

Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe

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Abstract

Aim: Identifying the factors that drive large-scale patterns of biotic interaction is fundamental for understanding how communities respond to changing environmental conditions. Mycorrhizal symbiosis is a key interaction between fungi and most vascular plants. Whether plants are obligately (OM) or facultatively (FM) mycorrhizal, and which mycorrhizal type they form – arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), ericoid mycorrhizal (ERM) or non-mycorrhizal (NM) – can have strong implications for plant species distribution at the continental scale and on the responses of plants to environmental gradients.

Location: Europe, north of 43° latitude and excluding Russia, Belarus and Moldova.

Time period: Undefined.

Major taxa studied: Vascular plants.

Methods: Using published sources, we compiled the most complete dataset yet of plant mycorrhizal and geographical information for Europe, comprising 1442 plant species. We mapped the European distributions of plant mycorrhizal status (OM and FM) and type (AM, ECM, ERM and NM) and analysed their relationships with climatic, edaphic and plant productivity drivers on a 50 km × 50 km equal-area grid.

Results: The distribution of mycorrhizal types in Europe was driven by mean temperature, soil pH and productivity. AM plant species predominated throughout the region, but at higher latitudes the share of NM and, to a lesser extent, ECM and ERM species increased. FM species predominated over OM species, and this increased with latitude and was dependent on temperature drivers. The high share of OM species in the central European mountains indicates a possible influence of historical glacial refugia.

Main conclusions: Our results challenge the prevailing view of parallel trends in the latitudinal and elevational distribution of mycorrhizal types and demonstrate distinctive responses of plants with different mycorrhizal status to climatic, edaphic and biogeographical drivers at the European scale.

KEYWORDS

arbuscular mycorrhiza, climate, ectomycorrhiza, ericoid mycorrhiza, facultative mycorrhizal, non-mycorrhizal, obligate mycorrhizal, soil

1 | INTRODUCTION

Mycorrhizae are ancient symbioses between fungi and plant roots which allow fungi to receive plant-synthesized carbon while providing plants with increased nutrient foraging ability and tolerance of abiotic and biotic stress (Smith & Read, 2008). The benefit gained from mycorrhizal symbiosis differs among individual plants and species, influencing plant–plant interactions (Moora & Zobel, 2010; Van Der Heijden, Bardgett, & Van Straalen, 2008) and the structure and functionality of plant communities (Van Der Heijden et al., 2008).

Multiple types of mycorrhizal symbiosis are recognized based on their morphology and the identity of both partners (Smith & Read, 2008). Arbuscular mycorrhizae (AM) are the most common type, being formed by more than 80% of vascular plant species, including herbaceous plants and various trees, while ectomycorrhizae (ECM) and ericoid mycorrhizae (ERM) are formed by approximately 2% of mostly woody plants, and 1% of plants limited to the Ericaceae family, respectively (Brundrett, 2009). About 6% of vascular plant species are believed to be non-mycorrhizal (NM). Such species do not seem to represent a particular plant life-form, although several plant families have been considered as predominantly NM (Brundrett, 2009).

The current theoretical understanding of how mycorrhizal types are distributed at large scales was proposed by Read (1991) and Read and Perez-Moreno (2003). They argued that the vegetation of different biomes changes in parallel along latitudinal and elevational gradients, reflecting similar climatic gradients and relating directly to the different roles of mycorrhizal types in plant nutrition. Their model was based on the ability of ERM and to a lesser extent ECM, but not AM, plants to decompose and access nutrients in organic compounds, especially in acidic and infertile soil conditions with a high organic matter content. Based on these assumptions, Read and colleagues proposed a gradual turnover with increasing latitude or elevation: from vegetation dominated by AM plant species (grassland, forest or shrubland); to forests dominated by ECM species and an understorey with AM or ERM species; to heathlands dominated by ERM species. There is currently empirical information about the distribution of mycorrhizal types and status in Germany (Menzel et al., 2016) and a map of potential mycorrhizal associations in the USA (Swaty, Michael, Deckert, & Gehring, 2016). To the best of our knowledge, however, neither the theoretical model of vegetation structure nor plant species distribution models focusing on mycorrhizal symbiosis have been empirically tested at a continental scale. In addition, detailed analyses of the precise environmental factors driving the distribution of plant mycorrhizal traits over broad spatial scales are largely lacking.

Previous studies addressing drivers of plant mycorrhizal trait distribution have been restricted to specific biomes, such as the polar regions (Newsham, Upson, & Read, 2009), targeted ecosystem succession (Dickie et al., 2013) or focused on global variation in root colonization rates (Soudzilovskaia et al., 2015; Treseder & Cross, 2006). However, integrating large-scale empirical data on the distribution and drivers of mycorrhizal types not only has the potential to enhance our understanding of the role of mycorrhizal symbiosis within and across

biomes, but may also help with predicting the impacts of global change, which is likely to affect plant mycorrhizal types differently (Cheng et al., 2012).

Based on the frequency of occurrence of mycorrhizal symbiosis among individuals of a mycorrhizal plant species, its mycorrhizal status can be categorized as consistently colonized (OM, obligately mycorrhizal) or sometimes colonized (FM, facultatively mycorrhizal) in nature (Smith & Read, 2008; page 28). Mycorrhizal status, mycorrhizal dependency (or responsiveness) and mycorrhizal colonization intensity represent different traits (Moora, 2014; Soudzilovskaia, et al., 2015). While mycorrhizal dependency describes the responses of plant growth to colonization and mycorrhizal colonization intensity the extent of root colonization at the level of the individual plant, mycorrhizal status reflects consistency in the presence or absence of fungal colonization within a species. Furthermore, large-scale patterns of plant mycorrhizal status can highlight conditions that determine the importance of mycorrhizal symbiosis across ecosystems (Menzel et al., 2016, 2017; Moora, 2014). The distribution of mycorrhizal status has previously been addressed in the regional floras of the UK for AM plants (Peat & Fitter, 1993) and of Germany (Hempel et al., 2013). Hempel et al. (2013) addressed the association between plant mycorrhizal status and known ecological requirements, and showed that OM plant species tend to prefer drier, warmer habitats with higher soil pH. They also showed that FM species have broader ecological requirements compared with to OM species at the regional scale. Although plant mycorrhizal status can be importantly related to habitat preferences and functional roles in ecosystems (Hempel et al., 2013; Van Der Heijden et al., 2008), large-scale information about the distribution of plants with different mycorrhizal statuses is scarce.

Information about the distribution and traits of vascular plants is gradually accumulating. Europe, with the exception of the most southern and eastern areas, is floristically one of the best-studied regions on the planet. Plant species distribution maps (Kalwij, Robertson, Ronk, Zobel, & Pärtel, 2014), together with relatively extensive plant mycorrhizal trait information (Akhmetzhanova et al., 2012; Hempel et al., 2013), namely plant mycorrhizal type and status data (Hempel et al., 2013; Moora, 2014), are available for this region. While plant distribution data alone do not allow species abundance to be incorporated into an assessment of the dominance of plant mycorrhizal types and statuses, the share of plant species with particular mycorrhizal traits in co-occurring species assemblages can still be estimated. Such data could provide the first empirical information about changes in the share of plant species with different mycorrhizal traits along environmental gradients in Europe.

Here, we provide a first empirical assessment of large-scale patterns of mycorrhizal association in Europe. We map the distribution of plant species with different mycorrhizal traits in Europe, excluding the most southern and eastern areas due to a shortage of reliable data from these regions. We also ask (a) whether the share of plant species exhibiting AM, ECM, ERM or NM mycorrhizal type, or OM or FM mycorrhizal status, changes along latitudinal and elevational gradients; and (b) which environmental variables drive the share of plant species

with different mycorrhizal types and statuses. Following Read's assumptions, we expect latitude and elevation to show parallel mycorrhizal patterns, driven by similar changes in soil and climate conditions (Read, 1991; Read & Perez-Moreno, 2003), such that the share of AM plant species decrease, while the proportions of ECM and ERM plant species increase, along latitudinal and elevational gradients. Nonetheless, we also expect relatively large proportions of AM and NM species to be apparent in high latitudes. While Read based his assumptions on the inability of AM species to take up organic N (Read, 1991; Read & Perez-Moreno, 2003), there have been recent suggestions that AM plants may obtain N from organic sources (Hodge & Fitter, 2010). Along with the ability of AM species to resist cold conditions (Kytöviita, 2005; Tibbett & Cairney, 2007), this might allow AM plants to occur in high latitudes to a greater degree than previously believed. On the other hand, NM species, which were not considered by Read, not only perform successfully in disturbed successional environments but also in stressful environments, such as the Arctic (Brundrett, 2009; Lambers & Teste, 2013). They may cope with nutrient limitation at high latitudes in ways that do not incur the costs of supporting mycorrhizal fungi: organic N uptake (Kielland, 1994), possessing root morphology analogous to proteoid roots (Shane, Cawthray, Cramer, Kuo, & Lambers, 2006) or specializing in the uptake of the most available form of N (McKane et al., 2002).

2 | METHODS

2.1 | Distribution of mycorrhizal types and statuses in Europe

To study the distribution of plants with different mycorrhizal types and statuses in Europe we used the most comprehensive available plant species atlas at the European scale (Kalwij et al., 2014). This atlas, which describes plant species occurrence in 50 km × 50 km grid cells, combines information from two pan-European atlases: the Atlas Flora Europaea (Jalas & Suominen, 1988) and the Atlas of North European Vascular Plants (Hülten & Fries, 1986). However, the Mediterranean area and some former Soviet countries in the east are not well represented, and were excluded from the analyses (see details in Appendix S2 in the Supporting Information). The distribution maps for European plant species were used in conjunction with a new database of plant mycorrhizal traits (Appendix S1). To assign mycorrhizal types (AM, ECM, ERM, NM) and statuses (FM, OM) to plant species we first compiled existing datasets of plant mycorrhizal traits (Akhmetzhanova et al., 2012; Harley & Harley, 1987; Hempel et al., 2013; Wang & Qiu, 2006) and then carried out an additional search for plant mycorrhizal trait data for the most abundant species not covered by previous datasets. To avoid errors and inconsistencies among these datasets, we checked and corrected all records to reflect the original source.

To assess the influence of possible undetected errors in the dataset, we artificially introduced errors to the mycorrhizal type and status affiliation of 20% of plant species (i.e., replacing the recorded trait category with a randomly selected alternative) and obtained qualitatively similar results to those derived from analysis of raw data (Appendix

S2). This suggests that conclusions based on this plant mycorrhizal trait dataset are robust, especially given that the error rate in plant species mycorrhizal trait databases has been estimated at around 10% (Brundrett, 2009). Besides, plant mycorrhizal datasets can be taxonomically biased, for example over-representing species from one family or not covering certain clades. We compared the family-level taxonomic affiliation of plant species in our list with that of plant species in Flora Europaea, and found no evidence of strong taxonomic bias (Appendix S2).

To map the share of different plant mycorrhizal types in Europe, we calculated the proportions of plant species with AM, ECM, ERM or NM types in relation to all plant species in each grid cell (e.g., % AM = number of AM species/total number of species). Arbutoid mycorrhizal symbiosis was pooled together with ECM, due to their very low frequencies and their structural and functional similarities (Smith & Read, 2008). Orchid mycorrhizal plants (ORM) were omitted from the study due to their low representation (41 species). Plants with dual mycorrhizal symbiosis (ECM + AM) were assigned to both ECM and AM for each individual-type analysis. Proportions of each plant mycorrhizal status were calculated as the number of species of each status (OM or FM) in relation to all mycorrhizal plant species in a given grid cell (e.g., % OM = number of OM species/number of mycorrhizal species) or in relation to AM plant species alone (Appendix S3). Maps were generated using an equal-area grid.

2.2 | Drivers of plant mycorrhizal trait distribution

Climatic, edaphic and productivity variables are known to be important drivers of the distribution of plant species and mycorrhizal fungi at large spatial scales (Davison et al., 2015; Read, 1991), and thus represent potential drivers of the distribution of plant mycorrhizal type (Smith & Read, 2008) and status (Gerz, Bueno, Zobel, & Moora, 2016).

Among climatic variables, we considered average evapotranspiration and temperature and precipitation variables from the Numerical Terradynamic Simulation Group and BioClim databases (Appendix S4), describing annual trends, seasonality and extreme or limiting environmental factors world-wide. We checked collinearity and multicollinearity among BioClim variables and evapotranspiration, and four representative and weakly correlated (Pearson correlation < .6 and variance inflation factor (VIF) < 3) BioClim variables were selected for further analysis: mean annual temperature (MAT), mean diurnal temperature range (MDR), annual precipitation (APP) and precipitation seasonality (PPS) (Appendix S4). MAT and APP represent annual average trends, while MDR and PPS represent variation, indicating to a certain extent the continentality of the climate.

Two relevant edaphic variables were available from the World Soil Information website (Appendix S4): soil pH and soil organic carbon (SOC). SOC and pH were highly negatively correlated (Pearson $r = -.8$), as acidification leads to reduced decomposition and a higher accumulation of organic matter, and vice versa (Brady & Weil, 2010). Thus, only pH was retained for use in the analyses. We also compiled estimates of net primary productivity (NPP) from the Numerical Terradynamic Simulation Group website (Appendix S4). When climatic variables are accounted for, a higher NPP may indicate fertile areas with higher plant

growth rates and thus potentially higher soil nutrient accessibility for plants.

Climatic, edaphic and productivity factors are expected to be closely related at large scales (Brady & Weil, 2010). In our dataset latitude was indeed correlated with temperature, pH and productivity. We found a high correlation of latitude with MAT ($r = -.9$), pH ($r = -.7$) and NPP ($r = -.7$; Appendix S4), and of MAT with NPP ($r = .8$) and pH ($r = .7$; Appendix S4). To prevent problems arising from multicollinearity, we prioritize the effect of pH and NPP over MAT as trends in temperature closely follow latitudinal ones, which are described in parallel. Therefore, MAT was replaced by the residuals of temperature after removing any pH or NPP effect on MAT (hereafter MATr). As the original data sources consistently had a spatial resolution of either 30 arc-sec or 1 km² grid cell (Appendix S2), all variables were scaled up to 50 km × 50 km resolution prior to all analyses.

2.3 | Modelling approach

To address the effect of climatic and edaphic gradients on the predominance of plant mycorrhizal traits in Europe, we used generalized linear models (GLM) with binomial error distributions and logit link functions. For each plant mycorrhizal trait value (e.g., AM, ECM, ERM and NM for mycorrhizal types), binary response variables were formed from the *successes*, that is, the number of species with that particular trait value, and the *failures*, that is, the number of species without that particular trait value. For plant mycorrhizal status with two levels (OM and FM), just one level was used to analyse the variation of the trait in relation to potential drivers. We accounted for model uncertainty by using a model averaging approach based on the average of the best models ($\Delta AIC < 7$; AIC, Akaike information criterion) (Burnham & Anderson, 2002). The final set of predictors included six variables: pH, NPP, MATr, APP, MDR and PPS. All predictors were standardized to avoid issues arising from scaling variance during model averaging (Burnham & Anderson, 2002).

Spatial autocorrelation in the residuals of all models was detected using Moran's correlogram and spatial residuals plots and was accounted for by adding selected spatial predictors to all models, following the spatial eigenvector mapping (SEVM) approach (Dray, Legendre, & Peres-Neto, 2006). After adding the selected spatial predictors to the models, no further significant spatial autocorrelation was detected (Appendix S5). The spatial predictors were considered fixed for the model averaging procedure, so they were included in all models.

All analyses were performed in R 3.2.1 (R Core Team, 2014), using the R packages Spacemaker, Packfor and MuMIn.

3 | RESULTS

Of the plant species included in this study, 948 (66%) formed AM, 61 (4%) formed ECM, 53 (4%) were dual mycorrhizal (AM + ECM), 19 (1%) formed ERM and 361 (25%) were NM. Regarding plant mycorrhizal status, 588 (41%) species were OM and 493 (34%) were FM.

3.1 | Distribution of plant mycorrhizal types and statuses in Europe

The proportion of plant species with each mycorrhizal type within 50 km × 50 km grid cells (Figure 1) was on average (\pm SD) 75 \pm 4% for AM, 7 \pm 1% for ECM, 1 \pm 1% for ERM, 21 \pm 2% for NM, 42 \pm 3% for OM and 55 \pm 4% for FM. All plant mycorrhizal types and statuses were present in all grid cells. The relative proportions of types changed significantly along latitudinal (Figure 2a) but not elevational (Figure 2b) gradients. The share of AM plant species peaked at low latitudes, with the exception of high mountain ranges, including the Alps, Carpathians, Balkans and Pyrenees (Figure 1a and Fig. S4.2h). NM plant species were the second most abundant type, peaking at high latitudes regardless of elevation (Figure 1d). The share of ECM plant species peaked at high latitudes, in northern Fennoscandia, and to a lesser extent at higher elevations in low latitudes, in the Alps, Carpathians, Balkans and Pyrenees (Figure 1b and Fig. S4.2h). Lastly, ERM plant species were confined to high latitudes but not high elevations (Figure 1c).

By contrast, the relative proportions of plant mycorrhizal statuses showed opposite trends along elevational and latitudinal gradients (Figure 2c,d). The share of OM plant species was higher towards southern latitudes, with a maximum of 48% of OM plant species per grid cell (Figure 1e). The share of OM plant species decreased and the share of FM plant species increased, peaking at 72% of FM species per grid cell at higher latitudes and in the coastal regions of north-western Europe (Figure 1f). At increasing elevations there was a steady increase in the share of OM plant species, while the opposite was observed for FM species (Figure 2d). The effect of elevation on the share of OM and FM plant species varied along the latitudinal gradient. A slightly higher proportion of OM plant species occurred at high elevations at lower latitudinal ranges, such as in the Alps, Balkans, Carpathians and Pyrenees (Figure 1e and Figs S3.1a, S4.2h and S6.1a), while there was a relative increase in the share of FM plant species at higher elevations in the Scandes and Scottish Highlands (Figure 1f and Figs S3.1b, S4.2h and S6.1b).

3.2 | Drivers of plant mycorrhizal trait distribution

The distribution of plant mycorrhizal types was mostly explained by MATr, soil pH and NPP (Figure 3a; models are fully described in Appendix S5). Higher proportions of AM plant species in grid cells were significantly positively related to MATr, soil pH and NPP. Higher proportions of ECM and ERM plant species were related to lower values of MATr, pH and NPP (Figure 3a). Proportions of ECM plant species were positively related, while proportions of ERM plant species were negatively related, to mean temperature diurnal range (MDR), indicating that ECM is favoured, and ERM disfavoured, by wider diurnal temperature variations (Figure 3a). Only the proportion of ERM plant species was related to higher precipitation seasonality (Figure 3a). Higher proportions of NM plant species were related to lower values of pH, NPP and MATr. This suggests that the proportion of NM plant species is higher in more acidic, unproductive, colder and lower-elevation areas at higher latitudes (Figure 3a). Higher proportions of OM plant species were related to higher values of MDR with relatively lower MATr, characteristic of

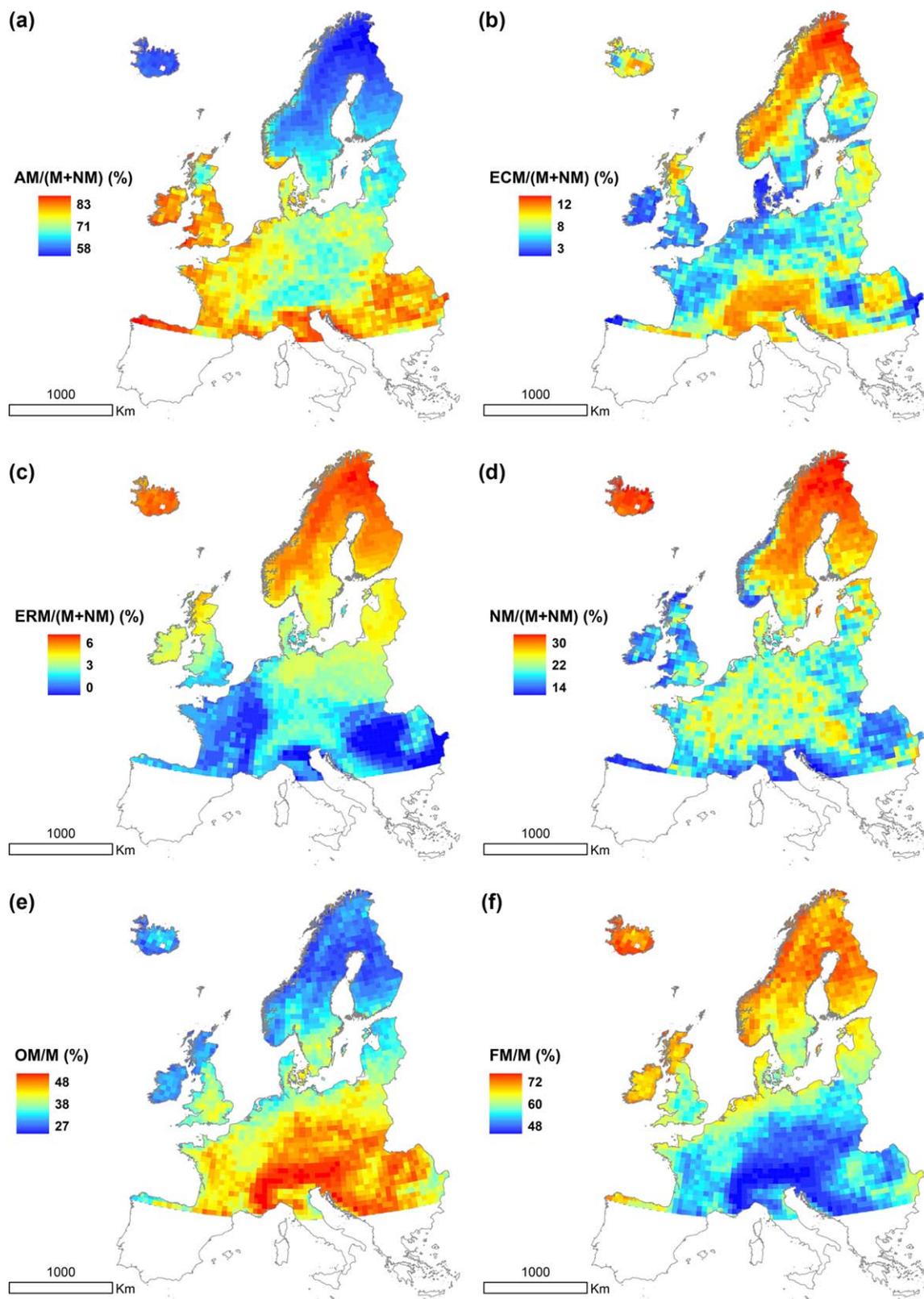


FIGURE 1 The share of plant species of particular mycorrhizal type and status in 50 km × 50 km grid cells in Europe: arbuscular mycorrhizal (AM; a), ectomycorrhizal (ECM; b), ericoid mycorrhizal (ERM; c) and non-mycorrhizal (NM; d) associations among all studied plant species, and obligately mycorrhizal (OM; e) and facultatively mycorrhizal (FM; f) associations among studied mycorrhizal plant species. Values in legends represent the respective maximum, median and minimum proportions. 'M' stands for mycorrhizal plant species

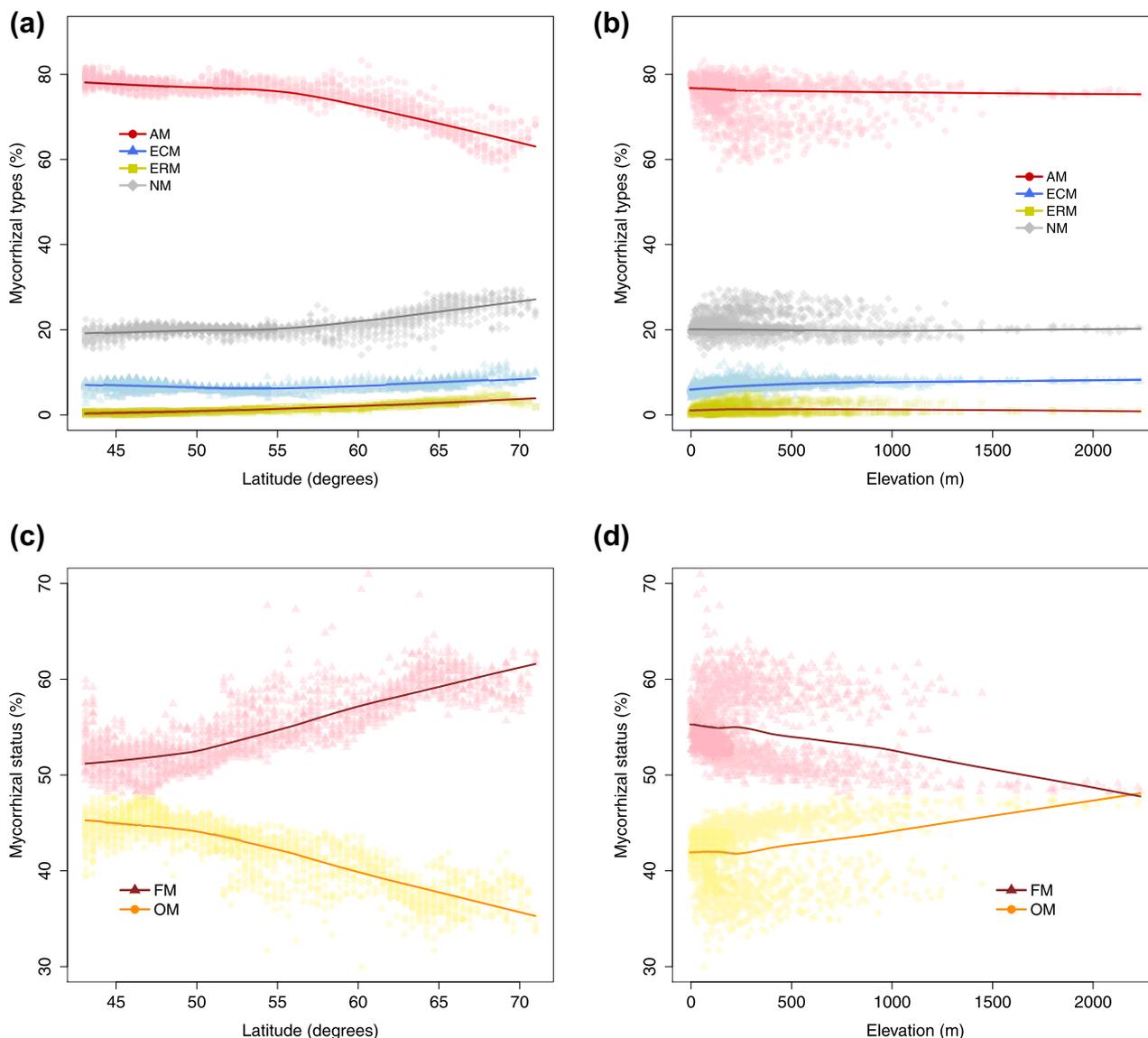


FIGURE 2 The predominance of different plant mycorrhizal types in relation to (a) latitude and (b) elevation and of different plant mycorrhizal statuses with (c) latitude and (d) elevation. Lines represent fitted curves from loess regression

more continental or high-elevation areas (Figure 3b). When only AM plant species were considered in the analysis of plant mycorrhizal status distribution, pH and NPP became more important predictor variables than MATr. The exclusion of ERM and ECM plant species, which generally have lower temperature preferences than AM plant species, and a greater preference of AM plant species for higher pH and NPP values among OM, compared with FM, species seem to underlie these associations when considering only AM plant species.

4 | DISCUSSION

We expected the predominance of mycorrhizal types (AM, ECM, ERM and NM) among co-occurring plant species assemblages to show parallel changes along latitudinal and elevational gradients in Europe. We show on the basis of empirical data that, in fact, all plant mycorrhizal

types respond differently to latitude and elevation. Moreover, the proportions of OM and FM plant species show opposite trends along latitudinal and elevational gradients. As we predicted, decreasing MAT, pH and NPP drive relative decreases in the number of AM plant species and increases in NM, ERM and ECM plant species with increasing latitude. The share of OM and FM plant species in assemblages is driven by the interaction of MDR and MAT. Finally, our results indicate a high share of NM plant species in the European flora – after AM species, NM plant species are the second most abundant in all geographical areas – and a latitudinal trend in the importance of this type.

We detected a decrease in the share of AM plant species and a parallel increase among ECM plant species with increasing latitude and to a lesser extent at higher elevations. This reciprocal trend among plant species with different mycorrhizal types can be explained by differences in their habitat preferences, which appear to reflect their evolutionary origins. The arbuscular mycorrhizal association originated in

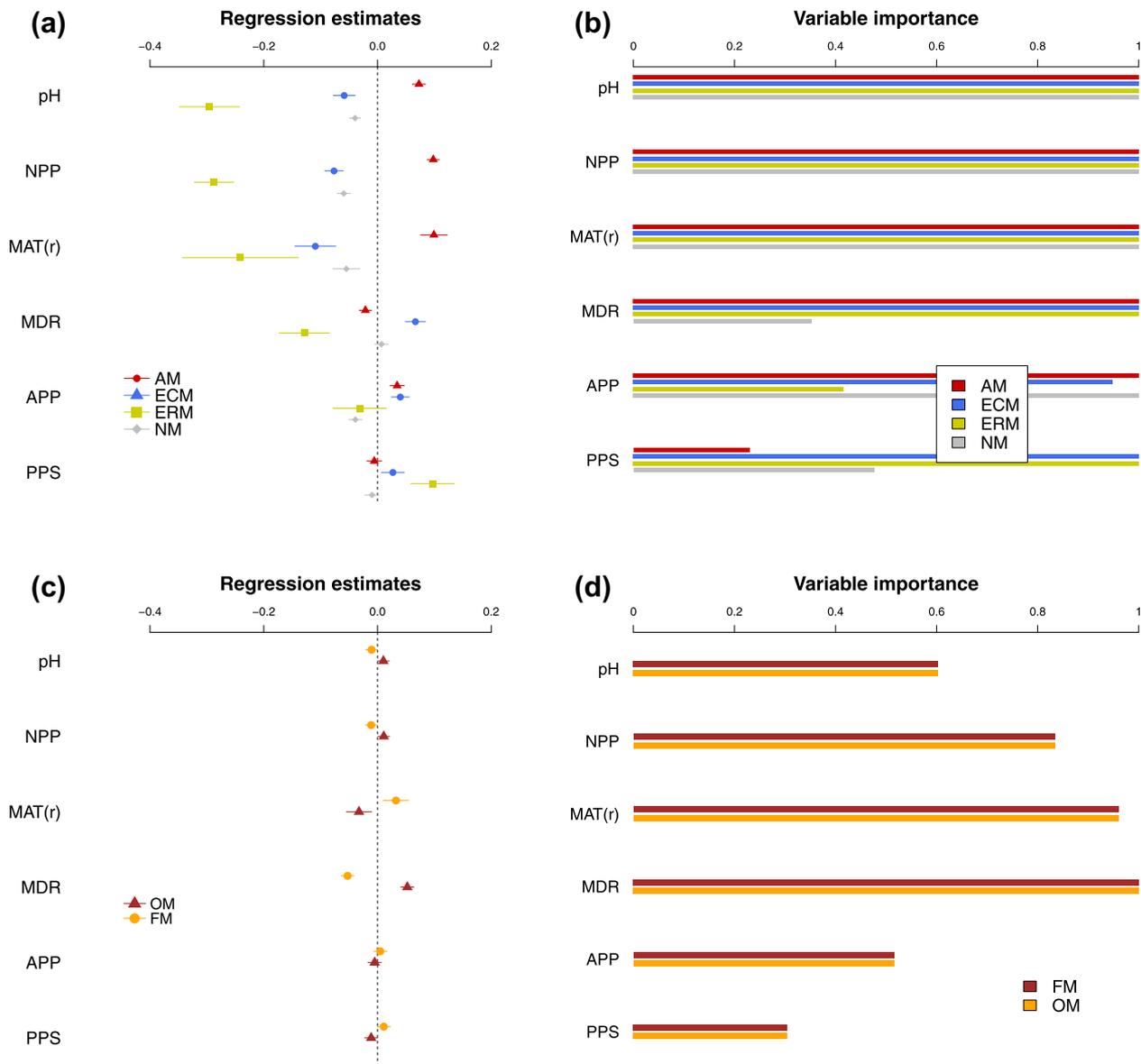


FIGURE 3 Model averaged ($\Delta AIC < 7$) predictor coefficients with one confidence interval and variable importance plots describing the proportion of plant species with plant mycorrhizal types (a, b) and statuses (c, d) in Europe. The importance for each variable was calculated as the sum of the Akaike weights for all the models where each particular variable appears. Variable importance is used to rank the relevance of the predictors, as it indicates the relative probability of each variable belonging to the best model set. AM, arbuscular mycorrhizal; ECM, ectomycorrhizal; ERM, ericoid mycorrhizal; NM, non-mycorrhizal; OM, obligate mycorrhizal; NPP, net primary productivity; MAT(r), residuals of mean annual temperature excluding the effect of pH and NPP; MDR, mean diurnal temperature range; APP, annual precipitation; PPS, precipitation seasonality

the tropics (Bonfante & Genre, 2008), while many ECM associations are of temperate origin (Tedersoo et al., 2012). However, concrete mechanisms that place a physiological limit on the formation and viability of AM in cold environments, and thus also potentially restrict the occurrence of AM plant species, are likely to be complex (Kytöviita, 2005; Tibbett & Cairney, 2007).

Besides temperature, soil pH and fertility were important drivers of the share of AM plant species in Europe. The relationship between plant mycorrhizal traits and pH is known from earlier ecophysiological experiments (Coughlan, Dalpé, Lapointe, & Piché, 2000; Van Aarle, Olsson, & Söderström, 2002) and descriptive studies (Hempel et al.,

2013; Peat & Fitter, 1993). For instance, preferences for more alkaline habitats have been shown by AM plant species (Peat & Fitter, 1993). Information about the link between mycorrhizal traits and soil fertility and related parameters is somewhat equivocal. In fact previous studies have shown all possibilities: AM fungi can decrease in fertile soils (Treseder, 2004), or their colonization intensity can peak in moderately fertile soils (Soudzilovskaia et al., 2015), or there may not be a clear association between soil fertility and the occurrence of AM plant species (Peat & Fitter, 1993).

NM plant species represented 25% of the flora analysed in this study and their share in co-occurring species assemblages was found

to increase in northern latitudes (Figure 1d), with MAT, pH and productivity being the most important drivers (Figure 3a). While this trend remained clear even when incorporating an artificial error rate of 20% in the mycorrhizal trait categorization (Appendix S2), the absolute percentages of each mycorrhizal trait level need to be interpreted with caution and placed in the context of the current incomplete mycorrhizal knowledge of the European flora. Being non-mycorrhizal is an evolutionarily recent plant characteristic (Trappe, 1987) that has started to gain greater attention in mycorrhizal research (Brundrett, 2009; Kytöviita, 2005; Lambers & Teste, 2013; Newsham et al., 2009). Peat and Fitter (1993) did not find any clear association of British NM plant species with particular environmental conditions such as soil pH or fertility. However, some previous studies have also noted an increased abundance of NM plant species at higher latitudes, although the mechanisms driving the pattern remain elusive (Brundrett, 2009; Kytöviita, 2005; Newsham et al., 2009). In cold areas, the occurrence of NM plant species has been attributed to inadequate nutrient acquisition by mycorrhizal fungi in cold conditions, with the fungus presenting a continued carbon drain on the host plant (Tibbett & Cairney, 2007). The performance of NM plants in high latitudes, where most nitrogen is available in organic forms, may also be enhanced by dark septate fungi (Newsham et al., 2009). Also, some plants are capable of taking up organic N directly (Kielland, 1994) through proteoid roots or analogous structures (Shane et al., 2006), or of specializing on forms of N that are temporarily or locally abundant (McKane et al., 2002). However, the precise mechanisms enhancing performance of NM plants in cold climates remain to be established.

The observed change in the relative number of ERM plant species along latitudinal and elevational gradients differed from our expectation that the highest proportions of ERM would occur at high latitudes and elevations. While higher shares of ERM plant species were associated with lower mean annual temperatures and soil pH values and the share of ERM plant species increased with latitude, the share of plant species with other mycorrhizal types remained considerably higher. In fact, we did not even observe high proportions (a maximum of 6%) of ERM plant species at the highest latitudes. Care should be taken when extrapolating this result to other high-latitude areas. Although vegetation in the northern part of European Russia is generally similar to that in Fennoscandia, with abundant ericaceous species, Siberian tundra is less homogeneous and more complex, with several dominant plant communities both with and without ericaceous species (Walker et al., 2005). Further studies are needed to determine the extent to which our result holds throughout the Holarctic region.

We did not find an elevational trend in the share of ERM plants, despite the overall strong negative relationship of this group with temperature. The proportion of ERM plants did not increase with elevation in any of the central European mountain ranges, as might be expected given the ability of such plants to cope with low temperatures and high soil organic matter. One plausible reason for this is that the occurrence of ericoid plants may have been suppressed by anthropogenic land use such as grazing, which replaces ERM-dominated forest or shrubland

with semi-natural grassland. A major conversion of land-use types in the central European mountains started as long as 4500 years ago (Giguet-Covex et al., 2014). Ericaceous shrubs may have been disfavoured since then due to trampling and cutting but also by herbivory (Carcaillet & Brun, 2000; Newton et al., 2009). Overall, our data confirm the observation by Rahbek (1995) of different effects of latitude and elevation on patterns of species richness. However, we cannot rule out the possibility that, depending on the spatial scale, different relationships between the proportions of plant mycorrhizal types and elevational gradients may be observed. Further work at various spatial scales is needed to confirm our findings.

The proportion of OM plant species was positively influenced by mean diurnal temperature range and elevation and negatively by latitude. Consequently, FM plant species showed the opposite pattern. Geographically, OM plant species were most abundant in the central European mountain ranges, while FM plants prevailed in northern Europe, regardless of whether the analysis included all mycorrhizal types or was restricted to AM plant species. This pattern is partially consistent with Hempel et al.'s (2013) finding that OM plant species prefer warmer, drier and more alkaline habitats, compared with FM plants, while avoiding acidic, moist and fertile soils. Also, Menzel et al. (2016) noticed that OM plant species are favoured by a high within-year temperature range. At the scale of our study, the distribution of OM and FM plant species appears to be driven by variation in temperature rather than pH and precipitation, as suggested by Hempel et al. (2013). One hypothetical explanation for this may be the influence of glacial history in Europe. FM plants may have survived in harsh conditions, unfavourable to mycorrhizal fungi, outside of glacial refugia, while OM plant species survived glaciations in the more hospitable refugia present in lower-latitude mountain ranges, such as the Alps, Pyrenees and Carpathians (Schönswetter, Stehlik, Holderegger, & Tribsch, 2005). As the classification of plant species into either OM or FM type might change as empirical data accumulate, these results should be interpreted with care. However, our parallel analysis indicated that data with even a 20% error rate did not change the main pattern of the results.

This study represents the first attempt to analyse the distribution of plant mycorrhizal traits in the European flora. Incorporating both plant distribution and mycorrhizal trait data from such a large area inevitably imposed some limitations. First, the availability of plant distribution data for Europe is somewhat limited, while abundance data from vegetation surveys are currently dispersed and extremely heterogeneous (Chytrý et al., 2016). Also, plant mycorrhizal trait information is scarce, with mycorrhizal trait information available for only about one-third of the central and northern European flora. Besides, the plant distribution data have a grid cell resolution of 50 km × 50 km, which limits our ability to detect relationships related to topographic or spatially heterogeneous variables. Nonetheless, our list of studied species was phylogenetically representative of the whole European flora, and the results were relatively insensitive to sample size. This suggests that our main results are an unbiased reflection of the coarse-scale variation in plant mycorrhizal traits in Europe.

In summary, the proportion of plant species with different mycorrhizal types changes along a latitudinal gradient, but these changes are less pronounced along an elevational gradient. At the same time, AM plant species predominate throughout the flora of northern and central Europe and the share of NM plant species is also relatively high throughout. Our study shows a clear trend for the share of OM plant species to decrease, and that of FM plant species to increase, with latitude and the opposite trend with elevation. The high share of OM plant species in the central European mountain ranges was unexpected, but can be hypothesized to reflect the influence of late Pleistocene conditions and the locations of glacial refugia. Our study reveals the importance of compiling information about plant distribution and mycorrhizal traits at large scales. Incorporating quantitative plant abundance data into future analyses could provide a more detailed insight into the prevalence of mycorrhizal types and statuses in vegetation (Gerz et al., 2016; Moora, 2014) and a better basis for understanding the role of the mycorrhizal symbiosis in ecosystem functioning in the face of global change.

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The research team is composed of researchers from the Plant Ecology Laboratory and the Macroecology Group from the University of Tartu, Estonia, and the Helmholtz Centre for Environmental Research of Salle, Germany. One of our research lines is to understand the role and distribution of mycorrhizal symbioses at large scales.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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