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MOUNTAIN TROPICAL FORESTS OF NORTHERN SOUTH AMERICA**

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**Universidad del Rosario
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ABSTRACT

Mycorrhizal fungi play key roles in the functioning of terrestrial ecosystems. The main types of mycorrhizal associations are arbuscular mycorrhizas (AM), ectomycorrhizas (EcM), ericoid mycorrhizas (ErM) and orchid mycorrhizas (OM). Previous studies have shown that the abundance of AM, EcM and ErM plants change gradually along latitudinal and altitudinal gradients driven by the effects of climate on decomposition, reflected in the accumulation of carbon and nutrients in the soil. The Colombian Andean mountain range reaches altitudes over 5,000 m and it is a great system to test the effects of altitude in tropical ecosystems. We aimed to understand how altitude and climatic and soil conditions shape the distribution patterns of mycorrhizal types in plant species distributed in this region. To test this, we used an herbarium plant record database and assigned mycorrhizal type based on the available literature. We also used bioclimatic and soil variables at a resolution of 10 km. We calculated the proportion of each of the different mycorrhizal associations types per grid cell and created a diversity index to explore their spatial distribution and their association with abiotic factors based on GLMs. We found that the diversity of mycorrhizal associations increases with altitude and soil carbon stock. We also found that the abundance of EcM and OM plants peaks around 2,000m and the abundance of ErM peaks around 2,300m, while AM plants preferred lower elevations (1,700m). Another interesting finding was that the abundance of AM plants increased when the proportion of nitrogen-fixing plants per cell increased. Our results suggest that climate change can alter the distribution of mycorrhizal types in tropical mountains with consequences for ecosystem function.

1| INTRODUCTION

Mycorrhizas are mutualistic associations between soil and plant fungi, where host plants receive nutrients and minerals from fungi and, in return, fungi receive carbon compounds obtained through plant photosynthesis (Smith and Read, 2008). Mycorrhizal associations play key roles in the functioning of terrestrial ecosystems, affecting the composition of the plant community (Klironomos et al., 2011), soil formation and structure (Leifheit, Veresoglou, Lehmann, Morris and Rillig, 2013), and the carbon (C) and macronutrient cycles (Averill, Turner and Finzi 2014; Veresoglou, Chen and Rillig, 2012). However, the mode and magnitude of the impact of mycorrhizas on ecosystem functioning are strongly related to the type of mycorrhiza involved (Van der Heijden, Martin, Selosse and Sanders 2015; Tedersoo and Bahram 2019; Tedersoo et al. 2020).

There are seven main types of mycorrhizal associations (Smith and Read, 2008) among which we can find: arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), ericoid mycorrhiza (ErM , typical of the Ericaceae family), and Orchid mycorrhiza (OM, unique to plants in the Orchidaceae family) (Read, 1996). These types of mycorrhizas are the most widespread in taxonomic and geographical terms being present in most terrestrial biomes. It has been estimated that approximately 84% of the earth's plant species form mycorrhizal associations with AM, EcM, ErM and OM fungi where 71% are arbuscular mycorrhizal, 2% are ectomycorrhizal, 1.4% are ericoid mycorrhizal, and 10% are orchid mycorrhizal (Brundrett and Tedersoo, 2018). Most plant species can form a single-type of mycorrhizal symbiosis (Wang and Qiu, 2006), with only a few exceptions in which the same plant species can be colonized by two types of mycorrhizal fungi (McGuire et al. 2008, Teste et al. 2020).

Associations with AM, EcM and ErM fungi predominate under specific edaphic and climatic conditions due to functional differences among these fungal guilds. Ectomycorrhizal and ErM fungi are more abundant in N-limiting conditions and are capable of decomposing organic matter by the expression of extracellular enzymes, which makes these associations more beneficial in organic soils (Readet *et al.* 2004, Lindahl and Tunlid 2015). On the contrary, the saprotrophic capacities of AM are less developed, which makes the AM fungi depend mainly on inorganic

compounds as a source of nutrients and, therefore, are more frequent in mineral soils with phosphorus limiting conditions (Smith and Smith, 2011).

In 1991 Read et al. proposed a theoretical model in which the abundance of plants with AM, EcM and ErM associations change gradually along latitudinal and altitudinal gradients, driven mainly by the effects of climate on decomposition, which is ultimately reflected in the accumulation of organic C and nutrients in the soil. According to this model, AM plants would dominate in grasslands and tropical forests; EcM trees would dominate in temperate and boreal forests; and plants with ErM associations would predominate in the heaths. Read's predictions were confirmed at the global scale by Steidinger et al. (2019) who found that regional variation in climate and rate of decomposition did predict the relative abundance of the different mycorrhizal types at the biome level. Another global study about the main factors driving the distribution of plants with different mycorrhizal associations found that changes in the climatic conditions, particularly temperature, can shape the distribution of plants with AM, EcM and ErM associations and suggested that climate change can significantly alter the distribution of mycorrhizal host plants, with a subsequent impact on the functioning of the ecosystem (Barcelo et. al. 2019).

Currently, there are not detailed studies about the distribution of mycorrhizal types in tropical mountains and all the available information is mostly based on modeling of the abundance of EcM vs AM plants at coarse scales (1° by 1° grid). In Colombia, the Andes mountain range has altitudes that can surpass the 5,000 m.a.s.l and have a surface of 299.540 km² that occupies approximately 26% of the total surface of the country (Veblen, Young and Orme, 2015). So, we aim to understand how the altitude and variations of climatic and soil conditions shape the distribution patterns of AM, EcM, ErM, and OM mycorrhizal plants as well as weakly or non-mycorrhizal and nitrogen fixers plants. We also aim to identify the areas and altitudinal ranges that hold the highest diversity of types of mycorrhizal associations. Even though we expect to find a predominance of AM associations as has been reported for the tropics, other types of mycorrhizal associations are present and are locally abundant in some tropical ecosystems. We expect to find a correlation between the type of mycorrhiza along the altitudinal-climatic gradient with AM plants being more abundant in the lowlands with warm climates and EcM and ErM plants being more abundant at high altitude and lower temperatures.

2|MATERIALS AND METHODS

2.1|Study area

Our study focuses on the Colombian Andes, which is a mountainous system located in northern South American (Figure 1). It occupies 299.540 km² which represents about 26% of Colombia's surface. This system also includes the Sierra Nevada de Santa Marta massif. The Colombian Andes have a great variability in altitude ranging from 100 m.a.s.l. in the inter andean valleys up to 5,775 m.a.s.l. at Cristóbal Colon peak (Figure 1.b) The tropical Andes region has one of the greatest plant diversity in the world and it is considered a biodiversity hotspot (Myers et al. 2000) due to the high endemism of plant species caused in part by its multiple environmental gradients (Rangel, 2005) and biogeographic history.

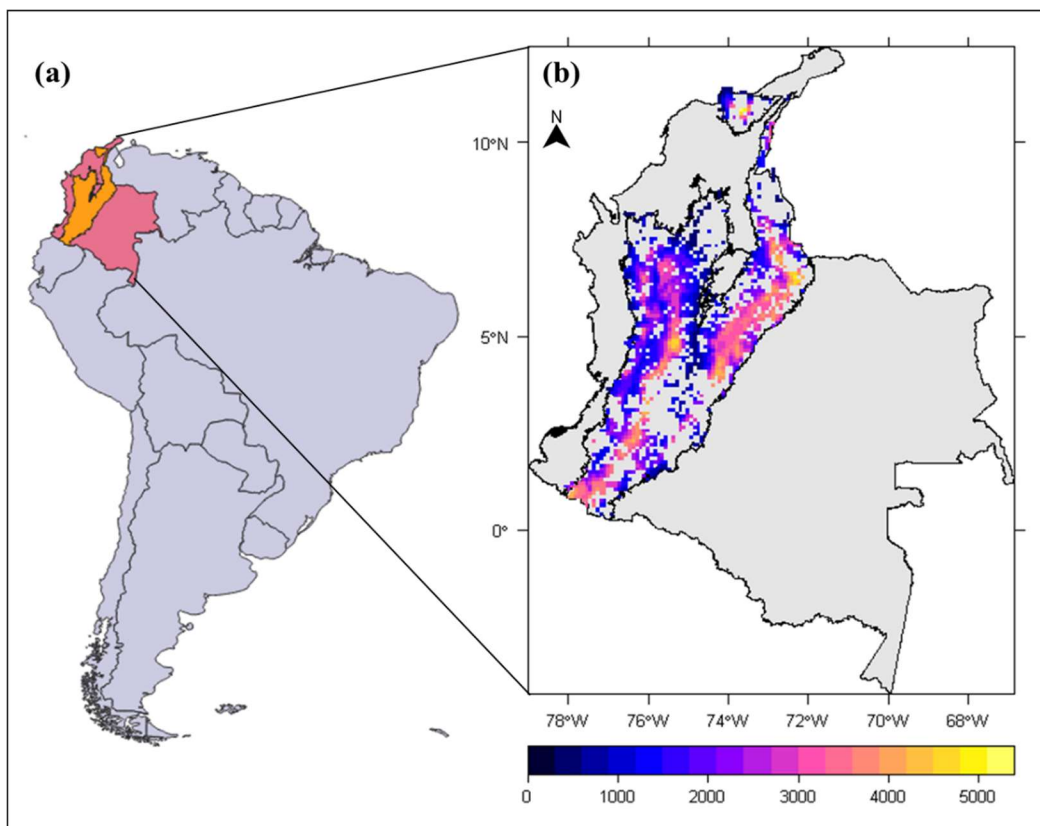


FIGURE 1. (a) Location of the country of Colombia in the north of the South America (pink) and the Andes mountain range in Colombian (orange.) **(b)** Altitudinal gradient (m.a.s.l.) of the Colombian Andes used for this study.

2.2 Plant database and assignment of mycorrhizal status

The database used for this study compiles 266,543 plant records from herbarium collections across the Colombian Andes and includes 3,094 plant genera. This database includes all the records previously published by Bottin et al. (2020) and details about the data standardization protocols are described therein. We assigned type of mycorrhizal association to plant genera based on the FungalRoot database (Soudzilovskaia et al. 2020) and the available literature (Wang and Qiu, 2006, Steidinger et al 2019, Vetrovsky et al. 2020). We started from the premise that the types of mycorrhizal associations are highly conserved among plant genera (Tedersoo and Brundrett, 2017, 2018). We were able to assigned type of mycorrhizal association to 2,410 plant genera, corresponding to 233,394 plant records.

From all the types of associations, we choose to work with the most abundant types of mycorrhizal symbiosis following Brundrett and Tedersoo (2018): arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), ericoid mycorrhiza (ErM), and orchid mycorrhiza (OM). We also classified some genera that have a weak AM relationship as slightly arbuscular or non-arbuscular (WamNM) and genera that form associations with nitrogen-fixing bacteria as nitrogen fixers (Nfix).

2.3 Soil and climatic databases

Soil variables were downloaded in raster format from the International Union of Soil Sciences website (ISRIC, <https://www.isric.org/explore/soilgrids/faq-soilgrids>) with a resolution 250 m at four depths 0, 0.05, 0.15 and 0.3 meters. These depths were averaged using Orfeo Toolbox (Grizonnet et al. 2017), We don't used the total carbon stock between 0 and 30 cm because we wanted an idea the representative value of carbon stock along to Colombia Andes . The downloaded variables included: soil water capacity (AWCh1; volumetric fraction, with Field Capacity = pF 2.0 percentage following de Oliveira *et al.* 2015), bulk density kg/m³ (BLDFIE), soil cation exchange capacity cmolc/kg (CECSOL), density of soil organic carbon kg/m³ (OCDENS), pH measured in water solution (PHIHOX), weight percentage of clay particles <0.0002 mm (CLYPPT), weight percentage of silt particles 0.0002–0.05 mm (SLTPPT), weight percentage of sand particles 0.05–2 mm (SNDPPT), texture class based on the USDA system (EXMHT), and soil organic carbon stock ton/ha (OCSTHA).

Climatic variables were downloaded in raster format with a resolution of 30 arc seconds from the Worldclim website (<https://www.worldclim.org/data/worldclim21.html>). Additionally, an elevation raster was downloaded from the same website to extract the elevation data from the logs also in raster format with a resolution of 30 arc seconds. The downloaded variables included 19 bioclimatic variables: BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)), BIO3 = Isothermality (BIO2/BIO7) ($\times 100$), BIO4 = Temperature Seasonality (standard deviation $\times 100$), 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, and BIO14 = Precipitation of Driest Month.

2.4 | Assembly of the spatial database

To evaluate the distribution patterns of the types of mycorrhizal associations we generated spatial grid data frame with a resolution of 10 square kilometers for all the Colombian Andes using the *Sp package* v1.4. To extract soil, climatic and elevation data, a resample was performed to adjust its resolution to the resolution of the types of grids used using the *raster* package v3.0. Once the resample for the variables was carried out, the values were extracted per cell. Geographic coordinates of the cells (longitude and latitude) were extracted using the coordinates function of the *raster* package v3.0 to be included within the variables for statistical analysis. All analysis were run in R statistical software v. 3.6.

We calculated the proportion of the different types of mycorrhiza per cell of the grid, by counting the number of records for each type of mycorrhizal association in the cell and dividing by the total number of records in the same cell. In addition, we calculated the ratio of the number of joint records of both EcM and ErM associations divided by the total number of records of AM per cell (EcRA, Equation 1). For statistical analysis we only used cells containing at least 10 records with known mycorrhizal type to prevent the models from being affected by empty cells.

$$EcRA = \frac{EcM \text{ records by cell} + ErM \text{ by cell}}{AM \text{ records by cell}}$$

EQUATION 1. Where *EcM* is number of ectomycorrhizal plant records per cell, *ErM* ericoid mycorrhizal plant records per cell, and *AM* is arbuscular mycorrhizal plant records per cell.

2.5 | Statistical analysis

The Shannon index was used to calculate an index representing the diversity of types of mycorrhizal associations using the relative abundance of each type of mycorrhizal association calculated as the number of records for each type of mycorrhizal association divided by the number of plant species records in the cell (Equation 2).

$$MycoIndex' = - \sum_{i=1}^M pi \log_2 pi$$

EQUATION 2. Where *M* is the number of types of mycorrhizal associations, *pi* is the relative abundance of the *i* type of mycorrhizal associations.

We used GLMs to explore the influence of our predictor variables on several response variables: 1) the proportions of the different types of mycorrhizal associations 2) the diversity index of the different types of mycorrhizal associations and 3) its spatial distribution in the Colombian Andes.

We implemented a stepwise analysis to select the final variables included in the models based on the AIC criterion using the *stepwise* function in the package Rcmdr v2.6. We also ran a variable inflation factor analysis on the final GLM models to verify the intensity of multicollinearity of the variables. We used an Anova to verify if there were significant differences in the elevation range for different types of mycorrhizal associations. We also ran a Tukey post-hoc test for a pairwise comparison of significant differences of the elevation mean between types of mycorrhizal associations. Finally, we used a variance partition analysis to examine the amount of variance explained by our predictor variables using four variables categories: edaphic, climatic, spatial, and biotic variables. We ran two variance partition analysis, one including data from all types of

mycorrhizal associations and one only including AM, EcM and ErM to be able to compare our results with previous studies.

Our group of climatic variables included mean annual precipitation and elevation (m), the latter being categorized in this case as climatic given its high correlation with temperature. The edaphic variables included available soil water capacity, bulk density, soil organic carbon density, pH, and soil carbon stock. The spatial variables included longitude and latitude. We also included the proportion of plants associated with nitrogen fixing bacteria (Nfix) per cell in the variance partition analysis and the GLMs models as a biotic predictor variable. Nfix roots associations have an important role in regulation of N soil-levels and this has a positive impact in the plant diversity (Xu et al. 2020). Therefore, we consider that this could influence the number of types of mycorrhizal associations in the altitudinal gradient of Colombian Andes. This analysis was run using the *vegan* package v. 2.6.

2.6 | Creating maps

We created maps of distribution of the different types of mycorrhiza based on relative abundance per cell and a map of the diversity of mycorrhiza types based on the Shannon index to identify hotspots of mycorrhizal type diversity and areas of higher abundance of each mycorrhizal type in the Colombian Andes. The maps were created using the *raster* package v3.0 and *Sp* package version 1.3-2. All the geographic data and geographical plots have a datum WGS84 and plotted using the *spplot* function of *Sp* package version 1.3-2 in R version 3.6

3|RESULTS

3.1| Distribution of types of mycorrhizal associations in the Colombian Andes

Our data included strong environmental gradients of many abiotic variables, i.e. the mean annual maximum temperatures ranged from a minimum of 2.6 °C at the highest peaks to 28.4 °C in the lowest valleys. Also mean annual precipitation ranged from 632 mm in dry areas to 6556 mm in very humid areas. We found a high correlation between elevation and carbon stock in the soil ($R^2 = 0.8, p < .0001$).

Table 1. Summary of the mycorrhizal type associations in the Colombian Andes

Type of symbiosis	Number of genera	% of total records	Most frequent genera	Most frequent families
AM	2,162	81.82	<i>Miconia</i> , <i>Solanum</i> , <i>Passiflora</i> , <i>Palicourea</i> , <i>Anthurium</i> , <i>Psychotria</i> , <i>Clusia</i> , <i>Pentacalia</i> and <i>Baccharis</i>	Melastomataceae, Solanaceae, Passifloraceae, Araceae, Rubiaceae, Clusiaceae and Asteraceae
EcM	27	0.61	<i>Quercus</i> , <i>Acacia</i> , <i>Alnus</i> , <i>Guapira</i> , <i>Coccoloba</i> , <i>Neea</i> , <i>Eucalyptus</i> , <i>Salix</i> .	Fagaceae, Fabaceae, Betulaceae, Nyctaginaceae, Polygonaceae, Myrtaceae, and Salicaceae
ErM	21	3.65	<i>Cavendishia</i> , <i>Gaultheria</i> , <i>Disterigma</i> , <i>Pernettya</i> , <i>Bejaria</i> , <i>Vaccinium</i> , <i>Macleania</i> , <i>Psammisia</i> , <i>Thibaudia</i> , <i>Themistoclesia</i>	Ericaceae
OM	174	3.27	<i>Epidendrum</i> , <i>Pleurothallis</i> , <i>Stelis</i> , <i>Elleanthus</i> , <i>Maxillaria</i> , <i>Cyrtorchilum</i> , <i>Oncidium</i> , <i>Ornithidium</i> , <i>Lepanthes</i> , and <i>Masdevallia</i>	Orchidiaceae
WamNM	49	7.67	<i>Piper</i> , <i>Asplenium</i> , <i>Geranium</i> , <i>Selaginella</i> , <i>Viburnum</i> , <i>Cecropia</i> , <i>Galium</i> , <i>Rhynchospora</i> , <i>Lycopodium</i> , <i>Gaiadendron</i>	Piperaceae, Aspleniaceae, Geraniaceae, Selaginellaceae, Adoxaceae, Urticaceae, Rubiaceae, Cyperaceae, Lycopodiaceae, Loranthaceae
Nfix	23	2.95	<i>Inga</i> , <i>Ocotea</i> , <i>Frullania</i> , <i>Morella</i> , <i>Desmodium</i> , <i>Calliandra</i> , <i>Mimosa</i> , <i>Erythrina</i> , <i>Lupinus</i> , <i>Machaerium</i>	Fabaceae, Lauraceae, Frullaniaceae, Myricaceae

The dominant type of symbiosis among plants from the Colombian Andes was associations with AM fungi (81.8% of the total, Table 1) followed by 7.7% of WamNM plants, and 3.7% of ErM. Based on the scatter plot of the mycorrhizal Shannon index with elevation (Figure 2a) the diversity of mycorrhizal associations increased with elevation and also with soil carbon stocks (Figure 2b), but show a decline after 3000 m. We also found that there was a greater concentration of diversity of types of mycorrhizal associations on the eastern mountain range of the Colombian Andes

(Figure 3). The point of the greatest diversity of types of mycorrhizal associations was at 3,158 m.a.s.l with a Shannon index of 1.27. The place with the least diversity of mycorrhizal types was found at 323 m.a.s.l with a Shannon index of zero, which means that there is only one type of mycorrhizal association in that cell.

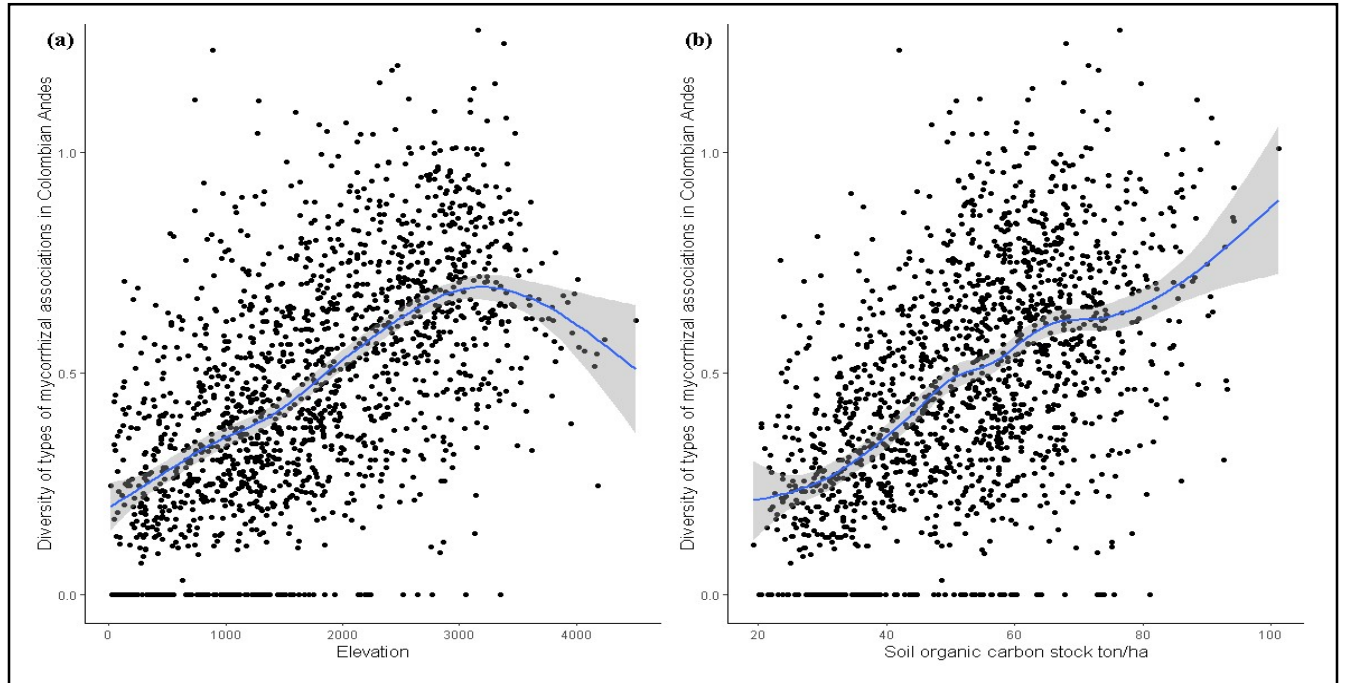


FIGURE 2. Diversity of types of mycorrhizal associations in the Colombian Andes along **(a)** the altitudinal gradient. **(b)** the soil carbon stock gradient.

The GLM results for the diversity of types of mycorrhizal associations shows that the soil carbon stock (OCSTHA) was significantly positively associated with the diversity of types of mycorrhizal associations ($t\text{-value} = 4.482, p = 7.92\text{e-}06$ ***). In the same way, elevation was highly significantly positive ($t\text{-value} = 10,939, p = <2\text{e-}06$ ***; Figure 3) and the proportion of Nfix plants was significantly negatively associated with the diversity of types of mycorrhizal associations ($t\text{-value} = -5.102, p = 76\text{e-}12$ ***).

Arbuscular mycorrhizal plants were amply distributed and had high relative abundance throughout the Colombian Andes (Figure 4a). The distribution of AM plants was negatively influenced by elevation ($t\text{-value} = -7.21, p = 8.24\text{e-}13$ ***) and was similarly negatively influenced by OCSTHA ($t\text{-value} = -4.87, p = 1.17\text{e-}06$ ***) but was positively influenced by the proportion of Nfix plants ($t\text{-value} = 5.74, p = 1.13\text{e-}08$ ***).

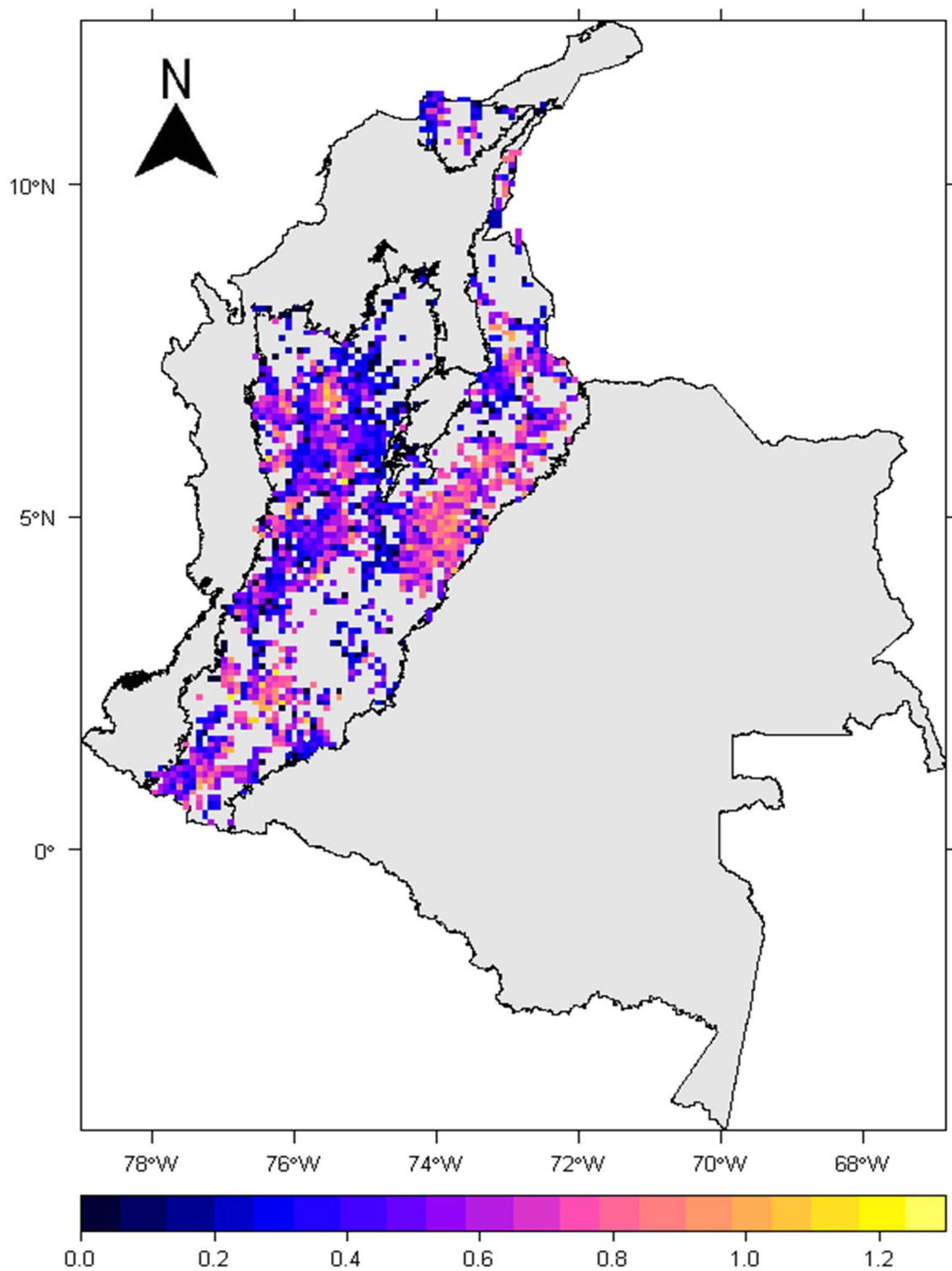


FIGURE 3. Spatial distribution of the diversity of types of mycorrhizal associations in the Colombian Andes. Diversity was calculated using the Shannon index.

Ectomycorrhizal associations were found in a low proportion throughout the Colombian Andes with points showing the highest proportion of EcM occurring at medium-high elevation (Figure 4b). We found that the EcM plant distribution was only negatively associated with mean annual precipitation (t-value = -3.75, $p = 0.000183$ ***). Ericoid mycorrhiza abundance increased with altitude showing a clustered distribution on small points of high concentration (Figure 4c). We found that the ErM plant distribution was positively associated with OCSTHA (t-value = 5.66, $p = 1.76 \times 10^{-8}$ ***), elevation was also positively significant for the distribution of ErM (t-value = 3.50, $p = 0.000466$ ***), while the proportion of Nfix plants plays a significant negative role in the distribution of ErM (t-value = -3.53, $p = 0.000428$ ***). The ratio between EcM and ErM vs AM was also positively influenced by OCSTHA (t-value = 5.66, $p = 1.76 \times 10^{-8}$ ***), and elevation (t-value = 3.50, $p = 0.00046$ ***), while the presence of N-fixers had a negative effect (t-value = -3.53, $p = 0.00042$ ***).

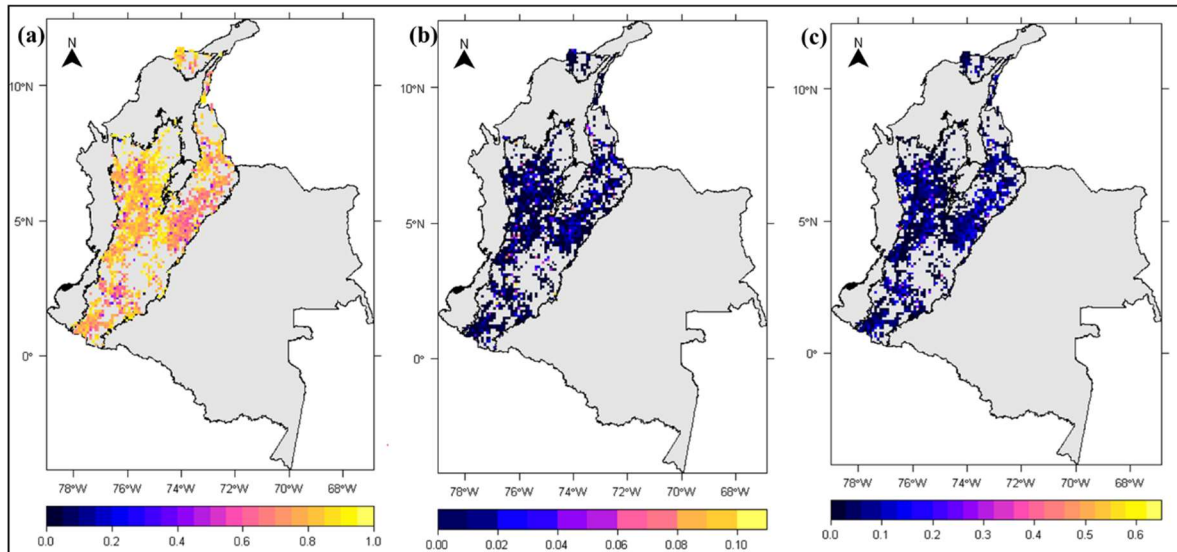


FIGURE 4. Spatial distribution in the Colombian Andes of the relative abundance per cell of (a) Arbuscular mycorrhizal plants (b) Ectomycorrhizal plants (c) Ericoid mycorrhizal plants.

We found that the OM plant distribution was positively associated with OCSTHA (t-value = 5.50, $p = 4.38 \times 10^{-8}$ ***), and negatively associated with the proportion of Nfix plants (t-value = -3.93, $p = 8.85 \times 10^{-8}$ ***). The proportion of WanNm plants was low throughout the Andes with high concentration in focal points in places of medium altitude (Figure 5b). We found that the WanNm

distribution was significantly positive associated with elevation (t- value = 7.734, $p = 1.81\text{e-}08$ ***) while OCSTHA (t-value = -2.67, $p = 0.0075$ ***) and the proportion of Nfix plants had significant negative association with WanNm ratio (t-value = -2,815, $p = 0.00494$ ***)).

The distribution of the proportion of Nfix plants was consistently low throughout the Colombian Andes with small areas of medium concentration (Figure 5c). Nitrogen fixing plant distribution was significantly positive associated with mean annual temperature (t-value = 4.316, $p = 1.68\text{e-}05$ ***) and negatively associated with OCSTHA (t-value = -5.538, $p = 3.55 \text{e-}08$ ***)).

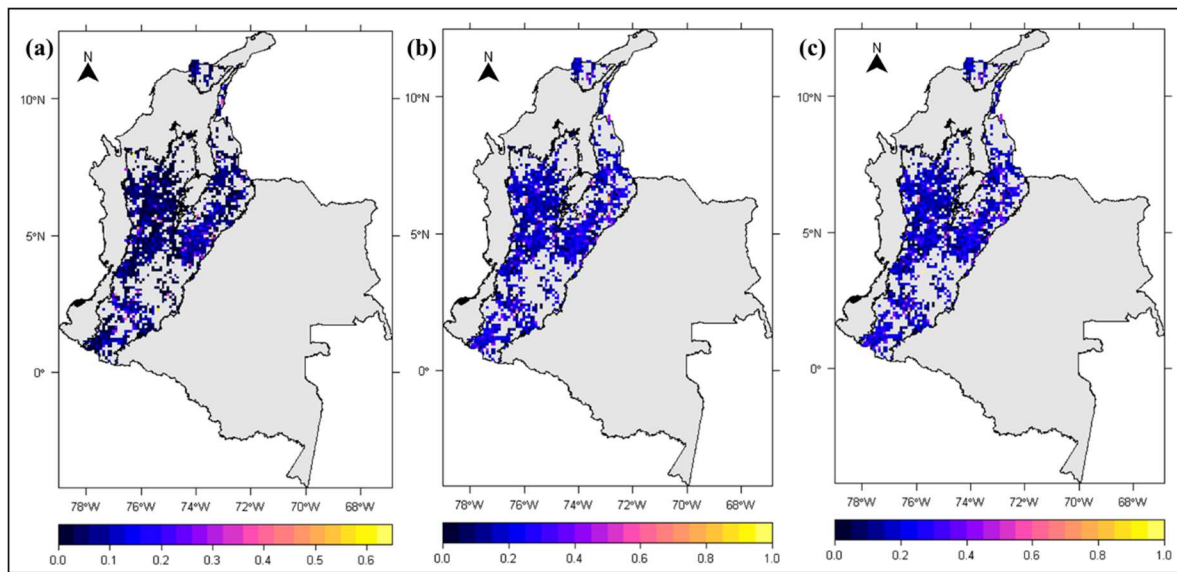


FIGURE 5. Spatial distribution in the Colombian Andes of the relative abundance per cell of **(a)** Orchid mycorrhizal plants, **(b)** Weakly arbuscular or non-mycorrhizal plants **(c)** Nitrogen fixing plants.

The ANOVA analysis shows that there were significant differences of the altitudinal ranges of the different types of mycorrhizal associations ($p = <0.0001$ ***, Figure 2). Arbuscular mycorrhizal associations had a median altitude of 1,760 m (highest point 4509 m - lowest point 18.82 m), EcM associations had a median altitude of 1,927 m (lowest point 43 m- highest point 4,246 m), ErM had a median altitude of 2,234 (lowest elevation 196 m - highest point 4,246 m) and OM had a median altitude of 2,047 m (lowest point 43 m - highest point 4,509 m). For the WanNM the median altitude was 1,825 (lowest point 19 m- highest point 4,509 m) and for Nfix was of 1,657

(lowest point 41.82 m - highest point 4,509 m). The Tukey test, revealed significant differences between the variances of the elevations of the AM vs EcM, ErM vs AM, OM vs AM, ErM vs EcM, Nfix vs EcM, Nfix vs ErM, WanNm vs ErM, Nfix vs OM, WanNm vs Nfix, and WanNm vs OM (Figure 6).

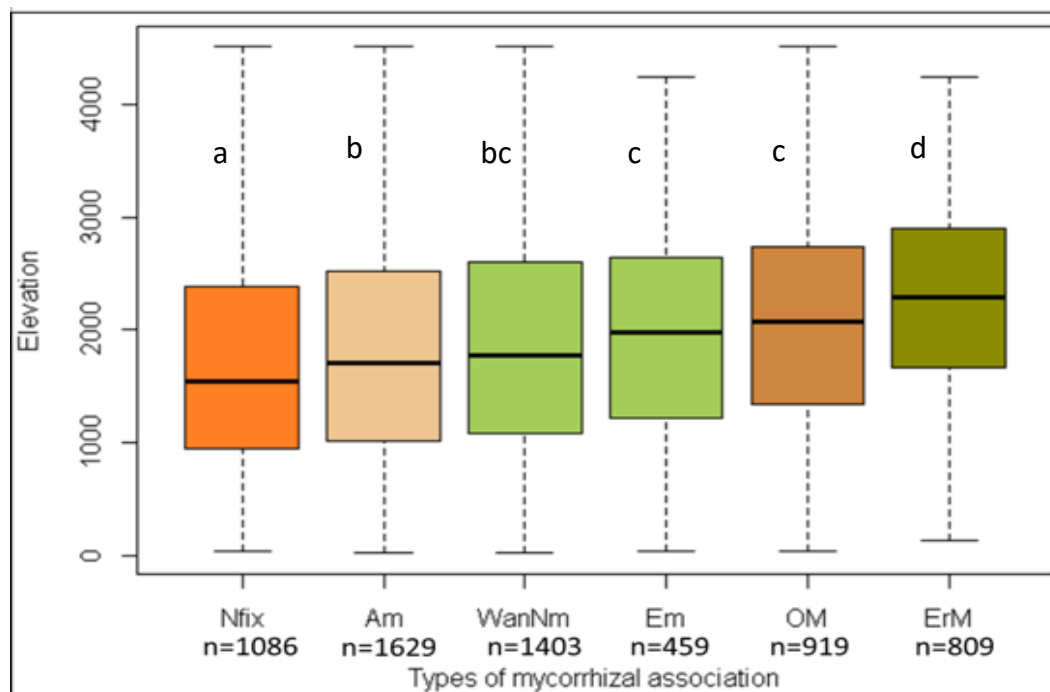


FIGURE 6. Distribution of the types of mycorrhizal associations along the altitudinal gradient of the Colombian Andes

Variance partition analysis including AM, EcM and ErM mycorrhizal plants show that climatic variables explained only 1.5% of the variation of the data, edaphic variables explained 0.9% and the interaction between the climatic and edaphic variables explained 16.2% of the variation. The spatial variables alone and their interaction with climatic, edaphic and biotic variables explained a very small proportion of the total variation (0.8% ,0.4%, 0.3%, respectively). The only biotic variable included in the variance partition, the Nfix abundance, alone explained 0.7% of the data variation, while the interaction of the Nfix with edaphic variables explained 0.2% and the interaction of Nfix with the edaphic and climatic variables explained 5.2%.

The variables included in the analysis only explained 25.5% of the total variation (Figure 7a) Variance partition analysis including all types of mycorrhizal associations showed similar results however we observed that the included variables explained only 17.2% of the variation of the data (Figure 7b).

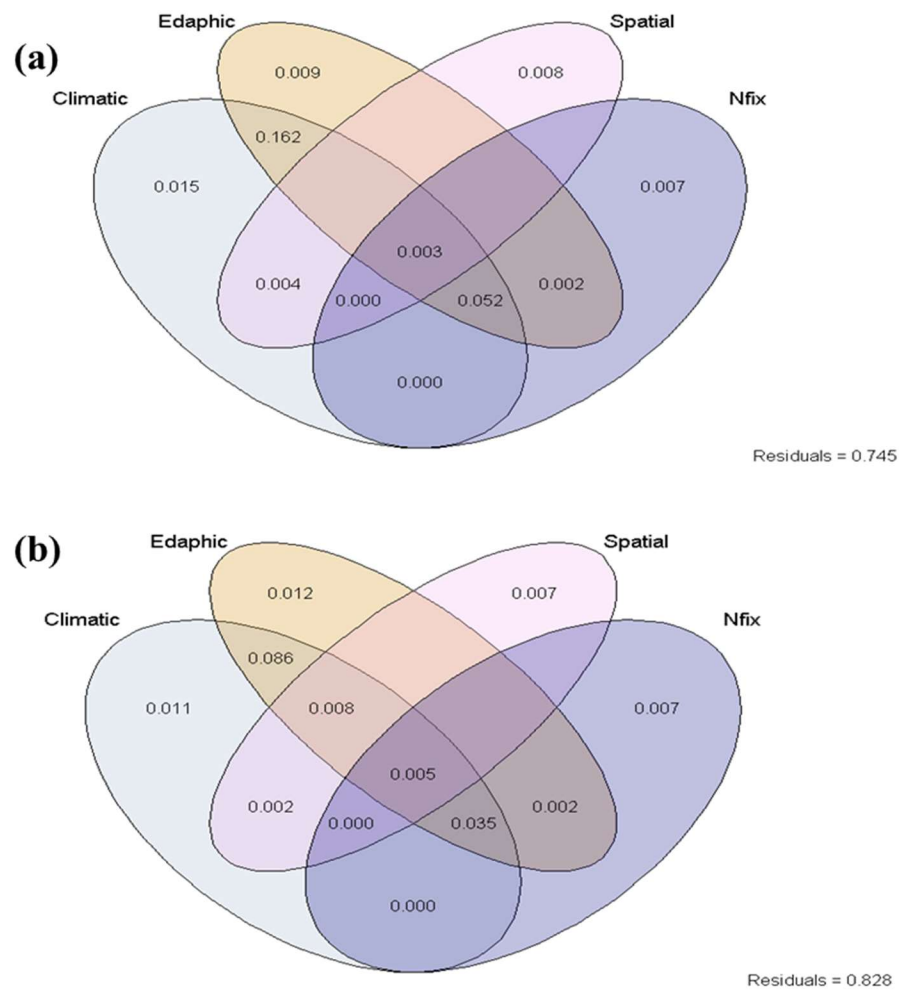


FIGURE 7. Variance partition plot for **(a)** All types of mycorrhizal associations included in this study **(b)** Excluding WanNm and OM plants.

4| DISCUSSION

This study shows for the first time the distribution patterns of the different types of mycorrhizal associations along tropical altitudinal gradients at a regional scale. Similar studies done with plants in the tropical Andes have been based on altitudinal gradients at smaller spatial scales and without including types of mycorrhizal associations and the implications of their distributions (Unger et al. 2012). Our work gives a new perspective on the distribution patterns of the different types of mycorrhizas along a broad altitudinal gradient and the interactions of altitude with edaphic and climatic variables. We found that there is a separation in the distribution of the different types of mycorrhizas along the altitudinal gradient in neotropical mountains. Our data also revealed that the three main factors influencing the distribution of the different types of mycorrhizal associations were elevation, soil carbon stock, and mean annual precipitation.

Regarding elevation as a predictor factor, it is relevant to understand the implications of this, not only as a spatial factor but also as a climatic factor with influence on edaphic conditions reflected on the existence of an inverse relationship between temperature and edaphic factors such as the stock of soil. Even though we don't have data about decomposition rate, it is well known that it decreases with altitude (van de Weg et al., 2009). Then we would expect our results to support the ones found at global scales by Steidinger et al. (2019). Our results partially supported the findings from Barceló et al. (2019) who found that climatic factors are the main drivers in the distribution of different types of mycorrhiza. Our results highlight the importance of edaphic factors in determining the altitudinal distribution of different types of mycorrhizal association in the Colombian Andes.

Even though our models show that soil carbon stock is one of the main factors associated with the distribution patterns of the different types of mycorrhizal associations along the altitudinal gradient of the Colombian Andes it would be difficult, without additional experimental evidence, to understand if the patterns found here correspond to niche preferences of plants with different mycorrhizal associations or to ecosystem changes created by microbially mediated feedbacks (Benett et al., 2017). For example, it has been shown that edaphic factors can be influenced by differences in the nutrient economy associated with AM vs EcM mycorrhizas (Unger et al. 2012; Phillips et al. 2013, Corrales et al. 2016). We also found that the distribution of Nfix plants may

be playing an important role in the distribution of different types of mycorrhiza through its influence on nitrogen cycling and nutrient availability (Xu et al. 2019; Xu et al 2020).

4.1 | Predictors of AM and WanNM associations

Our results show that the presence of Nfix plants is a very important factor for the distribution of AM plants in the altitudinal gradient, while high levels of carbon stock and high elevations are restrictive factors for its distribution throughout the altitudinal gradient. However, Am plants are not exclusive of lowlands since their distribution throughout the Andes is widespread compared to the other types of mycorrhizal associations.

Although elevation is the main factor that determines the distribution of AM in the altitudinal gradient, Nfix plant abundance could be playing an important role in facilitating AM plants. Nitrogen fixing plants perform biological nitrogen fixation (BNF) therefore increasing nitrogen availability in addition to having a possible effect in improving phosphate mineralization which could facilitate the colonization of AM plants (Nasto et al. 2014). This facilitation mechanism by Nfix can be a possible explanation for why AM distribution decreases with altitude as Nfix plants decline (Figure 4). With the reduction of Nfix plants with altitude, the availability of accessible N for AMs is reduced and inorganic nitrogen concentrations become more difficult to mobilize in the soil (Smith and Smith, 2011). Although the availability of the BNF provided by the Nfix plants is a factor that is important for its wide distribution at low elevation, it is not a limitation for AM plants distribution at a higher elevation, although it may be one of the reasons why the number of records is reduced. Also Barceló et al. (2019) highlights that temperatures below 15 °C significantly reduce intra-root colonization by AM to host plants, a factor that is of great importance for an effective propagation of this type of mycorrhizal association at higher altitudes (Gavito et al., 2012). The distribution of WanNM was associated with elevation, although soil carbon stock and the abundance of Nfix negatively affected their distribution.

4.2 | Predictors of EcM associations

We found that highest abundances of the EcM plants occurs in medium altitude forests with relatively low precipitation (Supplementary 1). This is a very interesting finding since it has been reported that EcM plants could have higher root hydraulic conductivity, higher water potentials, larger root systems, and higher CO₂ assimilation rates under drought conditions than non-EcM species (Lehto and Zwiazek 2011). These physiological advantages have been associated with the fact that EcM fungal mycelium can efficiently explore a large soil volume and access resources unavailable for plant roots (Lehto and Zwiazek 2011). We did not find an increase of EcM plants with elevation or temperature as found in previous studies (Steindinger et al. 2019) which could mean that the distribution patterns of tropical EcM plants could not be predicted based on global models.

The absence of native EcM conifer forests and the low abundance of EcM plants in the tropical Andes could account for the different distributional pattern. *Quercus* was the genus with the highest number of records. Particularly, in our database *Quercus* is represented by only one species in Colombia (*Quercus humboldtii*) that accounted for 21.3% of all EcM plant records. *Quercus humboldtii* shows a high dominance in the species composition and community structure of some montane forests of the Colombian Andes at elevations above 1,500 m.a.s.l. (González et al 2020) and it is distributed in sites with a mean annual temperature ranging from 9.3 to 27.1 °C (González et al, 2006).

Recent studies have demonstrated that EcM plants are associated with an organic nutrient economy (Phillips et al. 2013), which means that its main source of carbon comes from decomposing matter in the soil, such as leaf litter, lower pH levels, and much slower decomposition rates compared to what would be expected to be found in soils with AM dominance (Phillips et al ., 2013, Corrales et al. 2016; Cheeke et al., 2017). In addition EcM plants and their associated fungi have high phosphatase enzymes activity that allow them to improve the release of acids with low molecular weight, increasing their access to organic phosphorus (Jansa et al., 2011) and a greater number of forms of organic nitrogen (Read and Perez, 2003). The increase in dominance of EcM plants could help to conserve soil stock carbon due to its low decomposition rates of organic matter.

4.3 | Predictors of ErM associations

Our results show that the most important factors for the distribution of the ErM plants along the altitudinal gradient are soil carbon stock, elevation, and Nfix plant abundance. This result highlights the importance of soil variables as drivers of ErM plant distribution and is opposite to what was found by Barceló et al. (2019) that concluded that the main factor modeling the distribution of ErM was temperature. It has been shown that ErM plants have physiological adaptations to adverse climates (Marian, Krebs and Arora, 2004.) and it has been hypothesized that these adaptations are key to understand their distribution. We found that the higher the elevation, the greater the number of ErM plant records, however soil carbon stock turned out to be more important than elevation suggesting that it is not only the temperature but also edaphic conditions and nutritional requirements that may be influencing ErM plants distribution along the altitudinal gradient.

Edaphic conditions are relevant ecological drivers for ErM plants given their ability to access sequestered mineral nutrients within soil organic matter by releasing enzymes with cellulolytic, hemicellulolytic, pectinolytic, and ligninolytic activities, as reported by Cairney and Burke (1998). This suggests that ErM symbiosis have a high level of specialization for the acquisition of N and P from organic sources, which is something characteristic of species adapted to soils with a low rate of decomposition of organic matter and high acidity (Walker et al. 1994). These results added to the patterns described by Steidinger et al. (2019) showing that low rates of decomposition have a strong effect on EcM and ErM mycorrhizal distribution patterns.

4.4| Predictors of OM associations

Our results for OM plants revealed that the main factor that shapes the distribution of OM are soil carbon stock and Nfix plant abundance. These results suggest that for OM, temperature is probably not a limiting factor which was evidenced in the results of the variance partition (Figure 7b). The altitudinal range of OM was not significantly different from EcM based on the Tukey test, due in part to the great influence of the soil carbon stock in their distribution. This is an interesting result worth of further exploration given that there has been several reports of orchid plants that associate with the EcM fungi using a partially mycoheterotrophic strategy due to their non-photosynthetic

condition (Dearnaley et al. 2013). The Orchidaceae family, being the most diverse in the tropics, presents a great variety of strategies that range from autotrophic to total heterotrophic, many of them being saprophytes (Dearnaley et al. 2013; Geml et al. 2017). Our result suggest that the OM distribution could be at least partially influenced by the decomposition patterns of organic matter event though this requires further study and monitoring of EcM distributions in conjunction with OM distributions. It is important to note that most orchids are epiphytes, so their correlation with soil organic matter is more indirect at best, for this reason, this type of mycorrhizal association deserves further study, to understand their distribution drivers according to their ecology.

4.5| Predictors of nitrogen fixing associations

We found that the main factors affecting the distribution of Nfix plants were altitude, temperature, and soil carbon stock. Temperature increases the diversity, activity, and decomposition rate of organic matter which has a direct effect on the biogeochemical cycles of N and C (Zhou et al ., 2016) and increases BFN. We found, as expected, that the Fabaceae family accounted for the highest numbers of Nfix plant records. This result is very interesting given that there is a great debate around whether or not the presence of legumes increases the diversity of plants around them. Recently it was discovered that the increase in plant diversity due to the effect of legumes is a function of the amount of nitrogen available in soils, which reduces competition for the resource and favors and increase in plant diversity, but when there are poor N soils, legumes contribute to the fall on plant diversity, since legumes have very high requirements for N (Xu et al, 2020) (Supplementary 2). Our results show indirect support to the hypothesis of the decrease in the concentration of inorganic N available in soil with an increase in elevation.

4.6| Predictors of diversity of types of mycorrhizal associations

Our results indicate that the diversity of types of mycorrhizal associations is mediated mainly by elevation and soil carbon stock. We found an increase of the diversity of mycorrhizal types with altitude, with altitudes between 1,500 and 2,500 m.a.s.l holding the highest diversity of mycorrhizal types. Given the increase in soil carbon stock and the expected decrease in inorganic nitrogen with altitude, we can hypothesize that associating with different types of mycorrhizal

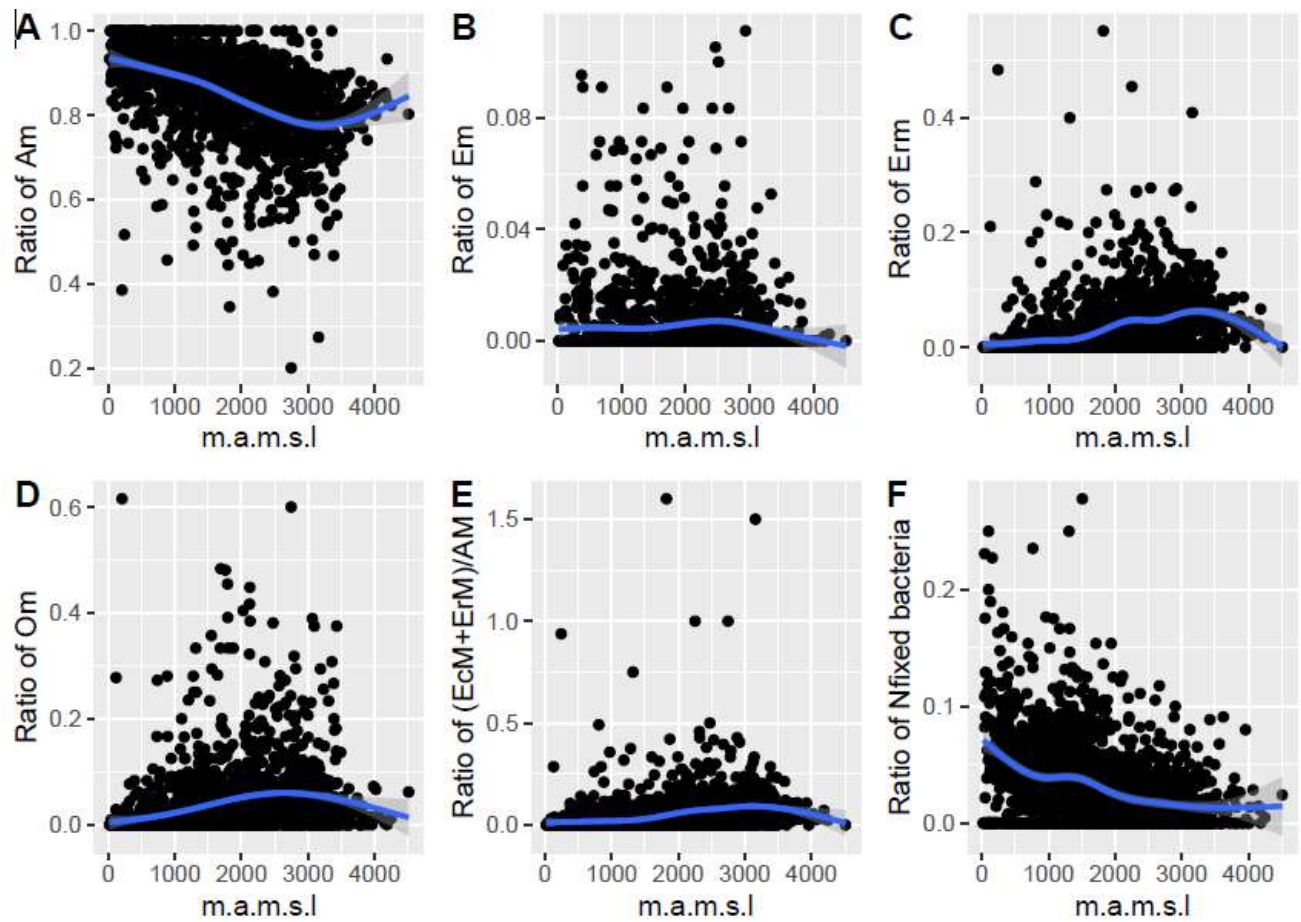
fungi are of great importance for reducing competition for limiting nutrients among plant species, improve nutrient uptake, maintain biogeochemical cycles and to increase accumulation of carbon in soils.

It is important to mention that mycorrhizal associations are of great importance in maintaining diversity in ecosystems (Van Der Heijden *et al.* 1998), but this diversity of types of mycorrhizal associations can be affected by fragmentation of the landscape. In Colombia, in recent decades, anthropic activities have led to the deterioration and fragmentation of ecosystems, with the Andes region being one of the most affected ones (Ayram *et al.* 2020). Habitat destruction could compromise the connectivity between fragments separated by anthropogenic effects becoming more difficult for different types of mycorrhiza to colonize these highly fragmented territories (Delavaux *et al.*, 2019) leading to a decrease in the diversity of different types of mycorrhizal associations and potentially altering feedbacks in the soil-microbial-plant continuum that could have consequences for ecosystem stability.

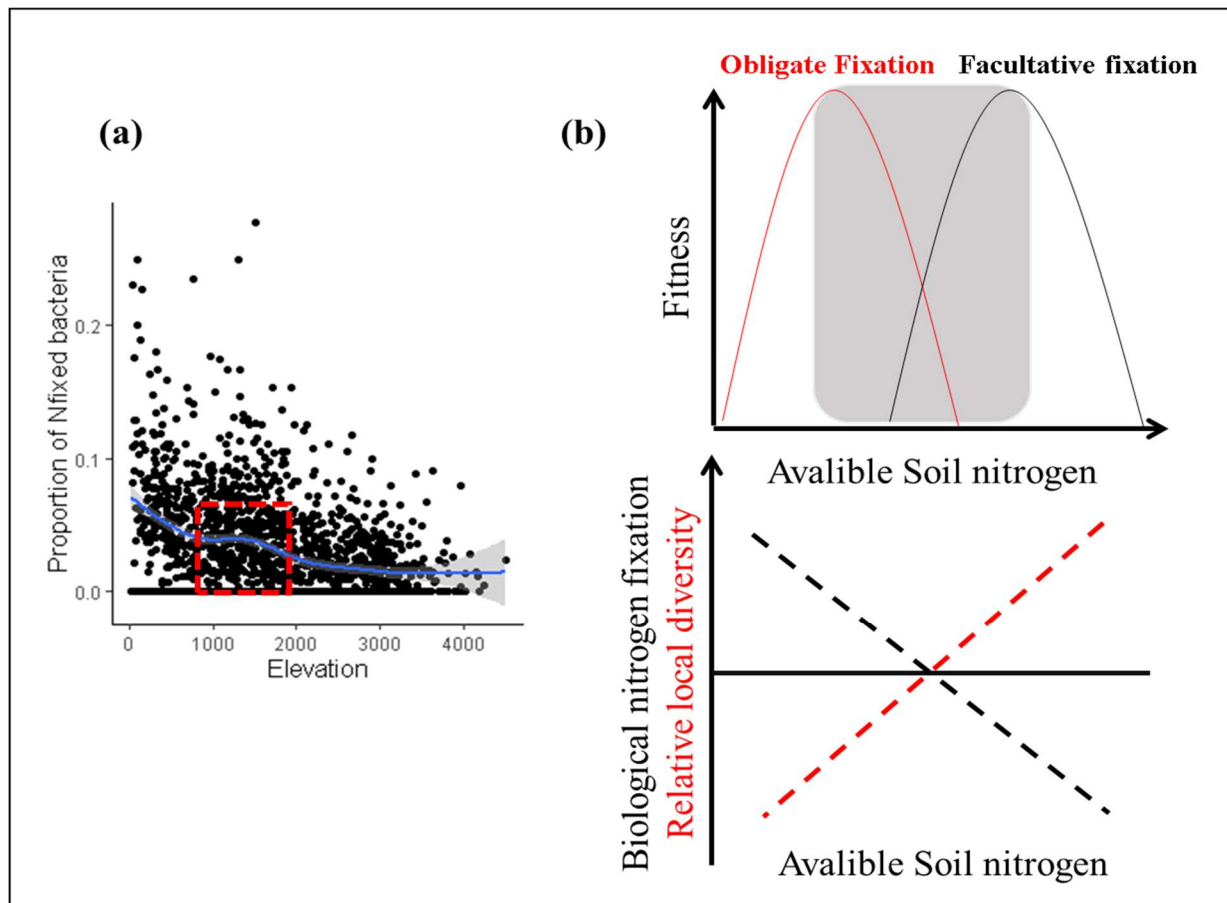
5|CONCLUSIONS

The aim of this study was to understand for the first time the factors that influence the distribution of different types of mycorrhizal associations in all the Colombian Andes. Our results partially support the results of Steidinger *et al.* (2019) and the hypothesis of Read (1991) mycorrhizal associations gradually change along a latitudinal and altitudinal climate on decomposition gradients. We found that not only do climatic factors affect the distribution of different types of mycorrhizal associations in the Colombian Andes, but the interactions between climatic and edaphic factors are the ones with greater explanation power. We also highlight the role that nitrogen fixing associations might be having in the diversity of mycorrhizal associations and consider important to continue investigating the relationship between Nfix bacteria and AM fungi and the possible effects that their interactions may have on plant diversity a context of climate change. Finally mycorrhizal associations play a very important role in biogeochemical cycles and ecosystem stability, then in the future it will be crucial to generate strategies for landscape conservation and connectivity to help preserve ecosystem stability.

6| SUPPLEMENTARY MATERIAL



Supplementary 1 Proportion of different mycorrhizal types association across the altitudinal gradient of Colombian Andes.



Supplementary 2. (a) Nitrogen fixing plant proportion along the altitudinal gradient of the Colombian Andes, framed in red, showing an increasing of the proportion of nitrogen fixing plant abundance with a decrease in elevation. (b) Differentiated fixation strategy hypothesis.

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