Global distribution patterns of mycorrhizal associations: abundance, environmental drivers and ecological impacts

Barcelo, M.

CHAPTER 2

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

Milagros Barceló., Peter M. van Bodegom &
Nadejda A. Soudzilovskaia

Journal of Ecology, 2019, 107(6):2564-2573

DOI: 10.1111/1365-2745.13275

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 aboveground 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 extents 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 AM, EcM and ErM 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.

2.1. 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 and Read 2008). It is widely recognized that mycorrhizal associations play a key role in the functioning of terrestrial ecosystems, affecting plant community composition (Van der Heijden et al. 1998, Klironomos et al. 2011), soil formation and structure (Rillig and Mummey 2006, Leifheit et al. 2013), and C and nutrient cycles (Read 1991, Veresoglou et al. 2012, Phillips et al. 2013, Averill et al. 2014). 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 et al. 2015).

According to differences in morphology and plant and fungal taxa, seven major types of mycorrhizas are distinguished (Smith and 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 and Tedersoo 2018). The majority of plant species is able to form mycorrhizal symbiosis of only one type (Wang and 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 et al. 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 and 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 et al. 2015), soil processes and structure (Rillig and 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 covers 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 aboveground 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.

2.2. Methods

2.2.1. Database assembly

2.2.1.1.Distribution of biomass fractions of different mycorrhizal associations

Estimates on the relative aboveground biomass of AM, EcM and ErM mycorrhizal associations were obtained from the high-resolution 10 arc-minutes (~315km^2 around the equator) gridded global maps from Soudzilovskaia et al. (2019b). An extended description of their procedure is provided in the Supplementary Information. Briefly: 1) All combinations of continents, 98 Bailey's ecological regions and 38 land cover types were considered for their mycorrhizal association. 2) The dominant species in each abovementioned combination were determined following an extensive compilation of vegetation surveys (see Supplementary Information in Soudzilovskaia et al. 2019b for a list of surveys used). 3) 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 et al. 2019a, Supplementary Table S2.3). 4) Each dominant species was attributed to a growth form and the relative aboveground biomass of each growth form for each land cover type was estimated based on rules detailed in the Supplementary Information. 5) 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, 6) 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 et al. 2019).

For the purpose of the current 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 270353 gridded cells were included in the final dataset.

2.2.1.2. Climatic and edaphic factors

We assembled a dataset of climatic and edaphic variables that have been proposed to be potential drives of mycorrhizal plants distribution at global scale (Read 1991, Smith and Read 2008). In total, our dataset includes information about 39 environmental variables (see Supplementary information, Tables S2.1 and S2.3). The inclusion of this large number of variables allowed us to evaluate the contribution of temperature, precipitation, seasonality and soil physicochemical 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 and Hijmans, 2017) at 10 arc-min resolution. In total 19 bioclimatic variables were included (see Supporting Information Table S2.1). 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 et al., 2008) was added to the climatic variables due to its ecological relevance. Global-

PET was calculated according to the Hargreaves equation (Hargreaves et al. 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 Supporting Information Table S2.2) from the soil top layer (0-30cm), which were scaled up to 10arc-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 plants 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 by 5 arc-minutes resolution. Only the soil top layer (0-20cm) 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 et al., 2014) at 30 by 30 seconds 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 2.3m. 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.

2.2.2. Statistical analysis

As climatic variables are highly correlated (Supporting Information, Table S2.3), 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 principal component analysis explained 79.6% of the total variance in climatic data. PC1 was mainly related to temperature variables; while PC2 incorporated mainly precipitation-related variables (Supporting Information Figure S2.1). 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 Supporting Information Figure S2.2).

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 non-linearity while detecting only general trends and avoiding overfitting issues. Assuming that different mycorrhizal plant types may vary independently to 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 Supporting Information Table S2.4) and Variance Inflation Factors (VIFs) 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 8 different variables, 6 competing models for EcM plant distribution (each including 6 different variables) and 2 competing models for ErM plant distribution (each including 3 variables) (see Supplementary information Tables S2.5,

S2.6 and S2.7). For each mycorrhizal plant type, the best model was selected according to the lowest Bayesian Information Criterion (BIC).

After the best models have been selected, a further variable selection was performed. We removed non-significant variables (with p-value >0.05) 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 non-linear 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 1) 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 et al. 2007), which can obscure the interpretation of the relative importance of the predictors. 2) Accounting for spatial autocorrelation 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 (270353), 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 Supplementary Information Figure S2.3) 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 Supplementary Information). As the main goal of the

models is to detect important predictors of mycorrhizal plants 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 2021) and gridded data was processed using ArcGis v10.2.2.

2.3. Results

The model selection applied to the AM host plant distribution retained in total 2 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, 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 2.2a). 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 2.1). 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.

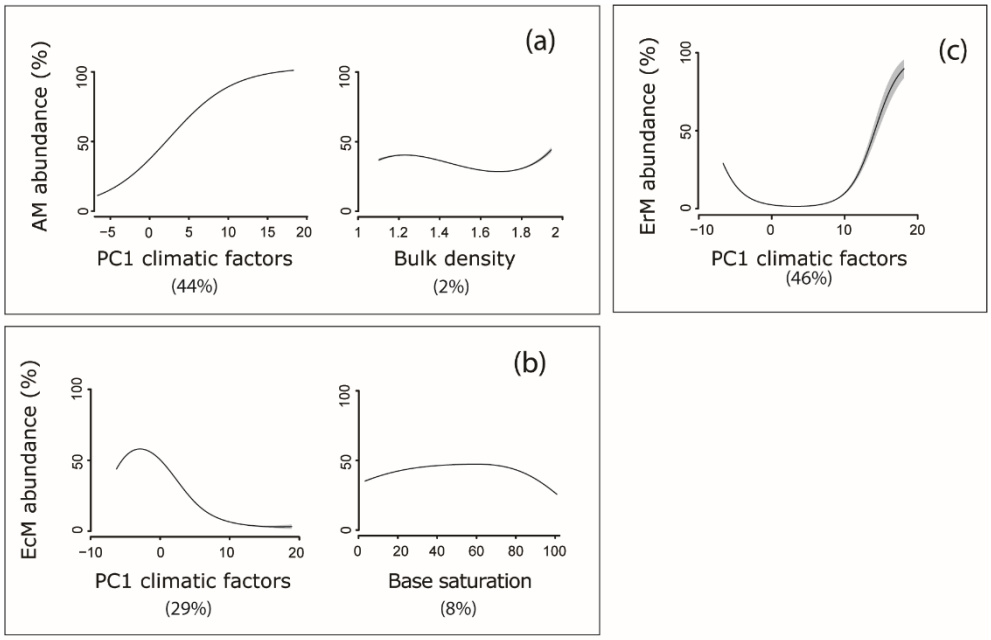

***Figure 2.1**: Predicted relation between AM (a), EcM (b) and ErM (c) relative abundances and the environmental factors maintained in the best models. Each relation was calculated setting the rest of the variables to the mean value. Light coloured shades represent the region within the upper and lower 95%-confidence limits. Numbers between brackets in the x-axes correspond to the individual variance explained by each factor in the models.*

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 2.1). 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 2.1). Figure 2.2b 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 explain EcM plants 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 40-70% (Figure 2.2b).

Table 2.1: 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-R2*
AM	*Bulk density*	*2*	*-98.94*	*<0.001*	**0.55**	0.02
	PC1 climatic factors	*1*	*449.42*	*<0.001*		0.44
EcM	*Base saturation*	*2*	*-54.58*	*<0.001*	**0.41**	0.08
	PC1 climatic factors	*3*	*-103.51*	*<0.001*		0.29
ErM	*PC1 climatic factors*	*2*	*140.2*	*<0.001*	**0.46**	0.46

*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.

For ErM plant distribution, only PC1 of climatic variables was retained in the final model, explaining 48% of the variance. Figure 2.2c 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 2.1 a-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.

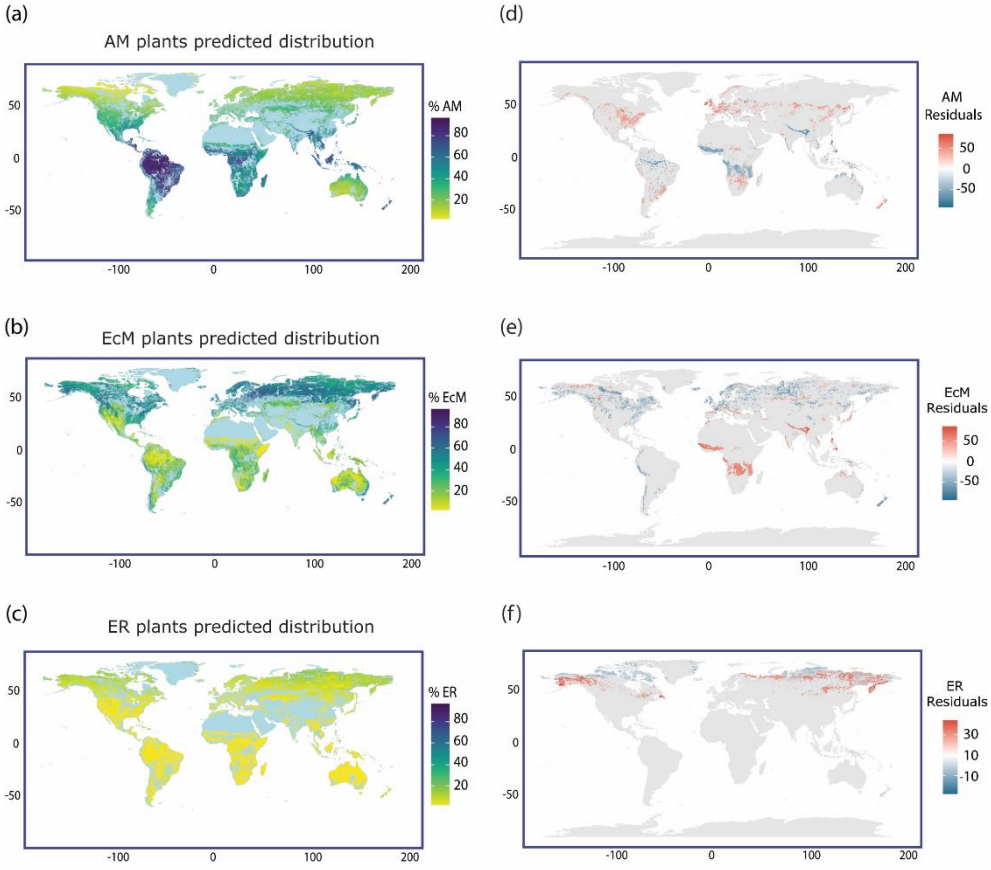

Figure. 2.2*: Predicted global distribution of AM (a), EcM (b) and ErM (c) mycorrhizal host plants and prediction residuals (d-f); here only the 5% of data points with the highest residual values are depicted. Light blue areas denote non-natural biomes, bare areas or regions for which no environmental 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.*

2.4. 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 at global scale.

The conclusion that edaphic factors do not control mycorrhizal plants distribution may be questioned based on three arguments: 1) 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 (Maire et al. 2015, Freschet et al. 2017), which supports the reliability of our results. This suggests that the patterns detected within our study reflect the true set of important predictors. 2) 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 and Janssens 2006, Doetterl et al. 2015). In line with this, our dataset shows that, at global scale, the principal components of climatic factors and soil properties are not highly correlated (see Supplementary Information Table S2.4), reinforcing the role of climate as a main driver of large scale distribution of mycorrhizal plants. 3) 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.

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 and 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.

2.4.1. Environmental predictors of AM plants 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 (Rillig et al. 2002, Gavito et al. 2003, Heinemeyer and Fitter 2004). Also, a reduction of intraradical colonization has been commonly reported at temperatures lower than 15°C (Hetrick and Bloom 1984, Gavito and Azcón–Aguilar 2012). 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 global scale, independent of soil properties.

In contrast, soil properties were not relevant in explaining AM abundances (Table 2.1). 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 et al. (2015a) reported no significant correlation between P limitation and AM root colonization. Similarly, using a meta-analysis approach, Allison & 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 of global temperatures expected for 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 2.1a and Figure 2.1d). These mismatches may be related to the higher proportion of facultative AM plants in northern latitudes (Hempel et al. 2013, Menzel et al. 2016, Bueno et al. 2017) 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 and 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 et al. 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.

2.4.2. Environmental predictors of EcM plants distribution

EcM plants relative abundance 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 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 (Sakai and Weiser 1973, Strimbeck et al. 2008, Kilpeläinen et al. 2016). 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 2.1e. In contrast, EcM abundance in tropical areas is not well represented, with a clear underestimation (Figure 2.1b and Figure 2.1e). 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 Africa continent is mainly dominated by EcM plants of the subfamily Detarioideae (family Fabaceae) (de la Estrella et al. 2017, Tedersoo 2017). 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 and 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 et al. 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 at 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.

2.4.3. Environmental predictors of ErM plants 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 and 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 2.1). 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 et al. 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 2.1). The fact that soil properties were not a good proxy for ErM plants 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.

2.5. 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 (Read and Perez-Moreno 2003, Smith and Read 2008, Phillips et al. 2013, 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 at large scale.

Given that our results point to climate as the main force shaping the distribution of AM, EcM and ErM host plants at the 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 1) higher resolution data of mycorrhizal plants distribution and 2) higher quality soil data and 3) 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 could not be considered in this work.

2.6. Acknowledgments

This work is supported by The Netherlands Organization for Scientific Research (NWO) grant 016.161.318 to N.A Soudzilovskaia.

2.7. Authors' contributions

MB performed modelling and wrote the first draft of the manuscript. PB and NS made substantial contributions during modelling process and revision of the manuscript.

2.8. Data Accessibility Statement

The data used in this research is compiled by joining publically available datasets:

- Mycorrhizal abundance maps: https://www.biorxiv.org/content/10.1101/331884v2; DOI: 10.1101/331884
- Climatic data: WorldClim database, Version2 (http://worldclim.org/version2)
- Annual Global Potential Evapotranspiration (Global-PET): https://cgiarcsi.community/category/data/

- Soil data:
    - Harmonized World Soil Database (HWSD): http://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) (http://globalchange.bnu.edu.cn/research/soilw)

2.9. Supporting information

2.9.1. Assembly of mycorrhizal vegetation maps

Soudzilovskaia et al, 2019 constructed the maps the biomass fractions of different mycorrhizal plant types, assigning values of mycorrhizal biomass fractions to in all possible combinations of continents, 98 Bailey's ecological regions and 38 land cover types (from here onwards referred to as ''combination''). The estimated fraction of each mycorrhizal type and of each growth form within each combination was based on the dominant plant species occurring in combinations, based on vegetation records (using for this purpose 1,568 sources of vegetation surveys, conducted in each combination). The maps construction process generally consisted of four steps (summary of which is provided below; for more information please consult Soudzilovskaia et al, 2019).

Step 1. Assigning mycorrhizal association to the dominant species within each combination. This information was extracted from a large database on the presence and type of mycorrhizal colonization of vascular plant species (36,303 plant species by site records) (http://biorxiv.org/cgi/content/short/717488v1). This information was provided by published reviews, data compilations, previously neglected or recent case studies on the type of mycorrhizal colonization (1,565 sources). By assembling the database classification of mycorrhizal type for a given species was performed following definitions of Brundrett and Tedersoo (2018) and based on the description of morphological criteria provided by the authors of a respective publication. Plant

records where the presence of intracellular arbuscules, coils or pelotons was corroborated were classified as AM, ErM or Orchid Mycorrhiza (OM), respectively. For EcM, the presence of a Hartig net or a well-developed mantle (>1 hyphal layer) was required. All plants of the families Diapensiaceae and Ericaceae were considered ErM, except for Enkianthus (AM), Arbuteae, Pyroleae, Monotropeae and Pterosporeae (all subtypes of EcM).

Because of multiple incorrect reports and alternative definitions for mycorrhizal types, plants were considered to belong to a given mycorrhizal type, only when this was supported by multiple independent studies and the proportion of conflicting reports was <50%. In other cases, the plant species were considered to feature a mixed type of colonization (for instance to be AM/EcM). Non-mycorrhizal species were assigned according to Brundrett, 2009 & 2017. While misdiagnosis of mycorrhizal type might be a problem in general (Bueno et al. 2019, Sun et al. 2019, Tedersoo et al. 2019) it is unlikely to have majorly affected our current analysis as the underlying maps were based on pre-dominant species only for which more consensus on mycorrhizal associations tends to exist, as such species are typically studied more extensively.

Step 2. Assigning growth form to each dominant species. This was done based on the vegetation records for each combination.

Step 3. Estimation of fractions of living biomass of each plant growth form within each combination. In these estimates, the following coefficients to translate information of plant growth forms into biomass fractions of plants were used:

- in forests that consist of two vegetation layers (trees and herbaceous/dwarf shrub understory vegetation), trees contribute 90±5% of the biomass, and the understorey vegetation comprises 5-10% of biomass;
- in forests that encompass a dense layer of shrubs, trees contribute 70±15% of the biomass, shrubs constitute 20±10% of biomass and understorey herbaceous/dwarf shrub layer constitutes 20±10%.
- In shrublands, shrubs account for 90±5% of the biomass, and herbaceous vegetation 10±5% of the biomass.

- Savannahs and forested steppes to harbor 30±10% of the biomass in trees, 30±10% of the biomass in shrubs, and the remaining biomass in herbaceous vegetation.

Step 4. Calculation of biomass fractions of mycorrhizal types and mapping those. The estimated proportion of a given mycorrhizal type per growth form was combined with the estimated growth forms biomass fractions to calculate the average biomass fraction of EcM, AM, ErM and non-mycorrhizal associations for each combination.

Finally, by overlaying the raster map of Bailey ecoregions, provided by the Oak Ridge National Laboratory Distributed Active Archive Center (10 arcmin), with the raster ESA CCI land cover dataset, spatially aggregated to 10 arcmin and a polygon map of continents, rasterized at 10 arcmin, global maps of mycorrhizal type association were created.

The maps were validated using four independent datasets: (i) forest biomass structure for Eurasia, (ii) a global dataset of forest biomass structure used for an analysis of mycorrhizal impacts on carbon vs nitrogen dynamics, (iii) estimates of mycorrhizal associations in the USA based on remote sensing, and (iv) West Australian map of mycorrhizal root abundance (Soudzilovskaia et al, 2019).

The maps of mycorrhizal vegetation have been assembled based on multiple published datasets, using a number of conversion factors. These conversions, as well as the fact that the plant species distribution data originates from multiple sources, constitute important uncertainty sources in the dataset. The average uncertainty of the biomass fractions of mycorrhizal plants per grid cell is 15-20% (Soudzilovskaia et al. 2019).

2.9.2. Environmental predictors

***Table S2.1**: List of bioclimatic variables included in the final dataset*

Abbreviation	Meaning
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Table S2.2: List of soil physicochemical properties included in the final dataset obtained from the Harmonized World Soil Database (HWSD), the ISRIC-WISE gridded database and the Global Soil Dataset for use in Earth System Models (GSDE).

Source	Soil properties	Abbreviation	Units	Original grid cell size	Comments
HWSD	Sand Fraction	Sand	% wt.	30 by 30 arc-seconds	
	Silt Fraction	Silt	% wt.	30 by 30 arc-seconds	
	Clay Fraction	Clay	% wt.	30 by 30 arc-seconds	
	Bulk density	Bulk density	kg/dm3	30 by 30 arc-seconds	Calculated with the Equations developed by (Saxton et al. 1986)
	Reference bulk density	Ref bulk density	kg/dm3	30 by 30 arc-seconds	SOTWIS Bulk Density estimation
	Organic carbon	Org C	% weight	30 by 30 arc-seconds	
	pH	pH	(H2O) - log(H+)	30 by 30 arc-seconds	pH measured in a soil-water solution
	Cation exchange capacity	Cat exc	cmol/kg	30 by 30 arc-seconds	
	Base saturation	Base sat	%	30 by 30 arc-seconds	

	Total exchangeable bases	Total exc bases	cmol/kg	30 by 30 arc-seconds	
	Calcium carbonate content	CaCO3	% weight	30 by 30 arc-seconds	
	Electrical conductivity	Conductivity	dS/m	30 by 30 arc-seconds	
ISRIC-WISE	Available Water Capacity	TAWC	c/m	5 by 5 arc-minutes	
	Total Carbon	Total C	g/kg	5 by 5 arc-minutes	
	Total Nitrogen	Total N	g/kg	5 by 5 arc-minutes	
	C/N ratio	C/N		5 by 5 arc-minutes	
GSDE	Bray Phosphorus	Bray P	ppm	30 by 30 arc-seconds	The amount of phosphorous using the Bray1 method
	Total Phosphorus	Total P	%	30 by 30 arc-seconds	

2.9.3. Statistical analysis

Table S2.3: *Pearson correlation matrix of climatic factors. Numbers in red indicate predictors with correlation >0.6*

	Evapo T	bio 1	bio 2	bio 3	bio4	bio5	bio6	bio7	bio8	bio9	bio 10	bio 11	bio 12	bio 13	bio 14	bio 15	bio 16	bio 17	bio 18	bio 19
Evapo T	1,00	**0,95**	**0,64**	**0,87**	**-0,79**	**0,94**	**0,88**	**-0,71**	**0,82**	**0,87**	**0,94**	**0,90**	0,14	0,26	-0,37	0,39	0,23	-0,31	-0,01	-0,12
bio1		1,00	0,42	**0,91**	**-0,89**	**0,88**	**0,97**	**-0,84**	**0,82**	**0,93**	**0,93**	**0,98**	0,29	0,38	-0,21	0,30	0,35	-0,15	0,10	0,05
bio2			1,00	0,42	-0,21	**0,66**	0,27	-0,07	0,40	0,36	0,55	0,33	-0,31	-0,18	-0,56	0,43	-0,21	-0,54	-0,30	-0,43
bio3				1,00	**-0,95**	**0,71**	**0,94**	**-0,90**	**0,71**	**0,86**	**0,75**	**0,95**	0,42	0,50	-0,09	0,24	0,47	-0,03	0,24	0,14
bio4					1,00	**-0,62**	**-0,96**	**0,98**	**-0,65**	**-0,86**	**-0,69**	**-0,96**	-0,50	-0,55	0,00	-0,15	-0,52	-0,07	-0,28	-0,23
bio5						1,00	**0,77**	**-0,54**	**0,78**	**0,83**	**0,98**	**0,79**	-0,01	0,10	-0,41	0,36	0,07	-0,36	-0,15	-0,14
bio6							1,00	**-0,94**	**0,75**	**0,93**	**0,83**	**1,00**	0,42	0,48	-0,07	0,20	0,45	-0,01	0,20	0,18
bio7								1,00	-0,59	**-0,82**	**-0,62**	**-0,92**	-0,53	-0,56	-0,07	-0,09	-0,54	-0,14	-0,31	-0,29
bio8									1,00	**0,63**	**0,82**	**0,77**	0,24	0,37	-0,20	0,37	0,34	-0,15	0,23	-0,12
bio9										1,00	**0,86**	**0,93**	0,25	0,31	-0,18	0,21	0,28	-0,12	-0,01	0,17
bio10											1,00	**0,85**	0,07	0,18	-0,33	0,34	0,15	-0,29	-0,07	-0,08
bio11												1,00	0,40	0,48	-0,11	0,24	0,45	-0,05	0,19	0,14
bio12													1,00	**0,94**	**0,60**	-0,21	**0,96**	**0,66**	**0,86**	**0,66**

bio13														1,00	0,39	0,07	**0,99**	0,45	**0,84**	0,47
bio14															1,00	**-0,78**	0,43	**0,99**	0,57	**0,81**
bio15																1,00	0,02	**-0,76**	-0,16	**-0,62**
bio16																	1,00	0,49	**0,85**	0,50
bio17																		1,00	**0,61**	**0,84**
bio18																			1,00	0,44
bio19																				1,00

***Table S2.4**: Pearson correlation matrix of soil predictors and the first two principal components of climatic factors. Numbers in red indicate pairs of predictors with correlation >0.6*

	Sand	Silt	Clay	Bulk density	Ref bulk density	Org C	pH	Cat exc	Base sat	Total exc bases	CaCO3	Conductivity	TAWC	Total C	Total N	C/N	Bray P	Total P	PC1_climatic	PC2_climatic
Sand	1,00	**-0,82**	**-0,70**	0,38	**0,83**	-0,22	-0,10	-0,50	-0,14	-0,47	-0,07	-0,02	-0,19	-0,11	-0,18	0,11	0,17	-0,09	-0,04	0,16
Silt		1,00	0,16	-0,33	-0,47	0,25	0,11	0,46	0,19	0,37	0,02	0,02	0,31	0,18	0,26	0,05	-0,11	0,17	-0,29	-0,20
Clay			1,00	-0,24	**-0,85**	0,08	0,03	0,28	0,00	0,35	0,09	0,01	-0,06	-0,03	-0,02	-0,25	-0,15	-0,05	0,43	-0,02
Bulk density				1,00	0,29	**-0,81**	0,23	**-0,67**	0,15	-0,29	0,06	0,01	-0,43	-0,46	-0,40	-0,25	0,12	0,06	0,09	0,22
Ref bulk density					1,00	-0,13	-0,10	-0,37	-0,11	-0,40	-0,12	-0,02	-0,02	-0,01	-0,05	0,25	0,16	-0,04	-0,28	0,06
Org C						1,00	-0,26	**0,82**	-0,14	0,34	-0,11	-0,03	0,44	0,56	0,47	0,36	-0,11	-0,11	-0,18	-0,17
pH							1,00	0,06	**0,87**	0,54	0,57	0,14	-0,26	-0,20	-0,12	-0,46	0,19	0,32	-0,11	0,50
Cat exc								1,00	0,14	**0,67**	0,04	0,00	0,39	0,44	0,41	0,19	-0,10	0,05	-0,22	-0,07

Base sat									1,00	0,56	0,42	0,10	-0,22	-0,13	-0,06	-0,36	0,25	0,32	-0,18	0,47
Total exc bases										1,00	0,42	0,07	0,14	0,15	0,18	-0,15	0,01	0,20	-0,16	0,21
CaCO3											1,00	0,15	-0,13	-0,13	-0,11	-0,31	0,01	0,12	0,02	0,30
Conductivity												1,00	-0,04	-0,03	-0,03	-0,07	0,03	0,04	0,00	0,09
TAWC													1,00	**0,67**	**0,65**	0,50	-0,05	-0,03	-0,33	-0,32
Total C														1,00	**0,92**	0,56	-0,11	-0,12	-0,22	-0,18
Total N															1,00	0,47	-0,10	-0,05	-0,26	-0,17
C/N																1,00	-0,12	-0,22	-0,33	-0,36
Bray P																	1,00	0,16	-0,09	0,23
Total P																		1,00	-0,22	0,11
PC1_climatic																			1,00	0,00
PC2_climatic																				1,00

Table S2.5: *Set of variables included in the 18 competing models for AM plant distribution and resulting BIC of the models. Model highlighted in yellow represents the selected model with lower BIC.*

AM									
Model	**Variables**								**BIC**
1	Clay	Total exc bases	pH	TAWC	C/N	Bray P	Total P	PC1_climatic	-3054.7
2	Clay	Total exc bases	pH	Total C	C/N	Bray P	Total P	PC1_climatic	-3063.5
3	Clay	Total exc bases	pH	Total N	C/N	Bray P	Total P	PC1_climatic	-3107.9
4	Clay	Total exc bases	Base sat	TAWC	C/N	Bray P	Total P	PC1_climatic	-3048.2
5	Clay	Total exc bases	Base sat	Total C	C/N	Bray P	Total P	PC1_climatic	-3043.3
6	Clay	Total exc bases	Base sat	Total N	C/N	Bray P	Total P	PC1_climatic	-3078
7	Ref bulk density	Total exc bases	pH	TAWC	C/N	Bray P	Total P	PC1_climatic	-3052
8	Ref bulk density	Total exc bases	pH	Total C	C/N	Bray P	Total P	PC1_climatic	-3043.5
9	Ref bulk density	Total exc bases	pH	Total N	C/N	Bray P	Total P	PC1_climatic	-3090
10	Ref bulk density	Total exc bases	Base sat	TAWC	C/N	Bray P	Total P	PC1_climatic	-3100.4
11	Ref bulk density	Total exc bases	Base sat	Total C	C/N	Bray P	Total P	PC1_climatic	-3079.3
12	Ref bulk density	Total exc bases	Base sat	Total N	C/N	Bray P	Total P	PC1_climatic	-3116.5
13	Sand	Total exc bases	pH	TAWC	C/N	Bray P	Total P	PC1_climatic	-3029.5
14	Sand	Total exc bases	pH	Total C	C/N	Bray P	Total P	PC1_climatic	-3043.5
15	Sand	Total exc bases	pH	Total N	C/N	Bray P	Total P	PC1_climatic	-3090
16	Sand	Total exc bases	Base sat	TAWC	C/N	Bray P	Total P	PC1_climatic	-3100.4
17	Sand	Total exc bases	Base sat	Total C	C/N	Bray P	Total P	PC1_climatic	-3079.3
18	Sand	Total exc bases	Base sat	Total N	C/N	Bray P	Total P	PC1_climatic	-3116.5

Table S2.6*: Set of variables included in the 6 competing models for EcM plant distribution and resulting BIC of the models. Model highlighted in yellow represents the selected model with lower BIC.*

EcM		
Model	**Variables**	**BIC**
1	Ref bulk density Total exc bases pH TAWC C/N PC1_climatic	3010.3
2	Ref bulk density Total exc bases pH Total C C/N PC1_climatic	3155.6
3	Ref bulk density Total exc bases pH Total N C/N PC1_climatic	3130.6
4	Ref bulk density Total exc bases Base sat TAWC C/N PC1_climatic	2562.7
5	Ref bulk density Total exc bases Base sat Total C C/N PC1_climatic	2608.8
6	Ref bulk density Total exc bases Base sat Total N C/N PC1_climatic	2560.1

Table S2.7*: Set of variables included in the 2 competing models for EcM plant distribution and resulting BIC of the models. Model highlighted in yellow represents the selected model with lower BIC.*

ErM		
Model	**Variables**	**BIC**
1	Total C C/N PC1_climatic	-6086
2	Total N C/N PC1_climatic	-6230

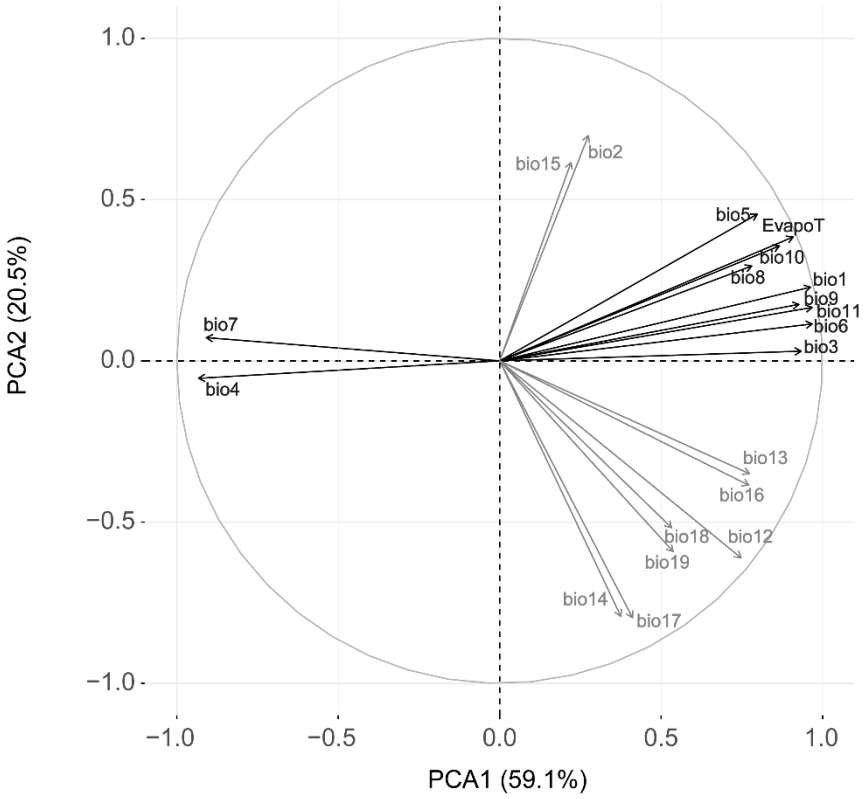

***Figure S2.1**: Principal component analysis ordination plot of climatic variables. Black arrows represent climatic variables mainly related to temperature factors and grey arrows represent climatic variables mainly related to precipitation factors*

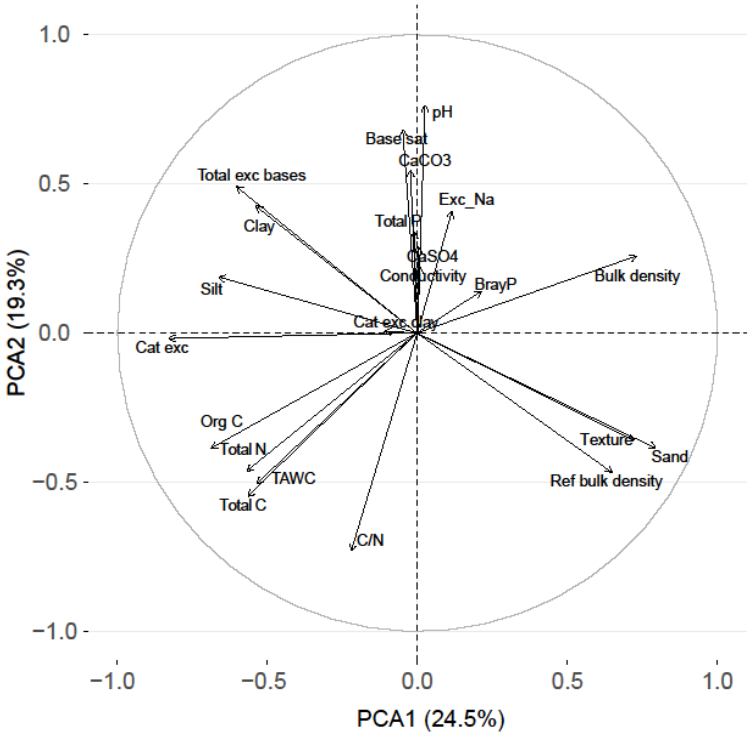

***Figure S2.2**: Principal component analysis ordination plot of edaphic variables.*

2.9.4. Spatial autocorrelation

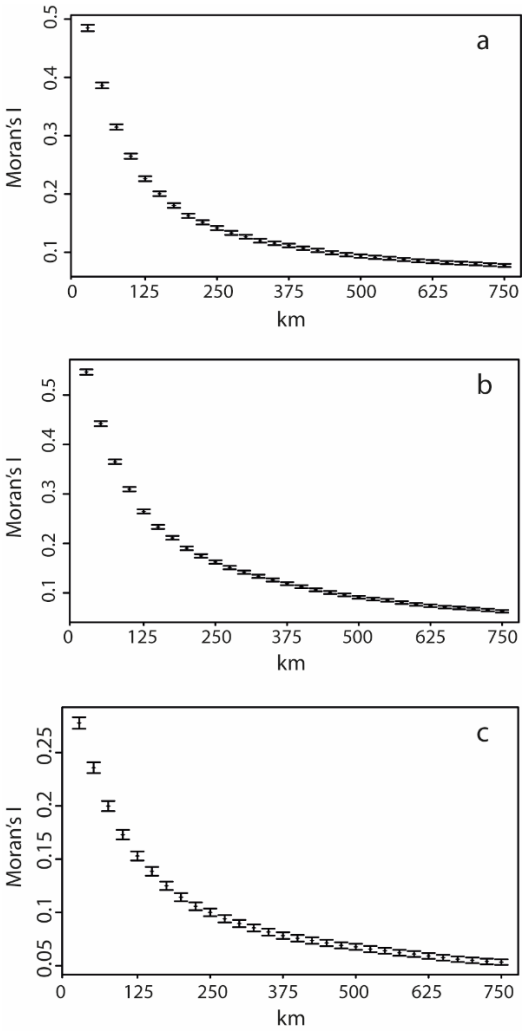

Figure S2.3: *Moran's I correlogram of AM (a), EcM (b) and ErM (c) model residuals.*

To evaluate whether the presence of SAC in the final model altered the final conclusion of this work, the complete dataset (n=270353) was subsetted according to two distance filters. In a first filter, we included only points that at least 250km apart from each other, resulting in 2337 data points. In a second filter, we included points

separated at least by 750km, resulting in 182 data points. The election of the distances is based on Moran's I correlogram (Figure S3) and correspond to distances at which the majority vs. virtually all spatial autocorrelation had disappeared.

The reduced model showed that, even when the distance between points is increased, climatic variables had the highest contribution in model R^2 (see Tables S8 and S9).

Table S2.8: *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 at a minimum distance of 250km.*

	Predictor	edf	t value	p-value	Pseudo-R^2	Contribution to Pseudo-R2*
AM	*Bulk density*	*2*	*-8.37*	*<0.001*	**0.48**	0.02
	PC1 climatic factors	*1*	*39.33*	*<0.001*		0.38
EcM	*Base saturation*	*2*	*-8.13*	*<0.001*	**0.31**	0.05
	PC1 climatic factors	*2*	*-24.6*	*<0.001*		0.25
ErM	*TOTN*	*2*	*5.99*	*<0.001*	**0.43**	0.01
	PC1 climatic factors	*3*	*-33.8*	*<0.001*		0.37

Table S2.9: *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 when including points at a minimum distance of 750km.*

	Predictor	edf	t value	p-value	Pseudo-R^2	Contribution to Pseudo-R2*
AM	*TOTN*	*2*	*-6.35*	*<0.001*	**0.43**	0.03
	PC1 climatic factors	*1*	*12.35*	*<0.001*		0.35
EcM	*TOTN*	*2*	*4.58*	*<0.001*	**0.20**	0.05
	PC1 climatic factors	*2*	*-8.05*	*<0.001*		0.15
ErM	*PC1 climatic factors*	*2*	*0.23*	*<0.001*	**0.33**	0.33