperms were mildly driving the central clustering in AM (Fig. 2b), while gymnosperms did the same in ECM (Fig. 2f), even though the latter pattern was statistically not significant. Drought dimension, that is the most studied abiotic stress parameter in plants[4] was noticeable only in case of AMs for gymnosperms (Fig. 2c), however this pattern was not statistically significant, probably due to relatively small sample size for such clustered analysis. The different patterns reflect, in a way, the traditional view on how mycorrhiza would benefit woody species—"Most woody plants require mycorrhiza to survive, and most herbaceous plants need them to thrive"[23]. While widespread AM generalist species[25] provide woody plants with opportunities to spread, much more endemic and specialist ECM species[5] mitigate the stress for better survival rates. Because of this, we also expect this hypothesis to apply only in the northern hemisphere, and not in the southern, where the dominating abiotic stress patterns are different.

As expected, obligate interactions are more abundant in the periphery of STS, especially in the shade tolerance end (Fig. 3a), as these interactions can render trees more shade tolerant by optimizing nutrient uptake and conserving carbon—a combination that is especially beneficial in the low-light, nutrient-poor conditions typical of many forest understories[2]. In contrast, facultative interactions that were more clustered in the center of STS and in the cold stress end (Fig. 3d), excel in cold environments likely by flexibly optimizing nutrient uptake and conserving carbon when fungal activity is limited.

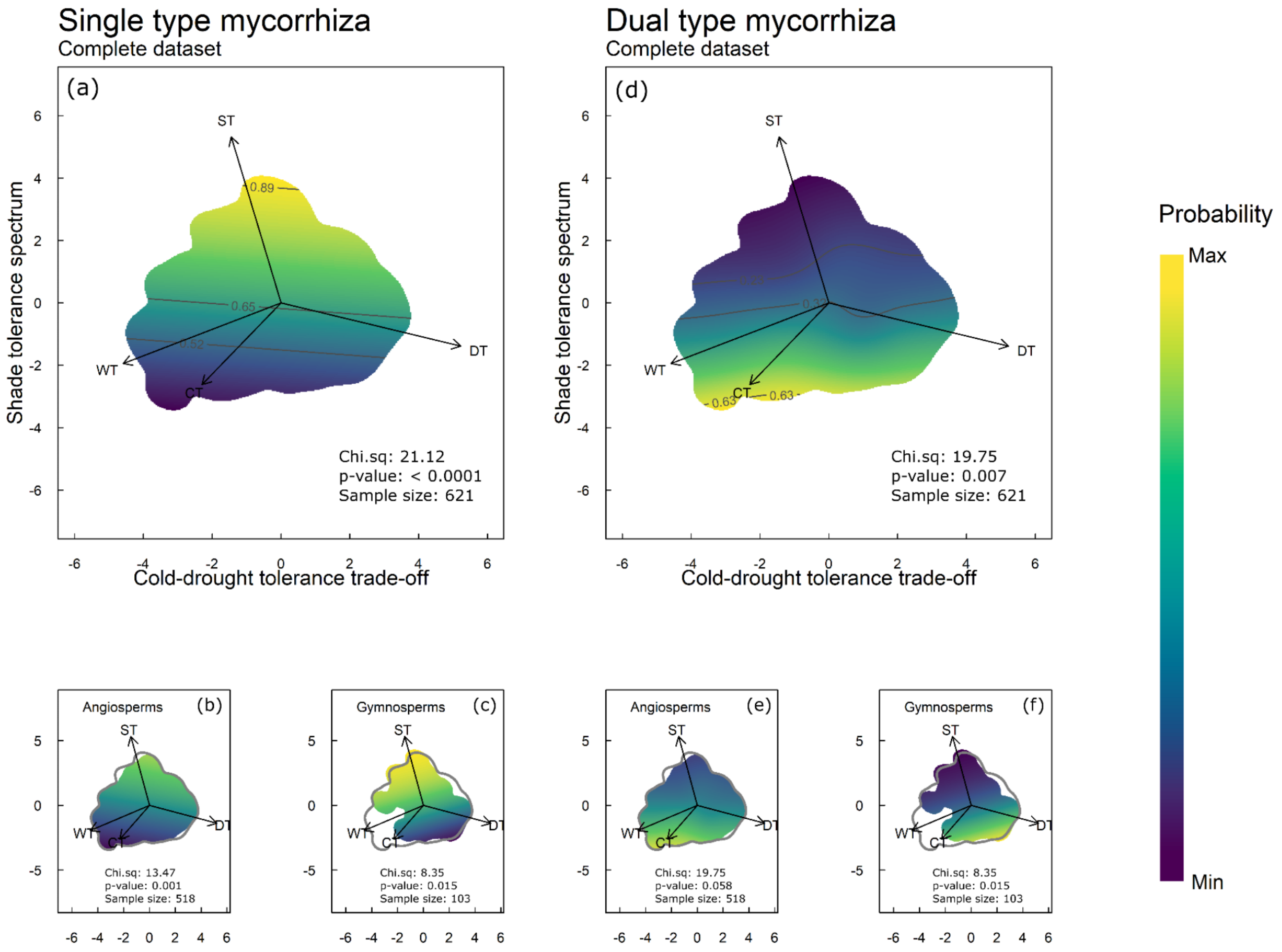

Fig. 1. Single versus dual type interaction plotted in the abiotic stress tolerance space (*sensu*[18]) of woody species. Panels (**a**,**b**) show the results based on the complete dataset, while panels (**c**–**f**) show the results separately for angiosperms and gymnosperms, for single and dual type interactions respectively. Color scale indicates the probabilistic distribution of trait combinations in the functional trait space created by PCA (yellow = high probability; violet = low probability). Contour lines are the quantiles of response variable predictions. Abiotic stress space dimensions are indicated with lines: *ST* shade tolerance; *WT* waterlogging tolerance, *CT* cold tolerance, *DT* drought tolerance. Kernel density heatmaps for the complete dataset analysis are in (Figure S1).

Despite the lack of mechanistic and quantitative understanding in how mycorrhiza regulates limiting resources in changing light conditions[41], obligate interactions in both angiosperms (Fig. 3b) and gymnosperms (Fig. 3c) were indeed mainly centered around the shade tolerance dimension, though the pattern in case of gymnosperms was not statistically significant. This trend appears to be consistent among woody plant species, albeit specifically within obligately mycorrhizal interactions. The concentration of obligate interactions in the peripheral areas, is relatively similar to ECM (Fig. 2d), and the woody species with ECM and obligate interactions are indeed correlated (Pearson's *r*: 0.36, p = < 0.001). Although obligately mycorrhizal associations avoid cold and waterlogged conditions and ECM species can be adapted to it. Although plants with facultative status are known to be better at long-distance dispersal[14] and their niche tend to be wider[15], facultative species have not established themselves in all stressful conditions, for example in the shade tolerant end. There seems to be a trade-off, similar to generalist vs. specialist plant species, between tolerating extreme stress with specific adaptations and capability of dispersing and invading new communities and habitats.

Overall, the correlative patterns of mycorrhizal interactions in relation to woody species abiotic stress tolerance depend significantly on the life form and the mycorrhizal trait preferences of the plant species. Different combinations of plant species and the functionality of the symbiotic association provide different types of services that are contingent on the tolerance strategy towards a specific abiotic stress factor. Deeper reliance on mycorrhizal interactions, whether expressed in dual type (Fig. 1), more species-specific types (Fig. 2), or status (Fig. 3), is significantly related to tolerating more extreme abiotic conditions, although the specific stress dimension is subject to the specific functional combination of both interaction participants.

The ability to form a dual mycorrhizal interaction with AM and ECM fungi provides the necessary resources for angiosperms to survive in cold and waterlogging habitats. These environments are marked by shorter

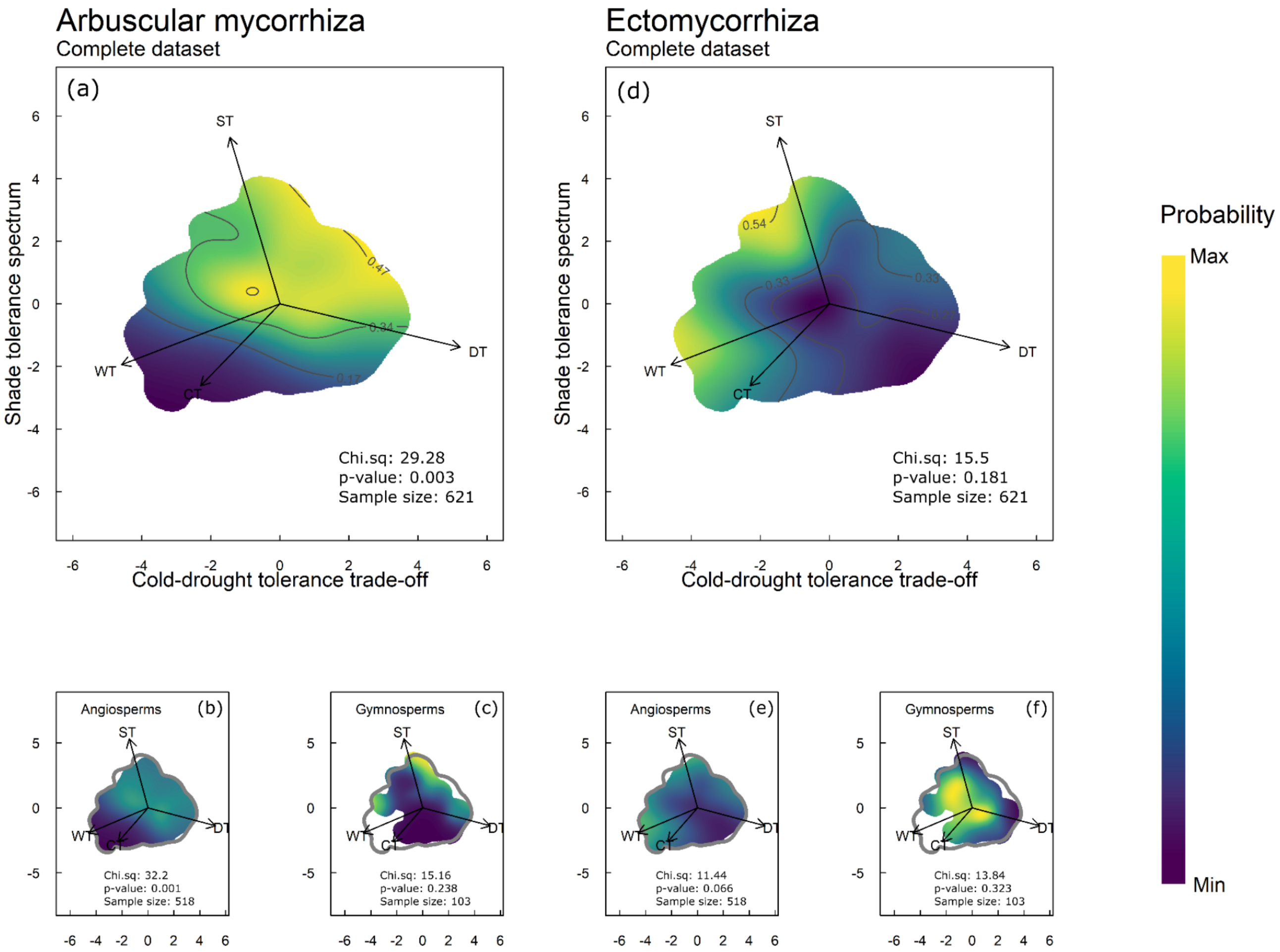

Fig. 2. AM versus ECM type interaction plotted in the abiotic stress tolerance space of woody species. Figure configuration follows (Fig. 1).

vegetation periods and the simultaneous presence of various stress factors. The benefits of more intimate interaction between ECM (which are more expensive than AM) and angiosperms and gymnosperms are apparent as this interaction mitigates cold and waterlogging stress. At the same time, obligate status may help to mitigate shade tolerance in both angiosperms and gymnosperms. The duality of mycorrhizal interactions might therefore reflect the variability of benefits from these interactions, ranging from nutritional benefits to non-trophic benefits (from soil water holding capacity to pathogen defense) that tend to be more associated with surviving stressful conditions. Similarly contrasting adaptational differences between gymnosperms and angiosperms in the abiotic stress tolerance space have previously appeared in biomass allocation patterns[21] and in the trait dimensions of global spectrum of plant form and function[22].

In summary, woody species occupying the extreme ends of stress dimensions need more abundant and intimate interactions with both AM and ECM in order to facilitate survival, while woody species in areas of STS have adapted to more moderate stress conditions and might use the symbiosis for enhancing the competitive edge. The survival-oriented combinations of mycorrhiza and woody plants seem to have strong roots in evolutionary and biogeographic history, and the thriving-oriented combinations in moderate or symbiotic limiting (cold) stress conditions are more sporadic and voluntary. This means that in the ongoing fast climatic changes, the species located in currently moderate stress conditions might also experience difficulties in finding the optimal mycorrhizal association to interact with, especially in case of ECM interactions, while the woody species in the extreme ends of stress dimensions could turn out to be more resilient to changes, as they already have multiple and intimate symbiotic relationships with mycorrhiza.

Methods

Woody plants polytolerance stress

Estimates of woody species tolerance of shade, drought, cold and waterlogging used for defining the STS were obtained from two published sources[17,19], which include species-specific stress tolerance scores for ~800 Northern Hemisphere woody species. Initial data compilation[19] included shade, drought and waterlogging tolerance, which were independently estimated by cross-calibrating multiple tolerance scales reported in the literature where multiple measurements for one species were available across tolerance scales. In addition, cold

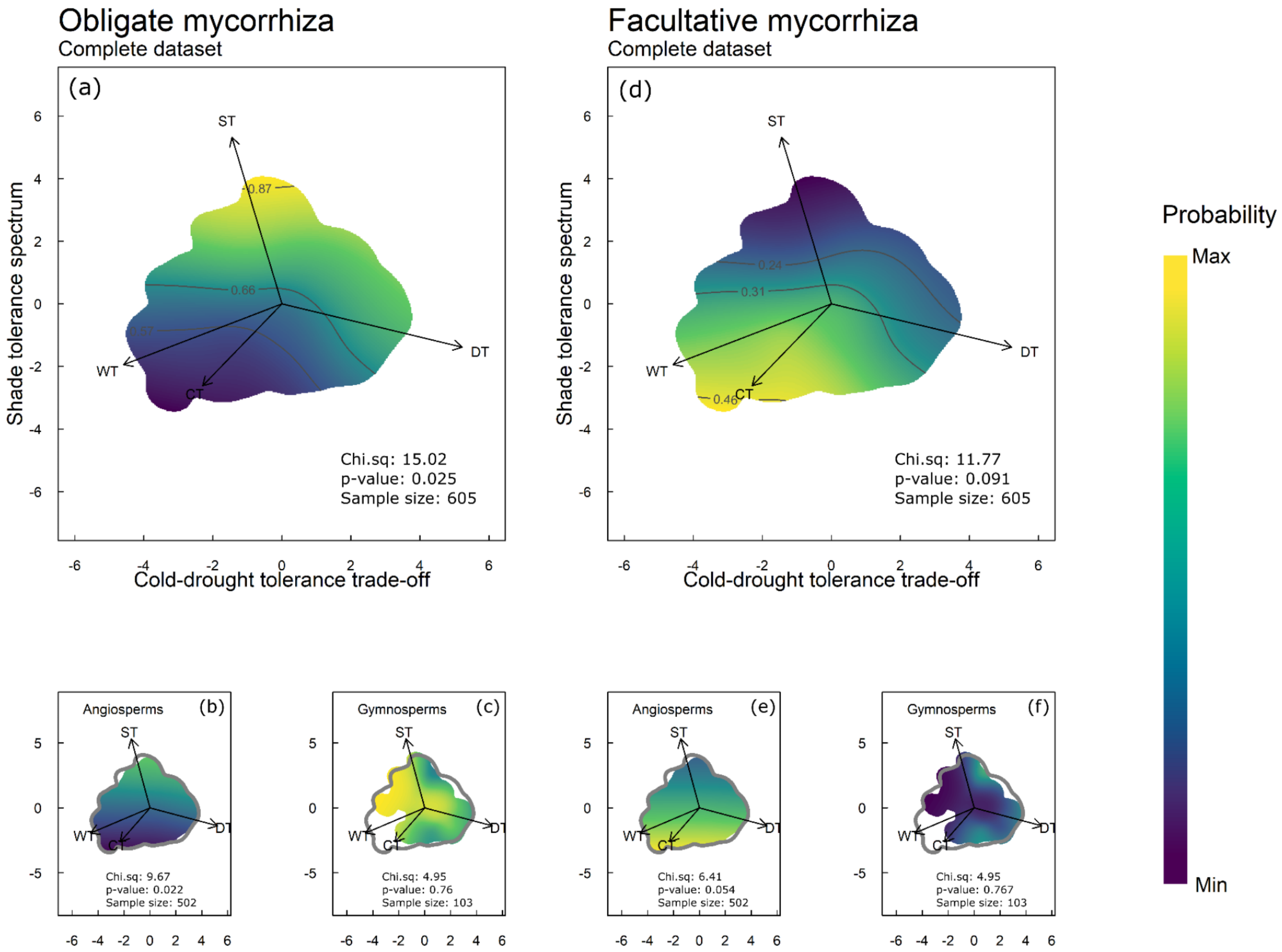

Fig. 3. Obligate versus facultative type interaction plotted in the abiotic stress tolerance space of woody species. Figure configuration follows (Fig. 1).

tolerance data were extracted from USDA plant hardiness data, and transformed to the same tolerance scale as in initial data compilation[17]. Stress tolerance scores for all abiotic stress factors varied in a continuous fashion between 1 - very intolerant species - to 5 - very tolerant species[17,19].

The formalization of the STS[18] revealed that the two dimensions in the principal component analysis captured ~ 80% of the variance in species-specific combinations of shade, drought, cold and waterlogging. Each pair of coordinates in the STS corresponds to a species-specific stress tolerance syndrome. Stress Axis 1 is positively correlated with drought tolerance and negatively correlated with both waterlogging and cold tolerance. There is a positive covariance in the model between cold and waterlogging tolerance. Stress Axis 2 is positively correlated with shade tolerance, and represents a shade tolerance dimension that is independent of other stress factors.

Mycorrhiza data

We added species-specific mycorrhizal interaction data to the abiotic stress tolerance dataset. Based on plant and fungal taxonomy and the mycorrhizal symbiotic structures found in the plant roots[2], the main woody plant mycorrhizal types were two: arbuscular mycorrhiza (AM), and ectomycorrhiza (ECM), as other types (i.e. ericoid or non-mycorrhizal plants) were not abundant enough to be considered. The presence of glomeromycotan fungi, arbuscules, or vesicles in roots were considered as pieces of evidence of the AM type[2,36,44]. The plant mycorrhizal statuses identified were obligate mycorrhiza (OM) and facultative mycorrhiza (FM), depending on whether the plant species are always, or sometimes colonized by mycorrhizal fungi, respectively[2].

To compile the plant mycorrhizal trait dataset, we used an empirical colonization approach at the species level, using all empirical mycorrhizal information of the species under study[36,44]. Thus, plant mycorrhizal trait data were obtained through the most up-to-date literature available[11]. These trait data were complemented with species-specific literature searches for the most abundant plant species lacking mycorrhizal trait information. In total, we compiled mycorrhizal trait information for 621 species (Table S2).

Statistical analysis

We defined the STS using principal component analysis (PCA) on the full dataset of stress tolerance combinations, as formalized by Puglielli and others[18]. The outer boundaries of the STS were defined at the 0.99 quantile of the multivariate probability distribution using the 'funspace' R function[45], which implements a kernel density estimation with unconstrained bandwidth selectors.

To test whether mycorrhizal symbiosis is associated with species-specific stress tolerance strategies within the STS, we classified the species in our dataset using binary variables summarizing either the type of mycorrhizal interaction (single type vs. dual type, $n = 391$ and $n = 201$, respectively), mycorrhizal type (only arbuscular vs. only ectomycorrhizal, $n = 225$ and $n = 166$, respectively), or mycorrhizal status (obligate vs. facultative, $n = 397$ and $n = 195$, respectively). We used multivariate kernel density estimated using the 'kde' function from the 'ks' R package[46] with unconstrained bandwith selectors at different quantiles (99th, 95th, 75th and 50th) to evaluate how the species described in terms of their mycorrhizal information were differently distributed within the STS defined across all species (Appendix S1, Fig. S1). Multivariate kernel density was estimated.

We then used logistic generalized additive models (GAMs) with a bivariate smoother to map the binary variables within the STS. We ran GAMs using the 'funspaceGAM' R function[45], setting a binary variable as the response variable and the axes defining the STS as the bivariate explanatory variable. Since species with different life forms occupy different and not always overlapping areas of the STS and previously displayed contrasting functional trait adaptations to tolerate abiotic stresses[22], we performed the GAM analysis by life form (angiosperm vs. gymnosperms). GAM predictions per each grouping variable were generated only within the portion of the STS occupied by each sub-group (Appendix S1, Table S1). This approach was taken to avoid the GAM smoother extrapolating model predictions outside the STS regions actually occupied by the available data points for each sub-group. The predicted probability values from the logistic GAMs were then mapped within the STS using the plotting function of the 'funspace' function package[45]. We used the same approach to analyze the relationship between mycorrhizal trait and stress tolerance strategies for species with different biogeographic affinity by using the species native origin (North America, Europe, East Asia, according to[19]) (Appendix S1, Fig. S2–S4). Full GAM statistics are available in Appendix S1 (Table S1). All statistical analyses were performed in R 4.2.2 (R Core Team, 2022).

Data availability

Data is available in the Supplement 2.

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Author contributions

LL, GM and CGB worked out the concept, MG, CGB, GP and LL gathered the data; NP, LL and GP did the analysis, LL wrote the first draft, all authors contributed to writing and editing the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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