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Climate drives the spatial distribution of mycorrhizal host plants in terrestrial ecosystems

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Abstract

1. Mycorrhizal associations have massive impacts on ecosystem functioning, but the mode and magnitude heavily depend on the mycorrhizal type involved. Different types of mycorrhizas are recognized to predominate under different environmental conditions. However, the respective importance of climate and soil characteristics in shaping mycorrhizal global distributions are still poorly understood.
2. We provide a quantitative and comprehensive global analysis of the main climatic and edaphic predictors of the distribution of plants featuring different mycorrhizal types. Estimates on per grid-cell relative above-ground biomass of plants holding arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) association were related to a set of 39 climatic and edaphic variables. We assessed their relationship by applying a Generalized Additive Models for Location, Scale and Shape (GAMLSS).
3. The best GAMLSS models were able to explain 55%, 41% and 46% of the variance in AM, EcM and ErM distribution, respectively. Temperature-related factors were the main predictors of distribution patterns for the three different mycorrhizal plant types. AM plants are favoured by warm climates, while EcM plants' dominance (and to some extent ErM plants too) is favoured by colder climates.
4. *Synthesis*. The observed lack of importance of soil drivers challenges the predominant view that mycorrhizal plants distribution mainly reflects soil type preferences—as related to its nutrient foraging strategies—of the different mycorrhizal types. Instead, our results highlight climate—and particularly temperature—as the main force shaping the distribution of arbuscular mycorrhiza, ectomycorrhiza and ericoid mycorrhiza host plants at the global scale and suggest that climate change can significantly alter the distribution of mycorrhizal host plants, with a subsequent impact on ecosystem functioning.

KEYWORDS

Arbuscular mycorrhiza, biogeography and macroecology, climate, ectomycorrhiza, environmental drivers, ericoid mycorrhiza, mycorrhizal distribution, soil properties

1 | INTRODUCTION

Mycorrhizas are mutualistic associations between soil fungi and plants, where host plants receive mineral nutrients from fungi and, in exchange, fungi obtain photosynthetically derived carbon (C) compounds from plants (Smith & Read, 2008). It is widely recognized that mycorrhizal associations play a key role in the functioning of terrestrial ecosystems, affecting plant community composition (Klironomos et al., 2011; Van der Heijden et al., 1998), soil formation and structure (Leifheit, Veresoglou, Lehmann, Morris, & Rillig, 2013; Rillig & Mummey, 2006), and C and nutrient cycles (Averill, Turner, & Finzi, 2014; Phillips, Brzostek, & Midgley, 2013; Read, 1991; Veresoglou, Chen, & Rillig, 2012). However, the mode and magnitude of mycorrhizal impacts on ecosystem functioning are strongly related to the mycorrhizal type involved (Phillips et al., 2013; Van der Heijden, Martin, Selosse, & Sanders, 2015).

According to differences in morphology and plant and fungal taxa, seven major types of mycorrhizas are distinguished (Smith & Read, 2008). Among these types, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) are the most taxonomically and geographically widespread, being present in the majority of terrestrial biomes. It has been estimated that approximately 80% of the Earth's plant species form mycorrhizal associations with AM, EcM and ErM fungi (Brundrett & Tedersoo, 2018). The majority of plant species is able to form mycorrhizal symbiosis of only one type (Wang & Qiu, 2006), with only a few exceptions in which the same plant species can be colonized by two mycorrhizal fungi types (McGuire et al., 2008).

AM, EcM and ErM associations predominate under distinct edaphic and climatic conditions. This differentiation is presumed to be strongly associated to the different nutrient uptake strategies among AM, EcM and ErM fungi. For example, EcM and ErM fungi are capable of breaking down organic matter through the expression of extracellular lytic enzymes, making these associations more suitable for organic soils (Read, Leake, & Perez-Moreno, 2004). In contrast, AM saprotrophic abilities are less developed, causing AM to mostly rely on inorganic compounds as a source of nutrients, and therefore more prevalent in mineral soils (Smith & Smith, 2011). Based on these insights, Read (1991) and Read and Perez-Moreno (2003) proposed a theoretical model where the abundance of AM, EcM and ErM host plants gradually changes along a latitudinal and altitudinal gradient, driven mainly by the effects of climate on decomposition, which is ultimately reflected in the accumulation of organic C in the soil and the availability of nutrients for plants. According to this model, AM plants dominate in grasslands and tropical forests; EcM trees are abundant in temperate and boreal forests; and, finally, plants featuring ErM associations predominate in heathlands.

Since Read's first approach, only a few attempts have been made to understand quantitatively which environmental drivers explain the distribution of distinct types of mycorrhizal plants. Menzel et al. (2016) focused on AM and analysed the geographical distribution and environmental drivers of AM plants status (obligate, facultative or non-mycorrhizal) on a regional scale (Germany). Bueno et al. (2017) examined how the number of plant species featuring distinct mycorrhizal traits (type and status) varied with different climatic and soil factors at the European scale. Only recently, Steidinger et al. (2019) performed a coarse resolution (1 degree) global analysis on mycorrhizal trees distribution and its environmental drivers although focusing specifically on forest ecosystems. Despite these efforts, the contribution of the different driving forces (e.g. dispersal, climatic factors, edaphic characteristics or evolution) in shaping the biogeography of mycorrhizal vegetation of the entire plethora of plant functional types at global scale and covering all natural biomes and plant growth forms needs better understanding. Moreover, most of the previous studies were based on the number of plant species capable of forming different mycorrhizal associations, without taking the relative abundance of these species in the ecosystems into account.

A quantitative understanding of the relationships between environmental drivers and the relative abundance, in terms of biomass or plant cover, of AM, EcM and ErM host plants is important, because the relative abundance of mycorrhizal types largely underpins ecosystem functioning. Changes in relative abundance of the different mycorrhizal plant types lead to changes in C and nutrient cycling (Phillips et al., 2013; Soudzilovskaia, Van Der Heijden, et al., 2015), soil processes and structure (Rillig & Mummey, 2006), and can even cause deeper modifications in plant community assembly (Van Der Heijden, 2002). In an era of human-induced environmental changes, unravelling the relative importance of soil and climatic factors in shaping the geographical distribution of plant species featuring different mycorrhizal types will lead to better predictions of changes in ecosystem functioning under a future climate.

Here, we present the first quantitative global analysis of the role of climatic and edaphic factors in explaining the distribution patterns of the three main types of mycorrhizal plants that cover all natural biomes and includes all plant growth forms. Our analysis is based on a high-resolution gridded dataset (10 arc-minutes), which includes information about 39 environmental variables and the percentage of above-ground biomass of plant species featuring AM, EcM and ErM mycorrhizal associations. Following Read's hypothesis, we expect a relatively high contribution of soil properties related to organic C content.

2 | MATERIALS AND METHODS

2.1 | Database assembly

2.1.1 | Distribution of biomass fractions of different mycorrhizal associations

Estimates on the relative above-ground biomass of AM, EcM and ErM mycorrhizal associations were obtained from the high-resolution 10 arc-minutes (~315 km^2 around the equator) gridded global maps from Soudzilovskaia, Van Bodegom, et al. (2019). An extended description of their procedure is provided in the Supporting information. Briefly: (a) All combinations of continents, 98 Bailey's ecological regions and 38 land cover types were considered for their mycorrhizal association. (b) The dominant species in each above-mentioned combination were determined following an extensive compilation of vegetation surveys (see supporting information in Soudzilovskaia, Van Bodegom, et al., 2019 for a list of surveys used). (c) The mycorrhizal association of each dominant species was extracted from a large database on the presence and type of mycorrhizal colonization of vascular plant species (36,303 site records for 14,768 plant species) (complete database is available in Soudzilovskaia, Vaessen, et al., 2019, Table S3). (d) Each dominant species was attributed to a growth form and the relative above-ground biomass of each growth form for each land cover type was estimated based on rules detailed in Supporting information). (e) The fraction of biomass of EcM, AM, ErM and non-mycorrhizal plants in each combination of ecoregion, continent and land cover type was calculated from the combination of 3. and 4. Finally, (f) global maps were obtained by overlaying continents, ecoregions and land cover types at 10 arc-minutes and linking the results of 5. to this overlay. While these maps are composed of multiple sources of information and subjected to a number of conversion factors, their average accuracy was estimated at 80%–85% (Soudzilovskaia, Van Bodegom, et al., 2019).

For the purpose of this paper, non-natural biomes (croplands and urban areas) and bare areas were excluded from the analysis to ensure reliability. This exclusion was performed using the 2015 Land Cover Initiative map developed by the European Space Agency at 300m spatial resolution (https://www.esa-landcover-cci.org/) as a reference. As a result, a total of 270,353 gridded cells were included in the final dataset.

2.1.2 | Climatic and edaphic factors

We assembled a dataset of climatic and edaphic variables that have been proposed to be potential drives of mycorrhizal plant distribution at global scale (Read, 1991; Smith & Read, 2008). In total, our dataset includes information about 39 environmental variables (see Tables S1 and S3). The inclusion of this large number of variables allowed us to evaluate the contribution of temperature, precipitation, seasonality and soil physico-chemical properties to shaping the global distribution of different mycorrhizal plant types.

Climatic variables were obtained from the WorldClim database, Version2 (http://worldclim.org/version2; Fick & Hijmans, 2017) at 10 arc-minutes resolution. In total 19 bioclimatic variables were included (see Table S1). These bioclimatic variables are a combination of monthly temperatures and precipitation values. The inclusion of the 19 bioclimatic variables allowed us to determine potential correlations with seasonality or extreme and limiting environmental factors. In addition, Annual Global Potential Evapotranspiration (Global-PET) (https://cgiarcsi.community/category/data/; Zomer et al., 2007; Zomer, Trabucco, Bossio, & Verchot, 2008) was added to the climatic variables due to its ecological relevance. Global-PET was calculated according to the Hargreaves equation (Hargreaves, Hargreaves, & Riley, 1985) which includes mean temperature, daily temperature range and extra-terrestrial radiation.

Data on the main edaphic variables were obtained from the Harmonized World Soil Database (HWSD) (http://dare.iiasa.ac.at/; FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012). We included in total 12 variables (see Table S2) from the soil top layer (0–30 cm), which were scaled up to 10 arc-minutes resolution using the mean of the raster cells as aggregation criterion.

Data on water-holding capacity, Total C, Total nitrogen (N), Total phosphorus (P) and available P is not available in the HWSD database. We considered these variables to have a potential implication on mycorrhizal host plant distribution due to their high ecological relevance, and therefore we prioritized their inclusion.

Available water Capacity, Total C, Total N were obtained from the ISRIC-WISE gridded database (https://www.isric.org/explore/wise-databases; Batjes, 2012) at 5 × 5 arc-minutes resolution. Only the soil top layer (0–20 cm) was included and scaled up to 10 arc-minutes resolution.

Phosphorus content was obtained from the gridded Global Soil Dataset for use in Earth System Models (GSDE) (http://globalchange.bnu.edu.cn/research/soilw/; Shangguan, Dai, Duan, Liu, & Yuan, 2014) at 30 × 30 s resolution. Due to the high number of missing values of the different phosphorus measurements, only data of total phosphorus and phosphorus extracted by Bray method was retained. The edaphic information on these variables was presented in eight different depth layers ranging from 0 to 2.3 m. For each variable, we calculated the mean of the first four layers covering the top layer (0–26 cm) and aggregated it to 10-arcmin resolution.

2.2 | Statistical analysis

As climatic variables are highly correlated (Table S3), we applied a principal component analysis (PCA) to alleviate the problematics related to the high degree of collinearity while maintaining a high degree of variance in climate variables. The first two axes (PC1 and PC2) of the PCA explained 79.6% of the total variance in climatic data. PC1 was mainly related to temperature variables; while PC2 incorporated mainly precipitation-related variables (Figure S1). Soil factors were examined individually due to the low explanatory power of the principal components and difficulties with the ecological interpretation of the PCA axes of the soil variables (see Figure S2).

Generalized Additive Models for Location, Scale and Shape (GAMLSS) were fitted to relate the percentage of biomass of AM, EcM and ErM plants, respectively, to the soil factors and PC1 and PC2 of the climatic factors using the “gamlss” package. A GAMLSS allows fitting flexible regression and smoothing models and relaxes the assumption of the exponential family distribution for the response variable, replacing it by a general distribution family. Models were fitted using a zero-inflated beta distribution, which is appropriate for modelling proportional data that contain a high proportion of zeros. The smooth functions of each predictor were restricted to a maximum of 3 degrees of freedom, allowing for nonlinearity while detecting only general trends and avoiding overfitting issues. Assuming that different mycorrhizal plant types may vary independently of environmental drivers, EcM, AM and ErM plant distributions were modelled separately. For model simplification, interaction terms were not included.

Model selection was performed by testing competing models that included a set of variables within which each variable explained at least 5% of the data variance, had a Pearson pairwise correlations lower than 0.6 (see Table S4) and variance inflation factors lower than 3. This procedure allowed us to select for sets of non-correlated variables with high explanatory power and to avoid including suppressive variables that would obscure the interpretation of the models. In total, we tested 18 different competing models for AM plant distribution, each of which included eight different variables, six competing models for EcM plant distribution (each including six different variables) and two competing models for ErM plant distribution (each including three variables) (see Tables S5, S6 and S7). For each mycorrhizal plant type, the best model was selected according to the lowest Bayesian information criterion.

After the best models have been selected, a further variable selection was performed. We removed non-significant variables (with $p > .05$) and variables with low relative importance in the model. We considered that a variable had little explanatory power when the effect of removing the variable did not decrease the Pseudo R^2 (Nagelkerke, 1991) with more than 1%. Finally, degrees of freedom of the smooth terms were reduced to preserve only clearly nonlinear patterns.

The presence of spatial autocorrelation (SAC) in AM, EcM and ErM final model residuals was tested using Moran's *I* correlograms with the "sp.correlogram" function in the "spded" package. Moran's tests confirmed the presence of SAC in the model residuals. The existence of SAC may lead to an overestimation of degrees of freedom and Type I errors may be strongly inflated (Legendre, 1993). The presence of SAC can be alleviated by (a) Including spatial coordinates explicitly in the model as covariates: This can be problematic since they could covary with the environmental variables present in the model (Dormann, 2007; Miller, Franklin, & Aspinall, 2007), which can obscure the interpretation of the relative importance of the predictors. (b) Accounting for SAC in model residuals: There is a wide range of methods available in the mainstream software that allow alleviating SAC in model residuals (Dormann et al., 2007). However, their implementation in the context of a zero-inflated beta distribution is still extremely limited. This problem is even increased by the large number of data points included (270,353), which makes the computation of the spatial models unfeasible.

Due to these technical limitations, no correction of SAC could be applied to our global high-resolution data. However, filtering the dataset by distances where SAC is significantly reduced as they decrease exponentially with distance (see Figure S3) demonstrated that the presence of SAC does not alter the importance of the predictors in the final models and therefore their interpretation is not biased due to the autocorrelation (more detailed information about the reduced models is provided in the Supporting information). As the main goal of the models is to detect important predictors of mycorrhizal plant distribution and not to serve as a predictive tool, we further discuss the output of the model with the complete dataset.

The final models were validated by 10-fold cross-validation. A difference of less than 10% between the RMSE (root mean squared error) of the final models and cross-validated models was used as a criterion for model validity. Both in AM, EcM and ErM models, the difference was lower than 5%.

Statistical analysis was performed using R 3.5.3 (R Core Team, 2018) and gridded data was processed using ArcGis v10.2.2.

3 | RESULTS

The model selection applied to the AM host plant distribution retained in total two different climatic and soil predictors: temperature-related factors (PC1), and bulk density. Together, these predictors were able to explain 55% of the variance in AM plant distribution (as indicated by Pseudo-R^2). PC1 was, by far, the best single predictor,

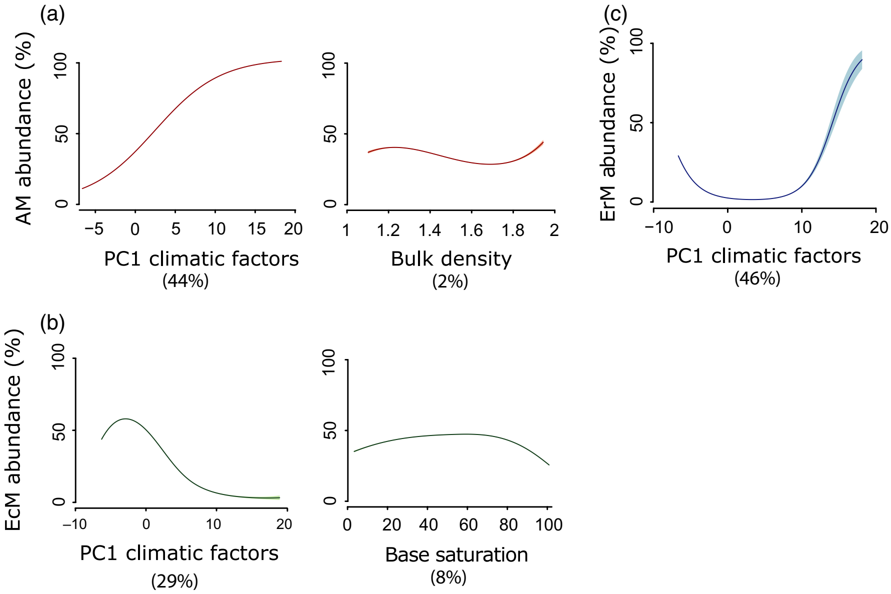

FIGURE 1 Predicted relation between AM (a), EcM (b) and ErM (c) relative abundances and the environmental factors maintained in the best models. Each relation was calculated setting the rest of the variables to the mean value. Light coloured shades represent the region within the upper and lower 95% confidence limits. Numbers between brackets in the *x*-axes correspond to the individual variance explained by each factor in the models

providing 44% of the total variance explained by the model. The model describes a positive logistic relation between AM host plant relative abundances and temperature-related factors (Figure 1a). These results suggest that AM plants dominate temperate and warm climates. Soil properties had little influence on the distribution of AM plants. Bulk density explained only 2% of the variance (see Table 1). The difference between the sum of Pseudo-R^2 of each variable (0.46) and the Pseudo-R^2 of the final model (0.55) indicates that 9% of the variance explained is shared between the two predictors.

For the relative abundance of EcM plants, the predictors retained by the best model were temperature-related factors (PC1) and base saturation. This set of predictors explained 41% of the total variance (Table 1). Similar to the patterns for AM, temperature-related factors arose as the most important predictor of EcM plant distribution, explaining 29% of the variance (Table 1). Figure 1b shows that EcM plants relative abundance peaks at relatively low values of PC1, and decreases exponentially at higher PC1 values. This suggests that EcM plants dominate under cold (but not extremely cold) climates. In contrast to the AM model, soil properties played a more important role in explaining EcM plant distribution. Although only base saturation remained in the final model, it was able to explain 8% of the variance. The model output shows that the dominance of EcM plants is mainly favoured by base saturation values between 40% and 70% (Figure 1b).

For ErM plant distribution, only PC1 of climatic variables was retained in the final model, explaining 48% of the variance. Figure 1c indicates that ErM relative abundance is favoured by both extremely cold and warm temperatures (low and high PC1 values). However, the rapid increase in high values of PC1 had higher uncertainties associated which indicate that predictions in that temperature range are less reliable and possibly influenced by the low number of points.

Examination of the model predictions and residuals (Figure 2a–f), suggests that our sets of predictors were able to capture a high degree of accuracy of the global patterns in the distribution of AM, EcM and ErM host plants.

4 | DISCUSSION

This study is the first global data-based analysis of the environmental variables (climatic and edaphic) explaining the global distribution patterns of AM, EcM and ErM mycorrhizal plants. The fitted GAMLSS models revealed that climatic factors were the main predictors for all mycorrhizal plant types. In contrast, soil properties played a secondary role in explaining mycorrhizal plants distribution on a global scale.

The conclusion that edaphic factors do not control mycorrhizal plants distribution may be questioned based on three arguments: (a) The larger extent of unaccounted variation in soil data compared to climate may lead to an underestimation of soil importance. However, the soil data used in this analysis has been proven to be robust enough to detect association patterns with above- and below-ground plant traits at global scales (Freschet et al., 2017; Maire et al., 2015), which supports the reliability of our results. This suggests that the patterns detected within our study reflect the true set of important predictors. (b) The theoretical overlap between soil properties and climatic condition may act as a confounding factor in detecting their relative importance in our models. However, although soil properties are theoretically influenced by climate (e.g. soil organic stocks are affected by temperature regimes), their actual values result from complex interactions between climatic, geochemical and biotic conditions (Davidson & Janssens, 2006; Doetterl et al., 2015). In line with this, our dataset shows that, at the global scale, the principal components of climatic factors and soil properties are not highly correlated (see Table S4), reinforcing the role of climate as the main driver of large-scale distribution of mycorrhizal plants. (c) The resolution of mycorrhizal plant maps (10 arc-minutes) may not be appropriate to capture the impacts of small scale variation of soil properties and, consequently, may reduce their explanatory power in the final models. However, given that the used resolution captures the main patterns in global soil distribution (Batjes, 2012), our models are likely capable of capturing global scale trends.

TABLE 1 Predictors, GAMLSS-estimated degrees of freedom (edf), *t*-value, *p*-values, Pseudo-R^2 of the final model for each mycorrhizal plant type and the Pseudo-R^2 that is attributed to each individual variable included in the final model

Predictor	edf	*t* value	*p*-value	Pseudo-R^2	Contribution to pseudo-R^{2a}
AM					
Bulk density	2	−98.94	<.001	0.55	0.02
PC1 climatic factors	1	449.42	<.001		0.44
EcM					
Base saturation	2	−54.58	<.001	0.41	0.08
PC1 climatic factors	3	−103.51	<.001		0.29
ErM					
PC1 climatic factors	2	140.2	<.001	0.46	0.46

[a] Due to the presence of joint effects (which refers to the shared contribution in the final model), the sum of the independent contribution of each variable to the model Pseudo-R^2 does not necessarily approximate to the Pseudo-R^2 of the final model.

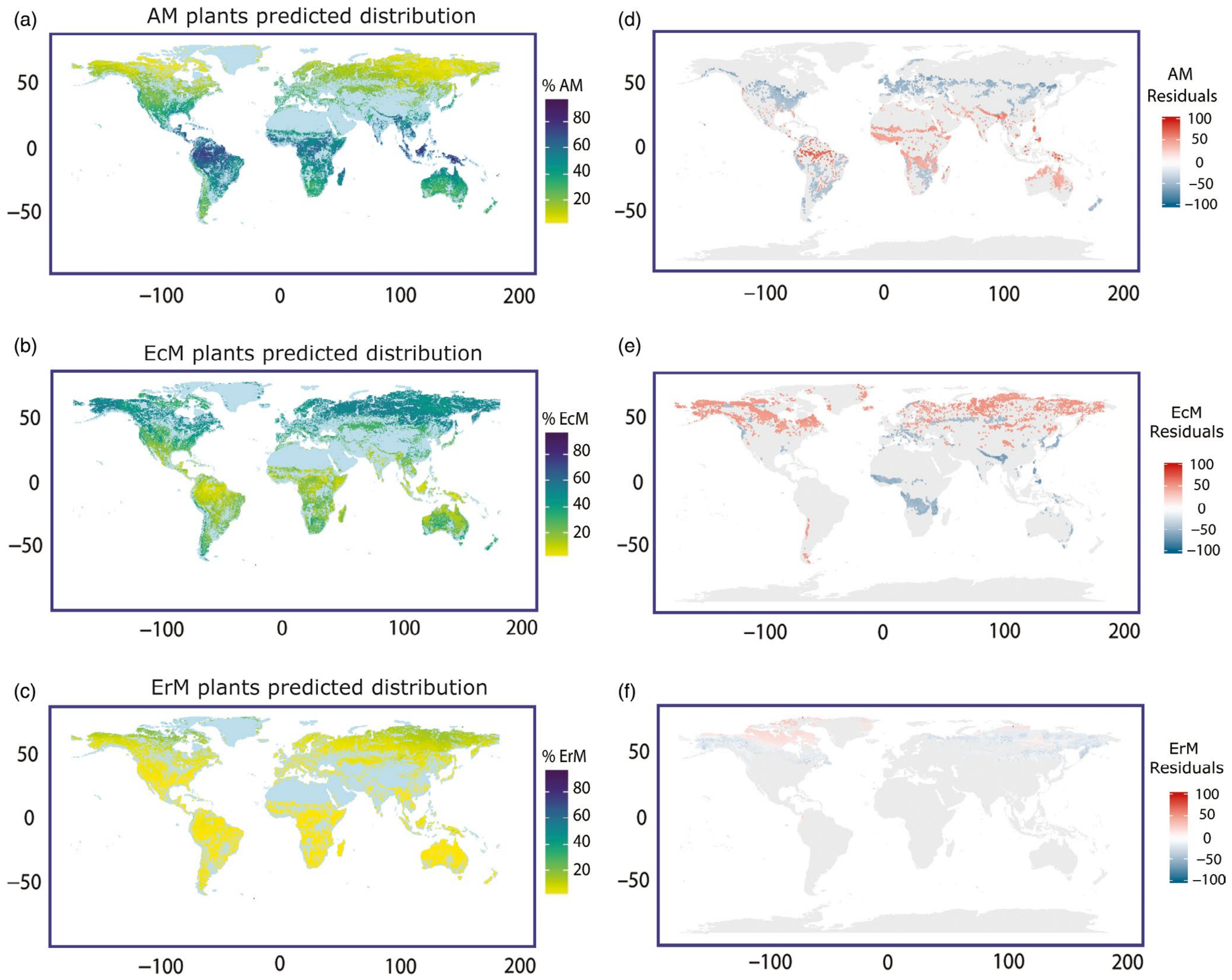

FIGURE 2 Predicted global distribution of AM (a), EcM (b) and ErM (c) mycorrhizal host plants and prediction residuals (d–f); here only the 5% of data points with the highest residual values are depicted. Light blue areas denote non-natural biomes, bare areas or regions for which no environmental data was available. Residues are expressed as the difference between predicted and observed AM, EcM, and ErM plant relative abundances. Red points (positive values) indicate zones where the predicted plant relative abundance was overestimated by the model and blue points (negative values) indicate underestimations

Thus, Read's paradigm of the latitudinal separation between AM, EcM and ErM plants being a reflection of their differential ability to take nutrient from organic sources (Read, 1991; Read & Perez-Moreno, 2003) is not supported by our findings. Our results also partially contradict the conclusion drawn by Steidinger et al. (2019), who as well found a strong climatic control over mycorrhizal trees distribution. Steidinger et al. (2019) related the mechanisms explaining this pattern purely to differences in decomposition rates, while they did not find a direct link with soil physicochemical properties. Our results suggest that other mechanisms play a role, as detailed below.

4.1 | Environmental predictors of AM plant distribution

Our results clearly highlight the impact of climate (especially temperature) on AM plant distributions. Several studies have reported temperature as an important limiting factor for the growth of AM extraradical mycelium (Gavito, Schweiger, & Jakobsen, 2003; Heinemeyer & Fitter, 2004; Rillig, Wright, Shaw, & Field, 2002). Also, a reduction of intraradical colonization has been commonly reported at temperatures lower than 15°C (Gavito & Azcón–Aguilar, 2012; Hetrick & Bloom, 1984). As an alternative mechanism, Veresoglou (2019) recently proposed that irradiance reduction in higher latitudes contributes to a reduction of AM fungi responsiveness, which may contribute to the detected decline of AM plant abundance in colder climates. In line with these studies, our findings suggest that the physiological restrictions of AM fungi to develop and provide benefits to its plant partner at lower temperatures might be a primarily important driver of AM plant distribution at the global scale, independent of soil properties.

In contrast, soil properties were not relevant in explaining AM abundances (Table 1). Especially surprising is the absence of soil P impacts in the final AM best model, which contradicts the view of AM associations being a key adaptation for P uptake. This view was already challenged by previous research. For instance, Soudzilovskaia, Douma, et al. (2015) reported no significant correlation between P limitation and AM root colonization. Similarly, using a meta-analysis approach, Allison and Goldberg (2002) showed that changes in P availability do not have a consistent effect on mycorrhizal infection at plant community level. These results indicate that, although P availability influences the performance of the plant-fungi relationship at the plant species level (Treseder, 2013), this does not necessarily translate into P availability driving AM distribution patterns at a global scale.

What is clear from these results is that climatic conditions are deeply affecting the global biogeography of AM associations. Therefore, the increase in global temperatures expected for the next decades (IPCC, 2014) can potentially modify the distribution range of AM plants and therewith their impacts on the functioning of terrestrial ecosystems.

Although climatic and soil factors were able to explain a large part of the variability in AM plant distribution, the model predictions tended to overestimate AM abundances in tropical zones (mainly central Africa) and underestimate abundances in temperate zones (Figure 2a,d). These mismatches may be related to the higher proportion of facultative AM plants in northern latitudes (Bueno et al., 2017; Hempel et al., 2013; Menzel et al., 2016), which suggest a differentiation in the environmental requirements between obligate and facultative AM plants. Also, the evolutionary and biogeographic history influenced by past geological and climatic episodes (such as tectonic movements, uplift of mountain ranges, climatic stability in different periods) and past human-induced changes (Kreft & Jetz, 2007), may influence the global distribution patterns of mycorrhizal vegetation and their correlation with environmental factors (e.g. different phylogenetic groups may have different adaptations to similar environments which could lead to a weaker correlation with environmental factors). Recent research also suggests that the ability of certain AM fungal species to colonize leaf litter may contribute to a higher abundance of this association in organic soils (Bunn, Simpson, Bullington, Lekberg, & Janos, 2019). Incorporating information about specific fungal functional traits and host identities will be key in future studies aimed to better understand AM plant biogeographical patterns.

4.2 | Environmental predictors of EcM plant distribution

The relative abundance of EcM plants was mainly explained by temperature-related factors, but showed trends opposite to those of AM. EcM plants showed preferences for moderately cold climates, which is consistent with their greater abundance in Northern temperate and boreal zones (Soudzilovskaia, Van Bodegom, et al., 2019). This climatic range possibly relates to the physiological adaptations of EcM plants present in boreal–temperate ecotones and their fungal partners to tolerate cold temperatures and frost periods (Kilpeläinen, Vestberg, Repo, & Lehto, 2016; Sakai & Weiser, 1973; Strimbeck, Kjellsen, Schaberg, & Murakami, 2008). Consequently, a temperature rise can also have serious consequences for EcM plant distributions.

Within the three mycorrhizal plant types studied, EcM plant distribution predictions by the model had the lowest accuracy. The model reflects the EcM distribution patterns in the Northern Hemisphere well, although with a tendency to underestimate its relative biomass; see Figure 2e. In contrast, EcM abundance in tropical areas is not well represented, with a clear underestimation (Figure 2b,e). This is especially visible in certain regions of central Africa where the EcM monodominant stands cannot be predicted by climatic and soil properties. This area of the African continent is mainly dominated by EcM plants of the subfamily Detarioideae (family Fabaceae) (de la Estrella, Forest, Wieringa, Fougère-Danezan, & Bruneau, 2017; Tedersoo,). These species are suggested to proliferate in nutrient-poor and acidic soils (Campbell, 1996) where specific traits of ectomycorrhizal fungal communities (e.g. the ability to obtain N from organic sources) may give them advantage over AM associations (Alexander & Högberg, 1986; Högberg, 1986). However, our model does not support this hypothesis since differences in soil fertility were not able to explain EcM plant distribution in these areas. It is likely that a combination of specific fungal and plant traits (e.g. high host specificity, poor seed dispersal, shade tolerance) create positive feedbacks resulting in a higher proportion of EcM plant abundance in these tropical areas (Peh, Lewis, & Lloyd, 2011). Another potential reason of a poor predictive power of our models in tropics is the limited amount of information about EcM plants in tropical areas. Therefore the EcM distribution map is likely to have higher uncertainties in these regions.

Altogether, with respect to EcM plant abundance, our results indicate that, although climatic conditions and soil properties play an important role in explaining EcM plant distribution, other complex ecological interactions between EcM fungal communities, their host plants and other non-EcM plants may influence the biogeography of EcM associations on a global scale. Increasing the information about distribution of EcM plants in tropical areas is crucial for getting a better understanding of the biogeography of this association.

4.3 | Environmental predictors of ErM plant distribution

The distribution of ErM plants has been traditionally associated with harsh environments, characterized by nutrient-poor and acidic soils (Read, 1991). This has been related to the ability of ErM fungi to produce hydrolytic and oxidative enzymes (Cairney & Burke, 1998) that would increase the fitness of their symbiont in these environments. However, our results suggested that, at a global scale, the abundance of plants capable to form ErM association is influenced mainly by temperature-related factors (Table 1). The strong contribution of temperature to explaining the distribution of ErM plants may be a reflection of their physiological adaptations to tolerate frost events (Marian, Krebs, & Arora, 2004) and therefore to survive in extreme temperatures where other plants are unable to establish.

Unexpectedly, soil conditions were only weakly correlated to the abundance of ErM plants (Table 1). The fact that soil properties were not a good proxy for ErM plant abundances could indicate the complexity and heterogeneity of strategies of ErM fungi to use organic substrates as a resource of nutrients. However, little information is available about ErM fungal traits or Ericaceae niche preferences that allow a deeper exploration of these results.

5 | CONCLUDING REMARKS

Our results point at temperature-related factors as the main predictors—instead of soil properties—for the global distribution of the three most abundant mycorrhizal plant types. The observed lack of importance of soil drivers contradicts the traditional view of climate-driven soil properties, such as the rate of organic matter decomposition and nutrient availability as the ultimate mechanisms explaining the latitudinal distribution of mycorrhizal plant types (Phillips et al., 2013; Read & Perez-Moreno, 2003; Smith & Read, 2008; Steidinger et al., 2019). In contrast, our findings support the role of temperature as a main driving force affecting the global distribution of plant ecological strategies (Moles et al., 2014), and reinforces the view that mycorrhizal type constitutes an important part of these strategies. We suggest that the latitudinal transition between AM, EcM and ErM plants is likely to be associated with ecological mechanisms that involve direct effects of climate on plant and fungi performance and survival. In line with this hypothesis, the indirect effects of climate on decomposition and nutrient availability would play a secondary role on a large scale.

Given that our results point to climate as the main force shaping the distribution of AM, EcM and ErM host plants on a global scale, and taking into account the importance of mycorrhizas on ecosystem functioning (Phillips et al., 2013), we suggest that climate change can significantly alter the distribution of mycorrhizal host plants, with subsequent impact on the functioning of terrestrial ecosystems and provisioning of associated ecosystem services. However, an accurate prediction of changes in mycorrhizal vegetation abundances under future climatic scenario will require (a) higher resolution data of mycorrhizal plant distribution and (b) higher quality soil data and (c) to increase the knowledge of mycorrhizal associations in plant species that have not been investigated yet to extend the analysis beyond the dominant species. This will allow to account for the large heterogeneity of soil properties and to evaluate the importance of smaller-scale processes that cannot be taken into account in this work.

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AUTHORS' CONTRIBUTIONS

M.B. performed modelling and wrote the first draft of the manuscript. P.M.v.B. and N.A.S. made substantial contributions during modelling process and revision of the manuscript.

DATA AVAILABILITY STATEMENT

The data used in this research is compiled by joining publically available datasets: Mycorrhizal abundance maps; https://doi.org/10.1101/331884. Climatic data: WorldClim database, Version2 (https://worldclim.org/version2). Annual Global Potential Evapotranspiration (Global-PET): https://cgiarcsi.community/category/data/. Soil data: Harmonized World Soil Database (HWSD): https://dare.iiasa.ac.at/. Available water Capacity, Total C, Total N: ISRIC-WISE gridded database (https://www.isric.org/explore/wise-databases). Phosphorus content: Global Soil Dataset for use in Earth System Models (GSDE) (https://globalchange.bnu.edu.cn/research/soilw).

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