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Asymmetric patterns of global diversity among plants and mycorrhizal fungi

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Abstract

Questions: Although the roles of mycorrhizal fungi in different vegetation types are widely acknowledged, it is still largely unknown how the diversity and frequency of different symbiotic partners vary among plant assemblages globally. We asked (1) how the global distribution of vascular plants correlates with the diversity (i.e. number of species) and frequency (i.e. relative abundance) of different plant mycorrhizal types (i.e. arbuscular mycorrhizal [AM], ectomycorrhizal [ECM], ericoid mycorrhizal [ERM], orchid mycorrhizal [ORM] and non-mycorrhizal [NM]); and (2) how the diversities of the most dominant plant mycorrhizal types (AM and ECM) correlate with those of their respective mycorrhizal fungal partners.

Location: Worldwide.

Methods: We retrieved all vascular plant occurrences available in the Global Biodiversity Information Facility database from sites worldwide where AM and ECM fungal diversity has been examined. Plant mycorrhizal types were assigned to plant species using expert-based imputation. Diversity and frequency indices were calculated using extrapolation and bootstrapping procedures in order to account for the heterogeneity and uncertainty of the datasets.

Results: Each plant mycorrhizal type correlated differently with the global diversity pattern of vascular plants, with higher total plant diversity in AM-dominated vegetation, compared with vegetation containing a larger share of ECM, ERM or NM plant species. The diversities of AM and ECM fungi were positively correlated with the frequency, but not diversity, of their respective plant mycorrhizal types; and weakly correlated with the frequency and diversity of other plant mycorrhizal types.

Conclusions: At the global scale, vascular plant distribution correlates, among other factors, with the frequency, and to a lesser extent diversity, of different mycorrhizal types of plants and fungi. Recognizing these relationships may help to predict changes in the frequency of ECM and AM plant mycorrhizal types under the different ongoing global changes.

KEYWORDS

arbuscular mycorrhizal, biogeography, cross-taxonomic, ectomycorrhizal, macroecology, mycorrhizal fungi, mycorrhizal types, vascular plants

1 | INTRODUCTION

Numerous mechanisms are believed to control the diversity of plant communities, but their respective roles and importance are still debated. Mechanisms related to belowground biotic interactions remain understudied although they represent potentially important drivers of ecosystem functioning (Bardgett & van der Putten, 2014; van der Putten, 2017). Mycorrhiza – an ancient symbiosis between soil fungi and plant roots – represents one of the most important belowground interactions (Smith & Read, 2008). Approximately 90% of vascular plant species form a symbiosis with mycorrhizal fungi (Brundrett, 2009). The fungus receives plant-synthesized carbohydrates while providing the plant with increased nutrient access and tolerance of abiotic and biotic stress (Smith & Read, 2008). Mycorrhizal symbiosis is known to importantly influence the performance of plant individuals, plant community composition and soil biogeochemical cycling (van der Heijden, Martin, Selosse, & Sanders, 2015). Varying plant growth responses to colonization by different fungal species and communities have been reported under experimental conditions (Klironomos, 2003; Treseder et al., 2018), suggesting that the distribution and diversity of plant species may be dependent on the local availability of appropriate fungal taxa. Thus, at the global scale, it is possible that vascular plant distribution and diversity depend, among other factors, on the different associations between plants and mycorrhizal fungi. Investigating large-scale patterns of diversity among plant mycorrhizal types, and correlations with their mycorrhizal fungi, can help to explain global patterns in vascular plant diversity, and can inform attempts to predict and mitigate ecosystem responses to ongoing global changes.

Distinct groups of plants and soil fungi form different types of mycorrhizal associations, each with particular physiological and functional properties; arbuscular (AM), ecto- (ECM) and ericoid (ERM) mycorrhiza being the three most common mycorrhizal types (Smith & Read, 2008). AM fungi associate with around 79% of all plant species, with the AM plant type correspondingly the most abundant type in all biomes (Brundrett & Tedersoo, 2018). By contrast, ECM and ERM fungi associate with a lower number of, mostly woody, plant species (<2%), but are expected to dominate in temperate and tundra environments, respectively (Brundrett & Tedersoo, 2018; Read & Perez-Moreno, 2003).

Earlier theoretical work explored the observation that ECM dominated plant communities were less diverse compared with AM-dominated communities (Allen et al., 1995; Connell & Lowman, 1989; Steidinger et al., 2019). This pattern was explained by the higher competitive ability of ECM plants due to their more specialized and hence supposedly more efficient partnership with fungi, in comparison with AM plants, which associate with a greater number of less host-specific fungal species. At the same time, there remains a lack of general empirical information about the distribution of plants with different types of mycorrhiza, and consequently about co-variation in the diversity and frequency of mycorrhizal types of plants and fungi. At the regional scale, there is accumulating empirical information about the distribution of plant mycorrhizal types in North and Central Europe (Bueno et al., 2017), North America (Soudzilovskaia, Vaessen, & van't Zelfde, M., & Raes, N., 2017; Swaty, Michael, Deckert, & Gehring, 2016) and Western Australia (Brundrett, 2017). Although general information about the distribution patterns of plants is also available for these regions (Kreft & Jetz, 2007), we are unaware of attempts to investigate relationships between the predominance of particular plant mycorrhizal types and plant species diversity.

Tedersoo et al. (2014) reported a positive global relationship between ECM host plant and ECM fungal diversity. However, aside from this, there is a scarcity of information about how the frequency and diversity of plant mycorrhizal types are associated with the diversity of mycorrhizal fungi. At the local scale, experimental evidence suggests that, for a given mycorrhizal type, high fungal diversity enhances plant diversity (van der Heijden, Bardgett, & Straalen, 2008; van der Heijden et al., 2015), although the opposite causal relationship – plant diversity favoring fungal diversity (Hausmann & Hawkes, 2009) – has also been indicated. It could be expected that such relationships are reflected in positive correlations between all different mycorrhizal plant types and their symbionts in natural ecosystems. For instance, there is indeed some field evidence of a positive local-scale correlation between plant diversity and the diversity of AM fungi (García de León et al., 2016; Hiiesalu et al., 2014; Neuenkamp et al., 2018) and ECM fungi (Gao et al., 2013; Tedersoo, 2016).

Studying different groups of mycorrhizal fungi at the global scale is very challenging due to a paucity of data, but information concerning global variation in the diversity of the two most widespread groups (AM and ECM fungi) is available (Davison et al., 2015; Pärtel, Zobel, Öpik, & Tedersoo, 2017; Tedersoo et al., 2014). Despite a lack of data about other mycorrhizal fungal types, it is possible to formulate hypotheses about ways in which the diversity and frequency of AM and ECM fungi relate to variations in other plant mycorrhizal types (e.g. non-mycorrhizal (NM), ericoid (ERM) and orchid (ORM)), based on the conditions where mycorrhizal associations have developed. For instance, it might be expected that colder conditions would be associated with low frequency and diversity of AM fungi and ORM fungi (Strullu-Derrien, Selosse, Kenrick, & Martin, 2018), which originated in the tropics, but would favor the cold-adapted and oligotrophic NM plant type (Delavaux et al., 2019; Kytöviita & Ruotsalainen, 2007) as well as the ERM plant type (Kohout, 2017; Read, 1991). Thus, we might expect that the occurrence and diversity of AM fungi negatively correlates with the occurrence of NM and ERM plant types, and positively with the occurrence of the ORM plant type.

In this study, we aimed to (a) describe the global distribution of the main five plant mycorrhizal types (i.e. AM, ECM, NM, ERM and ORM) and examine how they correlate with the diversity of vascular plants, (b) test associations between the frequency of the two most important plant mycorrhizal types – AM and ECM – and plant diversity at the global scale. Following Connell and Lowman (1989) and Allen et al.'s (1995), we predicted that ECM dominated

vegetation is less diverse than AM-dominated vegetation. Finally, we aimed to (c) analyze how the frequency and diversity of the plant mycorrhizal types correlate with the diversity of mycorrhizal fungi. We predicted negative relationships in frequency and diversity between plants and fungi belonging to different mycorrhizal types, as suggested by (a) contrasting patterns of regional distribution among plants forming AM and ECM (Bueno et al., 2017; Swaty et al., 2016) and (b) opposite trends in the diversity of ECM and AM fungal groups along latitudinal (Davison et al., 2015; Tedersoo et al., 2014) and altitudinal (Geml, 2017; Kivlin, Lynn, Kazenel, Beals, & Rudgers, 2017) gradients.

2 | MATERIAL AND METHODS

2.1 | Data sources

2.1.1 | Vascular plants and mycorrhizal types

We recorded the composition of large-scale plant assemblages for sites where AM or ECM fungal composition has recently been examined (708 sites in total): 343 sites for AM fungi represented in the Maarj*AM* database (Öpik et al., 2010) and 365 sites for ECM fungi represented in an extensive published dataset (Tedersoo et al., 2014). We used data from the Global Biodiversity Information Facility (GBIF.org, accessed 2016) as a source of information about vascular plant (i.e. Tracheophytes) distribution worldwide. The GBIF dataset is the only source that covers all of our global sample locations. However, it is evident that the GBIF database may suffer from strong spatial and taxonomic biases. We followed a careful data cleaning procedure prior to analysis of GBIF data: we removed duplicate records, corrected taxonomic misspellings where possible, and updated the taxonomy using the latest accepted species names, using the R package "taxize" (Chamberlain et al., 2016). We also assessed the level of agreement between GBIF and a comprehensive data set of global plant species richness (see section 2.3 below). In order to estimate correlations between plants and mycorrhizal fungi, we retrieved occurrences of all vascular plants within a 50-km circular buffer zone around each site represented in the Maarj*AM* database (Öpik et al., 2010) or ECM fungal dataset (Tedersoo et al., 2014). A 50-km circular buffer was considered a reasonable size to characterize the main vegetation type within a region because it is still expected to be spatially autocorrelated (i.e. more similar than random) (Tarnavsky, Garrigues, & Brown, 2008).

We assigned a mycorrhizal type to each plant species, using the latest expert-based imputation of plant mycorrhizal types (Tedersoo & Brundrett, 2017). We identified four plant mycorrhizal types according to their associations with mycorrhizal fungi: arbuscular (hereafter called AM plants), ecto- (ECM plants), ericoid (ERM plants) and orchid mycorrhizal (ORM plants) plants. We also identified plants that do not associate with mycorrhizal fungi as non-mycorrhizal plants (NM plants).

2.1.2 | Arbuscular mycorrhizal fungi

We used the Maarj*AM* database (Öpik et al., 2010) (accessed May 2016) as a source of AM fungal distribution data. Maarj*AM* collates AM fungal DNA sequence-based observations from published studies incorporating both soil and root samples, along with information about geographical location, and assigns them to Virtual Taxa (VT) (Öpik et al., 2010). The VT system is a phylogeny-based approach to classifying AM fungal small-subunit rRNA gene sequences (Öpik, Davison, Moora, & Zobel, 2014; Öpik et al., 2010). Hereafter, for simplicity, we use the terms "species" and VT interchangeably. VT have been used as pragmatic species proxies for AM fungi, with known benefits and limitations discussed elsewhere (Bruns, Corradi, Redecker, Taylor, & Öpik, 2018; Öpik & Davison, 2016; Öpik et al., 2014, 2010; Savary et al., 2018). The initial dataset included 343 unique geographic coordinates (i.e. latitude and longitude) and 361 VT. For further analysis, we selected only sites with natural or semi-natural vegetation (i.e. woodlands and grasslands) that were associated with at least 20 records (each record corresponds to a single sequence), since very low numbers of records might not allow precise extrapolations of species richness (see section 2.1.4 below). This resulted in an AM fungal dataset of 116 sites distributed worldwide.

2.1.3 | Ectomycorrhizal fungi

We used a global set of soil fungal distribution data (Tedersoo et al., 2014) as a source of information about ECM fungal distribution. Encompassing 365 sites across the world, each defined by unique geographic coordinates, the dataset benefits from uniform approaches to soil sampling and molecular fungal identification at all sites (Tedersoo et al., 2014). For further analysis, we selected only sites with at least 20 ECM fungal sequences (see section 2.1.4 below). This resulted in an ECM fungal dataset of 341 sites distributed worldwide.

2.1.4 | Diversity and frequency indices

For mycorrhizal fungi (i.e. AM and ECM), species richness was determined from the observations at individual sites defined by unique geographic coordinates in the Maarj*AM* database and in Tedersoo et al. (2014), respectively. Since the AM and ECM sites did not overlap, we used Generalized Additive Models (GAMs) (See section 2.4 below) to infer ECM fungal diversity at AM fungal sites and AM fungal diversity at ECM fungal sites in order to measure the correlation between the two fungal groups. However, for all other comparisons, only the values from the observations at individual sites were considered.

For all vascular plants and each mycorrhizal type, species richness and frequency (the abundance of a mycorrhizal type relative to other types — see below) was determined for each site from the vascular

plant observations within a 50-km radius of the site. Appendix S1 shows the number of records and observed species richness per site for all vascular plants and each mycorrhizal type.

To deal with scaling problems common in biodiversity studies, we followed the recommended approaches used in community ecology (Chase et al., 2018). Diversity was estimated using the Shannon index-based effective number of species to account for differences in sampling intensity between sites (i.e. the number of records in GBIF for plants, Maarj*AM* for AM fungi, and in Tedersoo et al. (2014) for ECM fungi). With this technique, it is possible to use most of the information in the original data, compared with standardizing data by rarefying approaches whereby many observations are removed from downstream analyses (Chao, Chiu, & Jost, 2016). In order to make sites with different sampling effort more comparable, we used extrapolation to an asymptote implemented in the iNEXT package (Chao et al., 2014), available in the R statistical environment (Hsieh, Ma, & Chao, 2016), for all vascular plants, each mycorrhizal type and all fungal taxa (i.e. AM and ECM fungi) separately. To improve comparisons of extrapolated values, we estimated their sampling distributions using the bootstrapping approach implemented in iNEXT based on resampling (with replacement) of records (10,000 times). Thus, for each taxonomic group and each site, we obtained 10,000 values of the Shannon index-based effective number of species (see Appendix S5, step 1a). With this framework, we estimated the diversity of all vascular plants, mycorrhizal types and mycorrhizal fungi. For statistical convenience, diversity metrics were natural-log-transformed.

Frequency was estimated for each plant mycorrhizal type and was calculated as the log ratio between the number of records of a certain mycorrhizal type and the number of records representing all other mycorrhizal types. We expect this value to represent the relative abundance of particular mycorrhizal types. In general, more common plants should have more records in GBIF, although we cannot discount sampling biases (e.g. very common species might be underrepresented). To improve the robustness of frequency estimates, we resampled plant records for each site with replacement (bootstrapping) 10,000 times, generating a distribution of records. The frequency of each mycorrhizal type was then re-calculated for each bootstrap iteration (see Appendix S5, step 1b).

2.2 | Statistical analysis

We investigated relationships between AM fungi and plants (i.e. all vascular plants and the five mycorrhizal types) on the one hand and between the ECM fungi and plants (i.e. all vascular plants and the five mycorrhizal types) on the other, both in terms of diversity and frequency (Appendix S5, step 2). To investigate co-variation, we used correlation rather than regression since the relationships may not be causal (but bidirectional) and may rather reflect the effect of other variables (e.g. historical, environmental). We calculated Spearman's rank correlation in order to account for non-normally distributed variables and/or non-linear relationships. We estimated

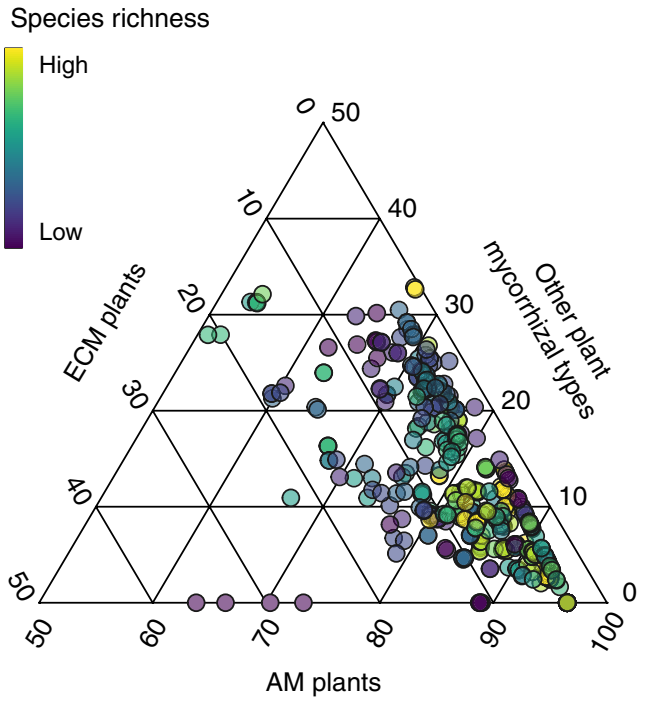

FIGURE 1 Ternary plot illustrating the proportion of different plant mycorrhizal types in the composition of 456 vascular plant assemblages. The axes represent the proportions of the two main mycorrhizal types (i.e. AM, ECM) and the other mycorrhizal types (i.e. NM, ERM and ORM). Point colors indicate total species richness in vascular plants along a gradient from low (blue) to high (yellow) species richness

correlations between the diversity of mycorrhizal fungi (i.e., AM and ECM fungi), vascular plants and mycorrhizal types; between the diversity of mycorrhizal fungi (i.e., AM and ECM) and the frequency of each mycorrhizal type; and between the diversity of vascular plants and the frequency of each mycorrhizal type (Appendix S5, step 2). The number of sites used for pairwise correlations varied depending on the number of records available for the different taxonomic groups.

2.3 | Sensitivity analysis

In order to test the effect of the community sample size (i.e. the 50-km buffer size) on correlations between aspects of plant and mycorrhizal fungal diversity, we compared estimates of diversity for all vascular plants as well as for each mycorrhizal type using the 50-km buffer circles and two smaller buffer sizes (40 km, 30 km; buffers <30 km could not be included since sites were associated with too few GBIF records). Estimates of plant diversity calculated using 40 km and 30 km were highly correlated with those derived from 50-km buffer sizes for all vascular plants (R^2 = 0.93 for 40 km and 0.81 for 30 km, Appendix S6) as well as for each mycorrhizal type (R^2 = 0.91–0.98 for the 40-km buffer size and 0.72–0.93 for the 30-km buffer size, Appendix S6), indicating that, within this range, diversity estimates are similar whatever the buffer size. The 50-km buffer zone

was thus chosen for the main analysis since this scale allowed those sites not well covered by GBIF at smaller scales (i.e. records <20) to be retained. However, we investigated all relationships using the range of considered community sample sizes, and interpreted them in the light of the different buffer zones in cases where the relationships were not consistent.

Because GBIF clearly suffers from a lack of data in some regions of the world, we tested how the data available in GBIF represent the global diversity of vascular plants, using for comparison the most comprehensive empirical observation-based vascular plant database available (Kreft & Jetz, 2007). Estimates of diversity in vascular plants derived from GBIF and those derived from Kreft and Jetz (2007) for the 456 sites considered in this study were positively correlated (Spearman's rank correlation test: $\rho = 0.69$, $p < 0.001$, Appendix S7b) confirming that estimates of diversity in vascular plants derived from the GBIF database match with models based on empirical data (Appendix S7). We note that Kreft and Jetz (2007) estimated species richness for ca. 12,100 km^2, whereas our 50 km radius corresponds to an area of 7,854 km^2. Thus, as seen in Appendix S7, Kreft and Jetz's (2007) values are larger than our estimates.

In order to account for the potential uncertainty of extrapolation, we calculated a correlation coefficient between each pair of diversity estimates obtained under bootstrapping (Appendix S5, step 2). We thus obtained 10,000 correlation coefficients for each pairwise correlation and the significance of the correlation from null expectations (i.e. no correlation) was tested using a two-tailed test ($\alpha < 0.05$). Thus, correlations were significantly different from 0 if 97.5% of the values were higher than 0 (i.e. significant positive correlation and reported as p-values > 0.975) or if 97.5% of the values were lower than 0 (i.e. significant negative correlation and reported as p-values < 0.025). All other outcomes represented non-significant correlations. For each correlation, the number of sites varied because only the sites with more than 20 records were considered (indicated in tables).

2.4 | Visualization of the global patterns

We used Generalized Additive Models (GAMs) with a smoothing spline-over-the-sphere algorithm to visualize global diversity and frequency patterns of vascular plants, mycorrhizal types and mycorrhizal fungi over the globe without producing edges (see Appendices S8 and S9).

We measured the predictive power of models using cross-validation by dividing locations into random 20% bins and estimating values for bins using the remaining data (Franklin, 2009). Pearson's correlation between observed and predicted values was calculated for diversity and frequency indices (Appendix S3). The spatial GAM models showed good predictive power for global vascular plant diversity (Pearson's $r = 0.71$, Appendix S3a) and the global diversity of each mycorrhizal type (Pearson's $r = 0.29$–0.98, Appendix S3a). Models describing the frequency of each mycorrhizal type had similar predictive power (Pearson's $r = 0.60$–0.90, Appendix S3b). For mycorrhizal fungal diversity, the spatial GAM models had slightly lower predictive power for ECM (Pearson's $r = 0.62$, $p < 0.001$, Appendix S3a), and the correlation between observed and predicted values of AM fungal diversity was not significant (Pearson's r: 0.17, $p = 0.06$, Appendix S3a). To measure the uncertainty in our predictions between regions across the world, we estimated the standard deviation of 100 predictions using random subsets to illustrate for each map region-to-region variability in the reliability of predictions (see Appendices S7 and S10).

All statistical analyses were performed in R software version 3.4.2 (R Core Team, 2017).

3 | RESULTS

3.1 | Data coverage

There were 20 to 478,489 GBIF vascular plant records (i.e. specimen) per site from the 456 sites worldwide (Appendix S1). Shannon index-based extrapolation of effective plant species richness ranged from 82 to 8,522 species per site (Appendix S1). AM plant mycorrhizal type represented the most dominant plant mycorrhizal type, comprising more than 75% of vascular plant species; and AM plant mycorrhizal type diversity was highly correlated with total vascular plant diversity (Spearman's rank correlation test, $N = 455$, $\rho = 0.96$, $p < 0.001$, Appendix S2). Each of the remaining plant mycorrhizal types comprised less than 10% of all vascular plant species (NM plants: 8.5%, ORM plants: 4.9%, ECM plants: 4.8%, ERM plants: 1.6%). The number of AM fungal records at these sites ranged from 22 to 815 (Appendix S1), and effective AM fungal species richness ranged from 6 to 216 species per site (Appendix S1). The number of ECM fungal records at the 341 sites ranged from 21 to 5,538 ECM fungal sequences (Appendix S1), and effective ECM fungal species richness ranged from 2 to 129 species per site (Appendix S1).

3.2 | Global diversity of plants and plant mycorrhizal types

The global diversity of vascular plants and plant mycorrhizal types was unevenly distributed globally. We found a latitudinal gradient in AM mycorrhizal plant type diversity, with decreasing frequency from tropical and subtropical regions (e.g. Central part of South America, East Africa, South East Asia) to high-latitude regions (Figure 2 and Appendix S9). Other mycorrhizal plant types exhibited high frequency and diversity in certain restricted areas, such as for the ECM plant type in temperate Eurasia and Australia, the NM mycorrhizal plant type in North America, the ERM mycorrhizal plant type in North Eurasia, and the ORM mycorrhizal plant type in Central Europe and Australia (Figure 2 and Appendix S9).

Across plant assemblages globally, total plant diversity was most tightly correlated with the frequency of the AM plant mycorrhizal

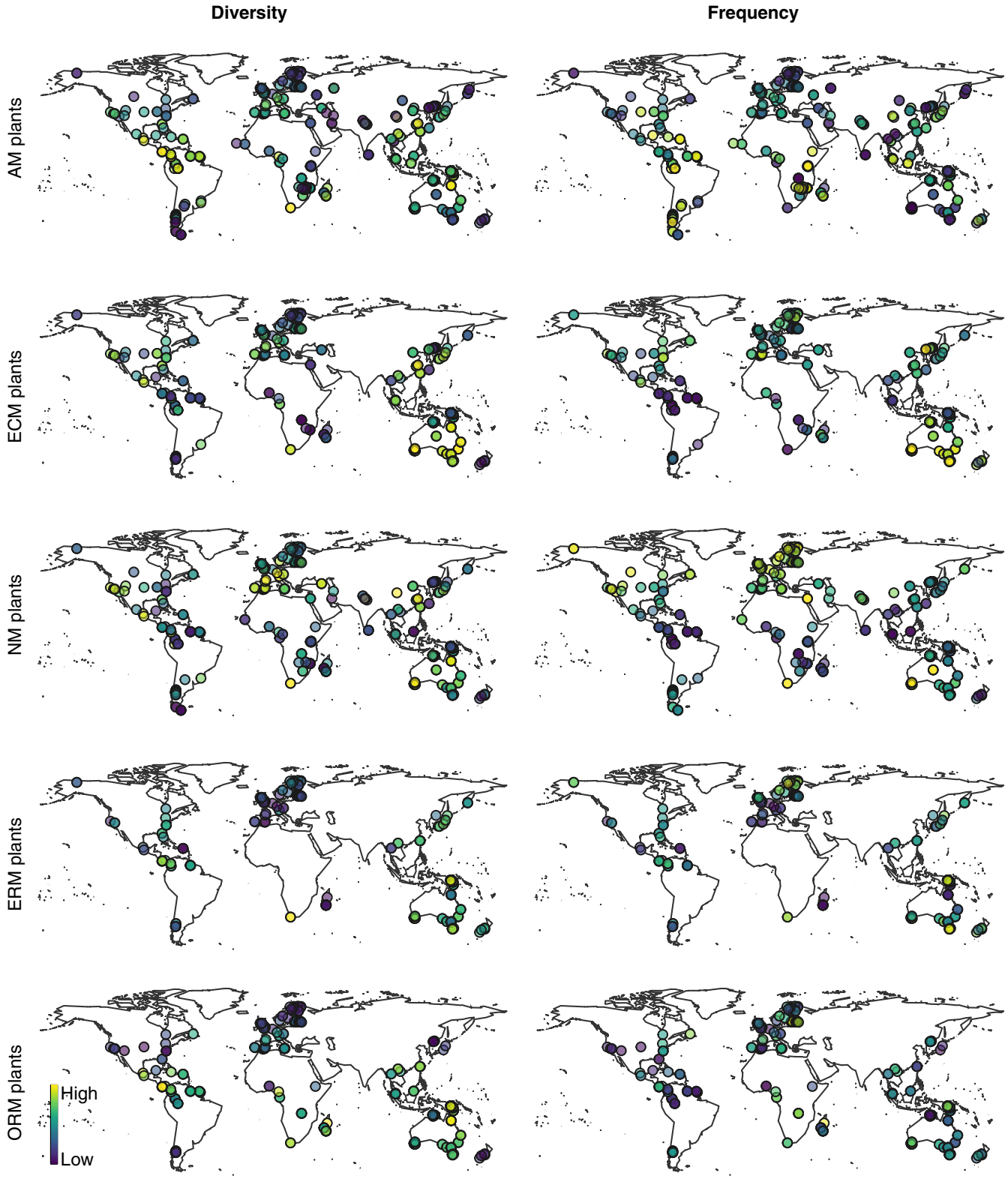

FIGURE 2 Global maps of diversity and frequency of mycorrhizal types. Panels in the first column show diversity; those in the second column show frequency. Diversity is calculated as the effective species richness (i.e. the number of species at each site after extrapolation using iNEXT) with a bootstrapping procedure (see Methods and Appendix S5 for details). The frequency of mycorrhizal types was calculated as the log ratio of the number of records corresponding to a particular mycorrhizal type and the number of records representing all other mycorrhizal types. Each row of panels corresponds to a different mycorrhizal type. Colors indicate the mean effective species richness at each site for each taxonomic group. Predictive maps showing smoothed variation in effective species richness and frequency worldwide are shown in Appendix S9

type (ρ = 0.212, $p < 0.001$, Appendix S12): the higher the frequency of the AM plant mycorrhizal type, the higher was the diversity of vascular plants (Figure 1). By contrast, the frequencies of plants of all other plant mycorrhizal types (i.e. ECM, NM, ERM and ORM) were negatively correlated with total vascular plant diversity (Figure 1, Appendix S12).

3.3 | Global diversity of mycorrhizal fungi

The global distribution of fungal diversity was uneven, with AM-species-rich sites in Africa and South America, and lower richness in northern regions (Figure 3b, Appendix S8B). By contrast, ECM fungal diversity exhibited a unimodal relationship with latitude, with species-rich sites in mid-latitude regions, such as North America, Central Europe and Japan, but lower diversity in high-latitude and tropical areas of South America (Figure 3c, Appendix S8C). The southern tip of South America (Patagonia) was the only high-latitude region with high ECM fungal diversity (Figure 3c, Appendix S8C). At the global scale we found a slightly negative correlation between AM and ECM fungi in terms of diversity ($N = 457$, ρ = −0.07, $p < 0.05$).

3.4 | Relationships between the diversity and frequency of plants and mycorrhizal fungi

Total plant diversity was not significantly correlated with AM fungal diversity ($N = 116$, ρ = −0.08, $p = 0.11$, Figure 4, Appendix S4), but there was a significant negative correlation with ECM fungal diversity ($N = 340$, ρ = −0.31, $p < 0.001$, Figure 4, Appendix S4). Moreover, we found positive correlations between the frequency (F) of AM and ECM mycorrhizal plant types and the diversity (D) of their associated fungal groups (AM fungi and ECM fungi, respectively; i.e. AM fungi–AM plants [F]: ρ = 0.17, $p < 0.001$ and ECM fungi–ECM plants [F]: ρ = 0.13, $p < 0.001$, Figure 4, Appendix S4). However, no significant correlation was found between the diversity of AM and ECM mycorrhizal plant types and the diversity of their associated fungal groups, respectively (i.e. AM fungi–AM plants [D]: ρ = −0.09, $p = 0.09$ and ECM fungi–ECM plants [D]: ρ = 0.03, $p = 0.43$, Figure 4, Appendix S4). These results were not strongly affected by the spatial buffer size used to calculate plant diversity and frequency (Appendices S13 and S14).

AM fungal diversity was significantly negatively correlated with the diversity of the NM plant type (ρ = −0.22, $p < 0.01$) and positively with the ORM plant type (ρ = 0.17, $p < 0.05$, Figure 4, Appendix S4), and negatively with the frequency of the ECM and NM plant types (ρ = −0.14, $p < 0.01$ and ρ = −0.12, $p < 0.05$, respectively, Figure 4, Appendix S4). There were variable correlations between the diversity of ECM fungi and the diversity of different plant mycorrhizal types: with positive (NM: ρ = 0.13, $p < 0.001$), non-significant (ERM: ρ = 0.05, $p = 0.24$) and negative correlations (AM: ρ = −0.29, $p < 0.001$, Figure 4, Appendix S4). Similar patterns were recorded in correlations with the frequency of the plant mycorrhizal types (Figure 4, Appendix S4) except for the frequency of the ORM plant mycorrhizal type (ρ = 0.34, $p < 0.001$).

4 | DISCUSSION

Using data from more than 450 sites worldwide, we showed that plant mycorrhizal types correlate differently with the global diversity of vascular plants. The uneven distribution of plant mycorrhizal types across the globe suggests that they are influenced by their fungal symbionts. For instance, the two main plant mycorrhizal types (i.e. AM and ECM) exhibited different, and often reciprocal, correlation. Importantly, their frequency, but not diversity, was significantly and positively correlated with the diversity of their fungal symbionts. These relationships suggest that ECM associations, which emerged relatively recently compared with the AM symbiosis (van der Heijden et al., 2015; Lutzoni et al., 2018) and which exhibited lower total plant richness (Figure 1), may represent a key driver of current and future global patterns of vascular plant and fungal diversity. Indeed, ECM plants may benefit from a fungal mantle creating a barrier that deters pathogens and root herbivores and thus prevents negative soil feedback (Bennett et al., 2017; Teste et al., 2017) or the ability of ECM fungi to mobilize organic nutrients and provide them to plants (Nicolás et al., 2019). These characteristics may render them competitively superior to AM plants, (Dickie, Koele, Blum, Gleason, & McGlone, 2014) and favor the dominance of ECM plant species. It is nonetheless important to note that uncertainty associated with diversity and frequency estimates varied from region to region for most taxonomic groups (Appendices S10 and S11). These analyses revealed variations in the precision of diversity and frequency estimates for different symbionts, including regions of generally low precision for AM fungi in North America, ECM fungi in northern high latitudes, and ECM, ERM and NM plants in parts of Africa. For AM fungi, the lack of available data in North America, combined with a relatively low number of sites worldwide, negatively affected the predictive power of the GAM model (Appendix S3a) and indicated that more data are needed for this region. While global patterns of AM and ECM fungal diversity are known (Pärtel et al., 2017; Tedersoo, 2017), our co-variation approach represents an important further step in understanding the interactions between symbionts of different plant mycorrhizal types and contributes to disentangling the drivers of plant diversity worldwide.

At the global scale, we found a negative relationship between the frequency of the ECM plant type and total plant diversity (Appendix S12), which has been hypothesized in earlier studies (Allen et al., 1995; Connell & Lowman, 1989), but not demonstrated quantitatively. In addition, we showed that lower plant diversity is associated with a higher frequency of ERM, NM and, to a lesser extent, ORM plant types. Many areas where ECM and NM plant types dominate are located in colder environments (Appendix S9),

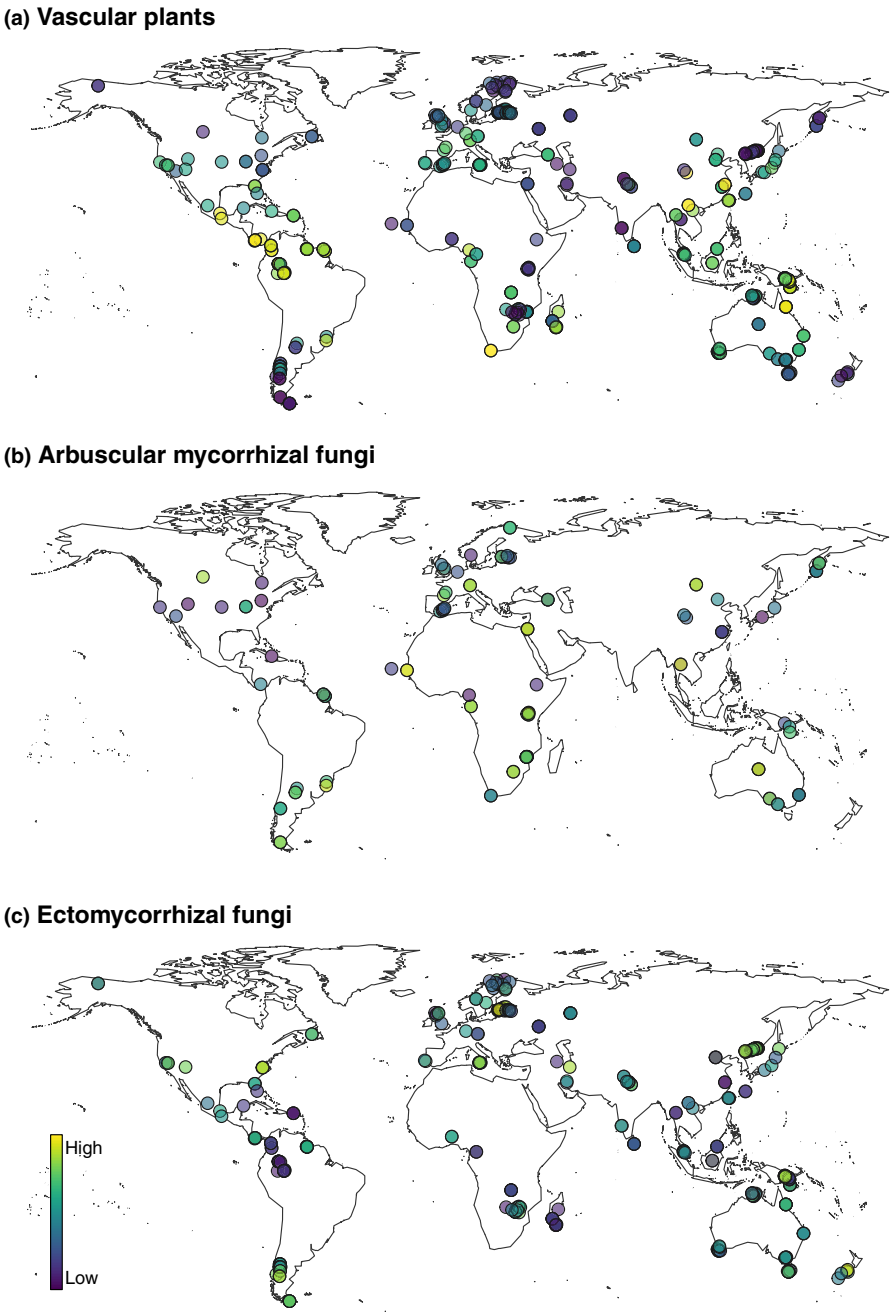

FIGURE 3 Global maps of the diversity of vascular plants and mycorrhizal fungi. Colors indicate the effective species richness at each site (i.e. the number of species at each site after extrapolation using iNEXT). The number of sites differs between the three groups (456 for vascular plants, 116 for Arbuscular mycorrhizal fungi, and 341 for ectomycorrhizal fungi). The reported values correspond to the mean of 10,000 bootstrapped estimates (see Methods and Appendix S5 for details). Predictive maps showing smoothed variation in effective species richness worldwide are shown in Appendix S8

which are evolutionarily recent habitats (Morley, 2000). The ECM symbiosis is also evolutionarily recent, having evolved multiple times since the early Jurassic and becoming increasingly dominant at higher latitudes in the Late Cretaceous, particularly after climate cooling in the Early Eocene and Mid-Miocene (Lutzoni et al., 2018; Tedersoo, 2017). Thus, the phylogenetically conservative cold sensitivity of plants and mycorrhizal fungi (Brown, 2014; Tedersoo, 2017; Tibbett & Cairney, 2007) may have hindered the expansion of plant lineages into high latitudes (Donoghue, 2008), and thus partly explain the low diversity of ECM, ERM and NM plant types. By contrast, the AM symbiosis emerged much earlier, in the Early Devonian (Lutzoni et al., 2018; Martin, Uroz, & Barker, 2017), under a warm tropical climate (Baars, 2017; Le Hir et al., 2011), and the highest diversity of both AM fungi (Pärtel et al., 2017) and plants (Kreft & Jetz, 2007) is still observed in the tropics.

Previous studies have shown that ECM fungi are relatively selective of host plant species, while AM fungi tend to be host generalists (Allen et al., 1995; van der Heijden et al., 2015). Hence, greater diversity of ECM plant species may provide more niches for ECM fungi, resulting in a positive correlation (Kernaghan, Widden, Bergeron, Legare, & Pare, 2003). Our results show that this expected positive correlation between the diversity of ECM fungi and their plant hosts was not evident at the global scale in terms of ECM plant diversity but was in terms of ECM plant frequency (Figure 4). Moreover, we found a non-significant correlation between the diversity of AM fungi and the diversity of their plant hosts, although positive relationships between AM plant and fungal diversity have emerged

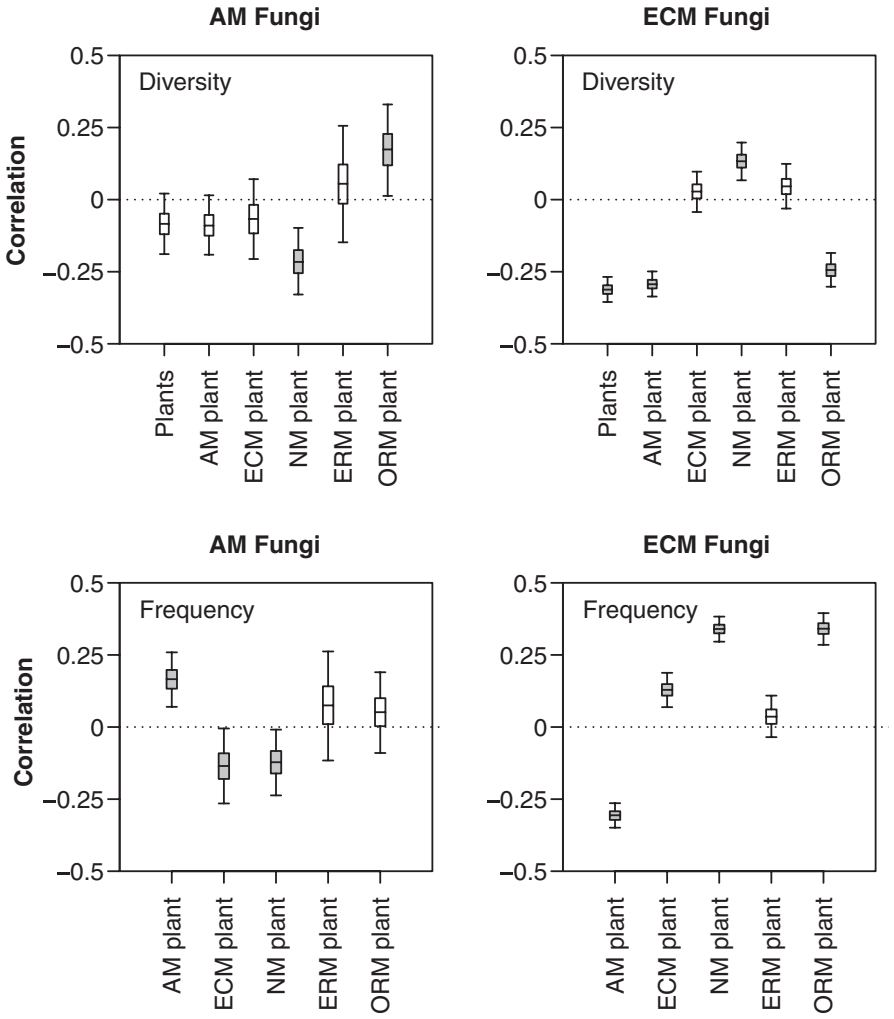

FIGURE 4 Correlations between the diversity of mycorrhizal fungi and the diversity and frequency of vascular plants and plant mycorrhizal types. Correlations were estimated for diversity (first row) and frequency (second row) metrics. Diversity is calculated as the effective species richness (i.e. the number of species at each site after extrapolation using iNEXT) with a bootstrapping procedure (see Methods and Appendix S5 for details). The frequency of mycorrhizal types was defined as the log ratio of the number of records corresponding to a particular mycorrhizal type and the number of records representing all other mycorrhizal types. Spearman's rank correlation was used. Whiskers correspond to 95% confidence intervals calculated from 10,000 correlation coefficients obtained using randomization (see Methods and Appendix S5 for details), boxes to 1st and 3rd quartiles and horizontal lines to median values. Filled rectangles correspond to confidence intervals excluding 0 (i.e. positive or negative correlation), whereas empty rectangles correspond to confidence intervals encompassing 0 (i.e. absence of correlation). The correlation coefficient (rho) and its associated *p*-value are reported in Appendix S4

in experiments (van der Heijden et al., 2008) and in local-scale descriptive studies (García de León et al. 2016; Hiiesalu et al., 2014; Neuenkamp et al., 2018). We showed, however, that high AM fungal diversity was associated with high AM plant frequency. AM fungi lack host specificity at the species level (Helgason & Fitter, 2009; Maherali, Oberle, Stevens, Cornwell, & McGlinn, 2016; Sanders, 2002) and hence the availability of broadly suitable "habitat" (i.e. the roots of any AM plant species) may be important for maintaining AM fungal diversity. Furthermore, the frequency of host plants in the past may also have promoted the current high diversity of AM fungi in particular regions (Pärtel et al., 2017). AM and ECM fungi exhibit different, and often reciprocal, correlation patterns with plant mycorrhizal types other than that of their hosts, both in terms of diversity and frequency (for NM and ORM plant types). This may reflect the influence of environmental conditions on the distribution of mycorrhizal associations. For example, in colder conditions, where ECM fungi are favored and AM disfavored, the frequency of cold-tolerant NM plants negatively correlates with the diversity of AM fungi and positively with that of ECM fungi, as expected.

Contrasting patterns of diversity and frequency in symbionts of different mycorrhizal types may also reflect the influence of direct ecological interactions. The ability of the ECM plant type and ECM fungi to outperform the AM plant type and AM fungi under certain conditions may be due to ECM fungi altering substrate stoichiometry in such a way to inhibit mineralization of soil nutrients, making them less available to the AM plant type (Dickie et al., 2014; Terrer et al., 2018). It is

also notable that the ECM plant type generally exhibits positive plant–soil feedback, compared with mostly negative feedback in the AM plant type (Bennett et al., 2017) and also exhibits wider niches than the AM plant type (Gerz, Guillermo Bueno, Ozinga, Zobel, & Moora, 2018). This difference might be due to the dense colonization of fine root surfaces by ECM fungi, which provides more efficient protection of host plants from microbial pathogens, compared with the AM association (Bennett et al., 2017; Teste et al., 2017). These ecological interactions may themselves be a result of evolutionary changes in plants and fungi facing historical climatic and environmental changes (Brundrett & Tedersoo, 2018; Ma et al., 2018).

Recognizing the relationships between plant and fungal mycorrhizal types in terms of diversity and frequency may allow the effects of ongoing climate change to be understood and predicted more clearly. For example, experimental evidence shows that the ECM plant type exhibits stronger growth responses than the AM plant type to increased CO_2, due to its ability to better overcome nitrogen deficiency (Terrer, Vicca, Hungate, Phillips, & Prentice, 2016; Terrer et al., 2018). If this is the case, the frequency of the ECM plant type is expected to increase under future global change scenarios (Tedersoo, 2017). Thus, the correlation patterns identified here suggest that such a process would be accompanied by decreases in the diversity and abundance of AM fungal and plant species, which could have profound effects on ecosystem functioning, such as carbon, nitrogen and phosphorus cycling (Fernandez & Kennedy, 2016; Lin, McCormack, Ma, & Guo, 2017; Rosling et al., 2016; Treseder & Lennon, 2015). In the future, there is a need to complement correlative studies with empirical tests concerning the quadripartite competition between ECM and AM symbiotic partners, and interactions involving ERM and NM partners, in order to better understand the distribution of mycorrhizal types and predict their responses to global change.

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AUTHOR CONTRIBUTIONS

AT, MM, MÖ, MZ, and MP designed the study. MÖ built the AM fungal database, LT built the ECM fungal database and AT performed the analyses. All the authors discussed the results and contributed substantially to the final manuscript.

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DATA AVAILABILITY STATEMENT

This publication is supported by multiple datasets, which are available at locations cited in the reference section. No new data were created during this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

APPENDIX S1. Number of records and effective species richness per site of fungi, plants and plant mycorrhizal types
APPENDIX S2. Correlations between plant mycorrhizal types in terms of diversity. Diversity
APPENDIX S3. Accuracy of GAM models for diversity and frequency of fungi, plants and plant mycorrhizal types
APPENDIX S4. Correlations in diversity and frequency between fungi and plants and plant mycorrhizal types
APPENDIX S5. Framework for calculating biodiversity indices for each taxonomic group using bootstrapping
APPENDIX S6. Relationships between estimates of plant diversity calculated using two different community sample sizes (buffer zone)
APPENDIX S7. Correlation between plant species richness from the GBIF and Kreft and Jetz (2007) databases
APPENDIX S8 Global maps showing the predicted diversity of mycorrhizal fungi and vascular plants
APPENDIX S9. Global maps showing the predicted diversity and dominance of different plant mycorrhizal types
APPENDIX S10. Uncertainty associated with predictions of diversity for mycorrhizal fungi and vascular plants
APPENDIX S11. Uncertainty associated with predictions of the diversity and frequency of different plant mycorrhizal types
APPENDIX S12. Correlations between plant diversity and the frequency of mycorrhizal types
APPENDIX S13. Correlations between AM and ECM fungal diversity and the diversity of plants and plant mycorrhizal types calculated using three buffer zone sizes
APPENDIX S14. Correlations between AM and ECM fungal diversity and the frequency of plant mycorrhizal types calculated using three buffer zone sizes

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