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PADRÕES NA COMPOSIÇÃO DE ESPÉCIES ARBÓREAS E DIVERSIDADE FILOGENÉTICA NA FLORESTA NEOTROPICAL PERENIFÓLIA NÃO INUNDÁVEL

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Padrões na composição de espécies arbóreas e diversidade filogenética na Floresta Neotropical Perenifólia não inundável

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SUMÁRIO

RESUMO

O Neotrópico é a região mais biodiversa da Terra. Diversos tipos de vegetação são encontrados nessa região, desde desérticas até a floresta úmida. A Floresta Neotropical Perenifólia não inundável (FNP) destaca-se pela elevada riqueza de espécies arbóreas, ampla ameaça à perda de *habitat,* além da variação ambiental e espacial como reflexo dos amplos gradientes latitudinais, altitudinais e longitudinais. Uma análise fitogeográfica abrangente ainda não foi realizada para a FNP. Nesse sentido, com base em dados de ocorrência de espécies arbóreas (518.004 registros de ocorrência de 15.134 espécies em 1.885 sítios) examinamos os principais padrões fitogeográficos da FNP, bem como seus preditores. Além disso, investigamos a variação da diversidade filogenética arbórea. Realizamos análises de agrupamento, ordenação, modelos canônicos e lineares com base em matrizes de dissimilaridade florística e filogenética, e investigamos o efeito de um amplo conjunto de variáveis ambientais e de barreiras à dispersão na composição florística e filogenética. Registramos nove grupos florísticos ao longo da FNP, cuja variação florística esteve associada principalmente à heterogeneidade ambiental. As barreiras à dispersão parecem atuar mais fortemente na Mata Atlântica em relação aos demais grupos da FNP. A dissimilaridade filogenética corroborou os principais grupos que emergiram da análise florística, tais como Amazônia, Floresta Atlântica, Floresta Nebular Andina, Andes Bolivianos e Caribe. A variação da diversidade filogenética ao longo da FNP responde consistentemente ao gradiente altitudinal. Amazônia e Floresta Atlântica são os blocos da FNP com maior singularidade florística e filogenética. Nesse sentido, a estruturação da FNP, assim como de toda a biota neotropical, está associada a múltiplos processos evolutivos e ecológicos, tais como conservadorismo de nicho, dispersão, migração e filtragem ambiental. Reforçamos assim a importância da preservação de áreas de FNP com identidade florística única.

Palavras-chave: assembleias arbóreas; barreiras à dispersão; Floresta Tropical; grupos florísticos; grupos evolutivos; gradientes de vegetação; NeoTropTree; preditores ambientais

ABSTRACT

The Neotropics is the most biodiverse region on Earth. Several types of vegetation are found within this region, from deserts to rainforests. The Neotropical Non-Flooded Evergreen Forest (NEF) stands out due the high tree species richness, wide threaten by habitat loss, in addition to environmental and spatial variation as a result of its wide latitudinal, altitudinal and longitudinal gradients. A comprehensive phytogeographic analysis has not yet been carried out for NEF. In this sense, based on an occurrence dataset of tree species (518,004 records of occurrence of 15,134 species in 1,885 sites), we examined the main phytogeographic patterns of NEF, as well as their predictors. In addition, we investigated the variation in tree phylogenetic diversity. We performed analyzes of cluster, ordination, canonical and linear models based on floristic and phylogenetic dissimilarity matrices, and investigated the effects of a wide range of environmental variables and dispersal barriers on floristic and phylogenetic composition. We recorded nine floristic groups throughout NEF, whose floristic variation was mainly associated with environmental heterogeneity. The dispersal barriers seem to act more strongly in the Atlantic Forest than in the other NEF groups. Phylogenetic dissimilarity corroborated the main groups that emerged from the floristic analysis, such as the Amazon, Atlantic Forest, Andean Nebular Forest, Bolivian Andes and the Caribbean. The variation in phylogenetic diversity along NEF, consistently responds to the altitudinal gradient. The Amazon and Atlantic Forest are the NEF blocks with the greatest floristic and phylogenetic singularity. In this sense, the structuring of NEF, as well as the entire neotropical biota, is associated with multiple evolutionary and ecological processes, such as niche conservantism, dispersion, migration and environmental filtration. We thus reinforce the importance of preserving NEF areas with a unique floristic identity.

Keywords: dispersal barriers; environmental drivers; evolutionary groups; floristic groups; NeoTropTree; tree assemblages; Tropical Forest; vegetation gradients

INTRODUÇÃO GERAL

A região Neotropical é reconhecida como propulsora da biodiversidade global (Antonelli et al., 2015). A diversificação da biota neotropical está associada a diversos processos históricos e evolutivos que ocorreram em diferentes tempos, intensidades e escalas e foram impulsionados tanto por fatores bióticos como abióticos (Antonelli & Sanmartín, 2011; Rull, 2020). O Neotrópico é a região mais rica em espécies de plantas com sementes do mundo, com cerca de 100.000 espécies (Antonelli & Sanmartín, 2011). Quando são consideradas apenas as espécies arbóreas estimativas apontam que a região neotropical possui entre 19.000 a 25.000 espécies (Slik et al., 2015).

Dentre os diversos tipos de vegetação presentes na região neotropical (Hughes et al., 2013), a Floresta Neotropical Perenifólia não inundável (FNP) destaca-se pela excepcional riqueza de espécies arbóreas. A FNP ocorre na forma de grandes blocos disjuntos que se distribuem do sul do México, América Central, Caribe, Andes Tropical, Amazônia até a costa atlântica, ao norte da América do Sul (Kappelle, 2004; Corllet & Primack, 2011). Além disso, a FNP apresenta abrangente gradiente altitudinal, pois compreende (i) a floresta tropical úmida, que pode ser definida como vegetação de copas fechadas e perenes que ocorrem em regiões de planícies com climas quentes e úmidos (geralmente >2.000 mm de precipitação anual) e que normalmente não experimenta estação seca pronunciada (Corllet & Primack, 2011) e (ii) a floresta tropical montana, que ocorre predominantemente entre 1.200 e 2.800 m acima do nível do mar, com pequenas áreas ocorrendo em regiões com mais de 4.000 m nos Andes (Kappelle, 2004), reconhecida também como floresta nebular devido à frequente cobertura de nuvens ou névoa que atua para manter a umidade, favorecendo seu caráter perenifólio (Stadtmüller, 1987). Assim, a FNP possui amplos gradientes latitudinais, altitudinais e longitudinais, o que implica em variações florísticas, ambientais e espaciais consideráveis em toda a sua extensão.

Vários blocos da FNP já foram reconhecidos como unidades florísticas distintas, tais como Floresta Atlântica, Amazônia, Chocó, Andes Tropical, Mesoamérica e Caribe (Gentry, 1982; Prance, 1989). Dentre esses blocos, Amazônia, Floresta Atlântica e Andes Tropical têm sido amplamente investigados sobre a diversificação de sua biota (e.g., Luebert & Weigend, 2014; Honorio-Coronado et al., 2015; Peres et al., 2020), enquanto outros, como por exemplo o Chocó, têm sido negligenciados (Pérez-Escobar et al., 2019). Nesse sentido, a distinção florística dos blocos da FNP pode estar associada à presença de barreiras que limitam o intercâmbio biótico, tais como (i) o Oceano Atlântico, que isola o Caribe da América continental; (ii) cadeias de montanhas de elevada altitude, como por exemplo os Andes, que separam a bacia Amazônica das florestas do Chocó e Mesoamérica; e (iii) regiões dominadas por climas sazonalmente secos, como por exemplo, a diagonal seca na América do Sul (Gentry, 1982; Prado & Gibbs, 1993; Hoorn et al., 2010; Jaramillo et al., 2010; Nieto-Blázquez et al., 2017; Bemmls et al., 2018). Além disso, o histórico geológico e climático da região neotropical implica em ampla heterogeneidade ambiental na FNP (Gentry, 1982; Hoorn et al., 2010; Antonelli & Sanmartín, 2011). Fatores estruturantes das variações florísticas têm sido investigados em diversos blocos da FNP, com destaque para: heterogeneidade topográfica na Mata Atlântica (Eisenlohr & Oliveira-Filho, 2015); gradientes de fertilidade do solo na Amazônia (Phillips et al., 2003; ter Steege et al., 2006; Bohlman et al., 2008; Coronado et al., 2009; Higgins et al., 2011; Pansonato et al., 2013); altitude e interação entre vento e topografia na floresta andina (Stadtmuller, 1987; Killeen et al., 2007); geomorfologia e fertilidade do solo no Chocó (Gentry, 1986; Faber-Langendoen & Gentry, 1991; Mosquera & Hurtado, 2014; Copete et al., 2019); heterogeneidade topográfica, gradientes geológicos e textura do solo na Mesoamérica (Pyke et al., 2001; Sesnie et al., 2009; Chain-Guadarrama et al., 2012; Morera-Beita et al., 2019); e geologia, tipo de solo e variação altitudinal no Caribe (Graham, 2003; Santiago-Valentin & Olmstead, 2004; Maunder et al., 2008; Ortiz et al., 2019).

Somado a isso, medidas de diversidade e estrutura filogenética permitem compreender de forma mais reveladora como os processos históricos atuaram na diversificação e estruturação das comunidades vegetais (e.g., Honorio-Coronado et al., 2015). Assim, a definição de unidades biogeográficas com base em medidas de diversidade beta filogenética permite a identificação de regiões evolutivamente únicas (Holt et al., 2013; Daru et al., 2017). Dessa forma, a definição de unidades biogeográficas ao longo da FNP com base em similaridade filogenética pode ser útil ao promover subsídios para a conservação dessas florestas, visto que permite que regiões com o mesmo histórico ecológico-evolutivo se tornem alvo de medidas protetivas semelhantes (Holt et al., 2013).

Considerando a inexistência de uma análise fitogeográfica abrangente incluindo todos os blocos da FNP, buscamos, com base em amplo conjunto de dados de ocorrência de espécies arbóreas (518.004 registros de ocorrência de 15.134 espécies em 1.885 sítios), compreender os principais padrões fitogeográficos ao longo da FNP e os preditores desses padrões. Examinamos aqui, além de questões relacionadas à distribuição das espécies, também as variações da diversidade filogenética. A relevância desse tipo de investigação é ainda mais urgente em ecossistemas que apresentam altas taxas de riqueza e endemismo de espécies e perda acelerada de *habitat*, como é o caso dos cinco *hotspots* presentes na FNP: Mesoamérica, Caribe, Choco, Andes tropicais e Mata Atlântica (Myers et al., 2000; Zachos & Habel, 2011).

Para investigar essas questões estruturamos a tese em três capítulos:

- Capítulo 01: investigamos a variação florística arbórea ao longo da FNP e abordamos as seguintes questões: (a) quais são os grupos florísticos do NEF e como eles se correlacionam com as variáveis ambientais; (b) quantas espécies, gêneros e famílias são compartilhados entre esses grupos florísticos e quais espécies são únicas e indicadoras de cada grupo; e (c) como a riqueza de espécies varia entre os grupos da FNP? Esse capítulo foi publicado como artigo científico na revista 'Applied Vegetation Science' (https://onlinelibrary.wiley.com/doi/abs/10.1111/avsc.12522).

- Capítulo 02: examinamos os preditores da variação da composição florística arbórea ao longo da FNP para responder às seguintes questões: (a) os blocos da FNP podem ser diferenciados com base em preditores ambientais?; e (b) como os preditores bioclimáticos, topográficos, edáficos e barreiras à dispersão contribuem para explicar a variação florística ao longo da FNP? Esse capítulo está submetido como artigo científico na revista 'Journal of Vegetation Science'.

- Capítulo 03: verificamos como ocorrem as variações da diversidade e da estrutura filogenética ao longo da FNP e buscamos responder às seguintes perguntas: (a) a dissimilaridade filogenética possibilita diferenciar a FNP em grupos evolutivos?; e (b) a variação da diversidade filogenética é consistente ao longo do gradiente altitudinal? Esse capítulo foi formatado para ser submetido como artigo científico na revista 'Journal of Biogeography'.

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CAPÍTULO I

Patterns of variation in tree composition and richness in Neotropical Non-Flooded Evergreen Forests

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ABSTRACT

Questions: We investigated tree floristic variation among the Neotropical Non-Flooded Evergreen Forests (NEF). We addressed the following questions: (a) which are the floristic groups among NEF and how are they correlated with environmental variables; (b) how many species, genera and families are shared between these floristic groups and which species are unique and indicative of each one; and (c) how does species richness vary between NEF groups?

Location: Neotropical region.

Methods: We investigated tree floristic variation among the Neotropical Non-Flooded Evergreen Forests (NEF). We addressed the following questions: (a) which are the floristic groups among NEF and how are they correlated with environmental variables; (b) how many species, genera and families are shared between these floristic groups and which species are unique and indicative of each one; and (c) how does species richness vary between NEF groups?

Results: We recorded 172 families, 1,276 genera and 15,134 species in 1,885 sites of NEF. The families most rich in species were Fabaceae, Rubiaceae and Myrtaceae. We identified nine groups among the NEF, which broadly correspond to floristic provinces reported in the literature. Altitude and annual mean temperature were associated with a species turnover gradient from Amazon to Andean Cloud Forest. Atlantic Forest (south) and Mesoamerica plus Caribbean (north) represented the extremes of a latitudinal gradient. The Atlantic Forest presented the largest number of exclusive and indicator species (2,477 and 265, respectively), while the Amazon showed the highest species richness (6,167 species).

Conclusions: Although it was possible to separate NEF into distinct floristic groups, this floristic dissociation seems to be recent, since it found support only in species data. The floristic groups identified in this study are largely congruent with their geographic distribution and spatial/ecological isolation, and seem to reflect historical, geological and climatic events that occurred in the Neotropics.

KEYWORDS
cluster analysis, floristic gradients, floristic groups, floristic similarity, forest conservation, NeoTropTree, plant distributions, species richness

1 INTRODUCTION

The Neotropical region has the richest flora on the planet (Antonelli and Sanmartin, 2011), harboring between 19,000 and 25,000 tree species (Slik et al., 2015). Evidence of rapid evolutionary turnover and a high rate of speciation of angiosperms during the last 66 million years in the Neotropics suggest that this region acts as a motor for global plant diversity (Antonelli et al., 2015). The Neotropics are covered by several types of vegetation, including rain forests, savannas and grasslands, seasonally dry forests and shrublands, and deserts (Hughes et al., 2013). However, rain forests stand out for their exceptional species richness and concentration of plant lineage diversity. Rain forests form large blocks that are distributed from southern Mexico through Central America, the Caribbean, the north and the Atlantic coast of South America, which, although physiognomically similar, differ in physiographic characteristics and species composition (Burnham and Johnson, 2004; Morrone, 2014). Despite this important role, neotropical rain forests are one of the most imperiled habitats in the world (Kim et al., 2015). Rampant habitat loss coupled with high rates of endemism of vascular plants resulted in five regions of neotropical rain forests recognized as hotspots for biodiversity conservation: Mesoamerica, Caribbean, Choco, Tropical Andes and Atlantic Forest (Myers et al., 2000).

Geological and climatic events contributed to the evolution and diversification of the neotropical flora (Hoorn et al., 2010; Antonelli and Sanmartín, 2011; Hughes et al., 2013; Antonelli et al., 2018). In fact, the discontinuity of neotropical rain forests is probably related to geological events, such as the uplift of the Andes (Hoorn et al., 2010), and to historical climatic events, such as the expansion of open vegetation in the Neotropics favored by the increase of seasonality during the Upper Miocene (Prado and Gibbs, 1993; Jaramillo et al., 2010). There are marked differences in the composition of the tree flora between blocks of neotropical rain forests, such as Amazon and Atlantic Forest (Miranda et al., 2018). However, these differences have not yet been quantitatively assessed across all neotropical rain forest units. Investigating the floristic distinction between regions would be important for conservation of biodiversity, because it can help portray the unique diversity of species (Banda et al., 2016).

In addition to historical events, floristic variation has been linked to differentiation in climatic, flood and topographic regimes among the neotropical rain forests (Antonelli and Sanmartín, 2011). Although generally restricted to wet and hot climates, rain forests occur in a considerable range of mean temperatures and rainfall seasonality. Part of the rain forests under seasonal climates has an evergreen characteristic, that is, there is no marked loss of leaves during the year due to the availability of water in the soil even in the dry season (Leigh-Jr, 2008). From the perspective of the flood regime, flooded forests experience essentially the same climate regime as surrounding non-flooded rain forests, but their distinctive structure and composition are determined by the flood spikes to which these forests are subject (Wittmann et al., 2013). In relation to topography, neotropical rain forests vary from lowlands to mountains (Prance, 1989). Lowland rain forests are the most abundant and biodiverse in the region (Thomas, 1999), occurring up to 700 m above sea level under hot and humid conditions (Burnham and Johnson, 2004). Tropical montane forests typically occur between 2,000 and 3,500 m above sea level, and have been largely defined by mild climates and frequent cloud cover or mist that acts to maintain moisture, favoring its evergreen appearance (Stadtmüller, 1987).

Neotropical rain forests occur as discontinuous blocks across the Americas, which, although physiognomically very similar, present floristic variations (Oliveira-Filho and Fontes, 2000; Rangel, 2004; Santiago-Valentin and Olmstead, 2004; Bruijnzeel et al., 2011; Antonelli et al., 2018; Miranda et al., 2018). Although many of these forests have been recognized as distinct units based on floristic knowledge (Gentry, 1982a; Burnham and Graham, 1999; Miranda et al., 2018), a comprehensive analysis using formal biogeographical methods and covering all the Neotropics is still lacking. We restricted our analysis to Neotropical Non-Flooded Evergreen Forests (NEF), defined here as wet non-flooded forests that lack a pronounced deciduousness. We excluded from our analyses flooded forests and seasonally dry deciduous forests, which display a floristic composition significantly different from that of non-flooded rain forests because of specific ecological requirements to cope with waterlogged soils and seasonally dry climate, respectively (Murphy and Lugo, 1986; Wittmann et al., 2013).

Here we investigated the floristic variation of the tree flora using a comprehensive data set covering all major blocks of NEF. We were guided by the following questions: (a) which are the floristic groups among NEF and how are they correlated with climatic, altitudinal and latitudinal data; (b) how many species, genera and families are shared between these floristic groups and which species are unique and indicative of each one; and (c) how does species richness vary throughout NEF groups?

2 METHODS

2.1 Floristic data

We obtained occurrence data from the NeoTropTree (NTT) database (http://www.neotroptree.info/; Oliveira-Filho, 2017). This database presents occurrence lists of native tree species - plants at least 3 m high, with free stems, that is, without relying on other plants - compiled from published and unpublished data, herbarium records and monographs during the years 1992-2017, for the entire Neotropical region. Thus, since they meet the above criteria, NTT occurrences may include trees, shrubs, palm trees, bamboos and ferns. In NTT, floristic lists are georeferenced and organized in circular sites within 10 km diameter. We restricted our analyzes to NTT sites located between 23°59'49"S; 48°18'57"W and 21°26'13"N; 99°09'09"W degrees of latitude and covered by NEF, occurring from lowlands to montane forests and where trees lose less than 30% of the leaf mass during the dry season. This cutoff defined sites subject to similar ecophysiological situations, avoiding comparisons between areas with discrepant ecological requirements such seasonal flooding or a marked dry season.

The verification of the taxonomic and geographic circumscriptions of all the species included in the NTT was performed by consulting the Flora do Brasil online project, Catalog of the Vascular Plants of Ecuador, Peru Checklist, Catalog of Bolivia (available at http://floradobrasil.jbrj.gov.br/, http://www.tropicos.org/Project/CE/, http://www.tropicos.org/Project/PEC and http://www.tropicos.org/Project/BC/, respectively) and published floras (Boggan et al., 1997; Steyermark, Berry, & Holst, 1995-2005; Bernal, Gradstein, & Celis, 2016). In addition, we performed additional checks in the floristic lists of

Cardoso et al. (2017) and Vascular Plants of Americas (Ulloa-Ulloa et al., 2018 onwards). We checked the correct spelling and the possible synonyms present in the occurrence data through the Flora do Brasil 2020 under construction (http://floradobrasil.jbrj.gov.br/), The Plant List (http://www.theplantlist.org/), IPNI (https://www.ipni.org/), TROPICOS (http://www.tropicos.org/), PLANTMINER (http://www.plantminer.com/) and iPlantCollaborative - Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/TNRSapp.html). We carefully revised the floristic database using the above-mentioned literature and online platforms, but it is important to mention that new taxonomic updates may arise. In fact, there have been a number recent of changes in the circumscription of several Neotropical groups of plants, including some of the largest and most abundant genera in the region (*Licania*, *Miconia*, *Protium*, *Psychotria*; eg. Steege et al., 2019), which were not implemented here.

After these steps, our database presented 1,885 sites/checklists, 15,134 species and 518,004 occurrence records of tree taxa for NEF, comprising a sample with broad representation in the Neotropics, including the main nuclei of NEF in the American continent. The NEF sites showed considerable variation in temperature, precipitation, altitude, and latitude (Karger et al., 2017; Appendix S1), although most of them comprise warm, humid and low altitude locations. Detailed information about each site, such as number of species, location and type of vegetation, is provided in Appendix S2.

2.2 Data analysis

i) Floristic similarity and main gradients

To answer the first question, we performed floristic similarity (clustering) and gradient (ordination) analyzes. We obtained binary matrices with species occurrence records per site and excluded 2,011 species that occurred in only one site ("uniques"). Firstly, we performed a cluster analysis of floristic information using the Unweighted Pair-Group Method using arithmetic Averages (UPGMA) (Borcard, Gillet, & Legendre, 2011). For the UPGMA we calculated the pairwise floristic distance between sites based on the dissimilarity index of Simpson. Simpson's index was chosen because it is less affected by variation in species richness when compared to others (Baselga, Jiménez-Valverde, &

Niccolini, 2007). This variation is a characteristic of our data set (26 to 1,315 species per site).

We executed the UPGMA in the ‘recluster’ package of R version 3.4.3 (Dapporto et al., 2013). In order to remove the bias caused by the order of the sites in the floristic matrix, we performed 1,000 randomizations (Dapporto et al., 2013) using the same package. In addition to summarize the results of the randomizations, we used a consensus tree with a 50% rule, because in this case the polytomies were significantly reduced in relation to the consensus tree with a 100% rule (see details on consensus rules in Dapporto et al. 2013). We performed this same routine for genera and families, but were unable to recognize floristic groups because of lack of variation in the data.

In the cluster analysis, the recognition of a group can be facilitated by the identification of a threshold explaining at least 90% of the dissimilarity in the taxonomic composition (Holt et al., 2013). The *recluster.expl.diss* function of the ‘recluster’ package implement this 90% cutoff based on the calculation of the difference between the sum of the distance between the clusters and the sum of all the dissimilarity values of the matrix (Dapporto et al., 2013). We here obtained 20 consistent subgroups. Subsequently, to evaluate the ability of these subgroups to associate floristically with each other, we performed bootstrap partitions (1,000 randomizations) in the ‘pvclust’ package (Suzuki & Shimodaira, 2006) of R. This method provides two bootstrap supporting values: bootstrap probability and AU (Approximately Unbiased) p-value computed by multiscale bootstrap resampling. Groups with AU values greater than 0.95 were considered to be strongly supported (Banda et al., 2016), and resulted in the combination of the 20 groups initially found into nine final groups.

In order to investigate the main floristic gradients throughout the NEF, we performed an ordination analysis using Non-Metric Multidimensional Scaling (NMS) (Kent, 2011) based on the nine floristic groups. Here, as in the cluster analysis, we used Simpson's coefficient of similarity. We obtained the stress value and evaluated it according to Clarke’s rules (Clarke 1993). To perform the NMS we used the *metaMDS* function of the ‘vegan’ package (Oksanen et al., 2018), with trymax = 100. The significance of the groups obtained in the UPGMA was tested using ANOVA based on the scores of the two NMS axes. A partitioned ANOVA with permutations was run in the 'coin' package through the function *IndependenceTest* (Hothorn, Hornik, Van De Wiel, & Zeileis, 2008). We obtained the ‘Maximum Type Independence Test Statistic’, which is the statistic of the permutation test (Hothorn et al., 2008). In turn, the partition had the objective of discounting the effects of the spatial autocorrelation (Appendix S3), which can inflate the type I error in statistical tests (Peres-Neto & Legendre, 2010). In this sense, spatial autocorrelation was considered in ANOVA through the insertion of spatial eigenvectors as covariables. We selected spatial eigenvectors from 21 Spatial Weighted Matrix (SWM; Bauman, Drouet, Fortin, & Dray, 2018) types by applying the *listw.candidates* and *listw.select* functions of 'adespatial' package (Dray et al., 2017). We optimized the selection of these filters by minimizing the spatial autocorrelation in the ANOVA residuals (Bauman, Drouet, Dray, & Vleminckx, 2018). The SWM selected for both ANOVAs (axes 1 and 2 of NMS) was a distance-based matrix obtained by a binary function (details on Dray et al., 2017). We applied an a posteriori test with permutations using the *pairwisePermutationMatrix* function of the 'rcompanion' package (Mangiafico, 2019). To avoid inflation in the type I error rate due to multiple comparisons we used the "fdr" method, which generates an adjusted p-value (Mangiafico, 2019). Finally, as a preliminary assessment of the influence of environmental predictors on species composition, we tested the correlation between a set of main synthetic variables of precipitation, temperature, altitude, and latitude (Appendix S1) and floristic composition summarized in the NMS ordination scores using the *envfit* function of ‘vegan’ package (Oksanen et al., 2018). The significance of correlations was controlled for spatial autocorrelation using the *modified.ttest* function of the ‘SpatialPack’ package (Osorio & Vallejos, 2019). We did not control such autocorrelation when testing correlations involving latitude, since this variable is inherently structured in space.

ii) Floristic characterization of groups and species sharing

To answer the second question, we obtained for each of the floristic groups identified in step (i) the exclusive species and the number of species, genera and families shared with other groups. In addition, we performed an indicator species analysis (ISA; De Cáceres & Jansen, 2016) to identify the species that characterize each group. We evaluated the statistical significance of the indicator values using 1,000 randomizations. To perform this analysis we used the package ‘indicspecies’ (De Cáceres & Jansen, 2016) of R. We considered as factor variable the different sites along the different floristic groups. In this analysis we used the algorithm of Tichý & Chytrý (2006), implemented in the *multipatt* function of the package ‘indicspecies’ by means of the argument "r.g" instead of "r" (De Cáceres & Jansen, 2016). This algorithm is useful for correcting distortions caused by different group sizes (Tichý & Chytrý, 2006). We considered as indicators the species that presented the indicator value above 0.5 and p-value <0.05.

iii) Species richness estimates

To answer the third question, we estimated the species richness for each floristic group detected in step (i) and for all the data together using the rarefaction/extrapolation integrated curves (Chao et al., 2014). We used the ‘iNEXT’ (Hsieh, Ma, & Chao, 2016) package of R. The confidence interval used was 95%, obtained by 1,000 bootstrap runs (Chao et al., 2014).

3 RESULTS

We recorded 172 families, 1,276 genera and 15,134 species along 1,885 sites of Neotropical Non-Flooded Evergreen Forest (NEF). The richest families in number of species were Fabaceae (1,475 spp.), Rubiaceae (1,254) and Myrtaceae (1,142) (Table 1); Fabaceae, Rubiaceae and Asteraceae comprised the richest families in number of genera (Table 1). The genera richest in species were *Eugenia* (467), *Miconia* (455) and *Ocotea* (313) (Table 1). Fabaceae and Rubiaceae presented the highest number of occurrences, with 54,356 and 38,261 occurrences, respectively (Appendix S4), followed by Melastomataceae, with 31,445 records (Appendix S4). The genera with the highest number of occurrences were *Miconia* (19,672 records), *Inga* (15,627) and *Ficus* (9,226) (Appendix S4). The three species with the highest number of occurrences were *Tapirira guianensis* (1,117), *Miconia prasina* (1,053) and *Piper arboreum* (1,028) (Appendix S4). Together, the 100 species with the highest number of occurrences represented only 12.4% of all occurrence records for NEF (Appendix S4).

TABLE 1 Top ten families in number of species and genera, and most species-rich genera recorded in 1,885 sites of Neotropical Non-Flooded Evergreen Forests.

Taxa	**Richness**
Family	N° of species
Fabaceae	1,475
Rubiaceae	1,254
Myrtaceae	1,142
Melastomataceae	969
Lauraceae	856
Annonaceae	608
Malvaceae	420
Euphorbiaceae	369
Chrysobalanaceae	349
Sapotaceae	341
Family	N° of genera
Fabaceae	151
Rubiaceae	96
Asteraceae	70
Malvaceae	55
Arecaceae	49
Euphorbiaceae	48
Rutaceae	35
Annonaceae	33
Melastomataceae	33
Lauraceae	29
Genera	N° of species
Eugenia L.	467
Miconia Ruiz & Pav.	455
Ocotea Aubl.	313
Inga Mill.	243
Myrcia DC.	238
Clusia L.	194
Pouteria Aubl.	181
Licania Aubl.	178
Palicourea Aubl.	152
Guatteria Ruiz & Pav.	147

(i) What are the floristic groups along NEF?

We obtained nine floristic groups: Amazon, Atlantic Forest, Mesoamerica, Andean Cloud Forest, Caribbean, Sub-Andean and Northern Lowland Forests (SANLF), Bolivian Andes, Choco, and North-Andean and Caribbean Montane Forests (NACMF), and the first five groups presented subdivisions (Figure 1). Detailed information on the environmental characteristics of each group is provided on Appendix S5. These groups were named based on the predominant geographic unit of their sites. Two groups (SANLF, and NACMF) cover sites with more than one geographic unit. Detailed floristic information on each group is provided in Appendix S6. In the NMS, we observed a gradient along the first axis separating the Amazon and Atlantic Forest groups from the other groups, mainly Andean Cloud Forest and Mesoamerica, whereas on the second axis Atlantic Forest sites were isolated from other groups (Figure 2). The stress of NMS (0.1733) was within the value indicated by Clarke's rule to obtain a structure not attributed to chance. Effect of the different NEF groups on the gradient provided by NMS was significant for both axes (axis 1: maxT = 29.682, p-value < 0.0001; and axis 2: maxT = 33.169, p-value <0.0001). Pairwise comparisons of groups highly supported the differentiation of NEF groups (Appendix S7). The floristic groups that demonstrate differences from all other groups in both axes were Atlantic Forest, Bolivian Andes and SANLF (Appendix S7). In turn, Caribbean and NACMF did not differ from any other group along either axis (Appendix S7). Annual mean temperature and altitude correlated significantly with floristic variation on the first axis of the NMS, and annual precipitation and latitude were highly correlated with the second NMS axis (Figure 2; Appendices S5, S8). We recorded a species turnover gradient from Amazon to Andean Cloud Forest associated with annual mean temperature and altitude (Figure 2; Appendices S5, S8). In addition, annual mean temperature was associated with the separation of Amazon in relation to the other NEF groups. We also found a latitudinal gradient associated with variation in floristic composition starting from Atlantic Forest towards Mesoamerica (Figure 2). Annual precipitation was associated with the separation of Mesoamerica (high precipitation) and Atlantic Forest (low precipitation) from other groups (Figure 2; Appendices S5, S8).

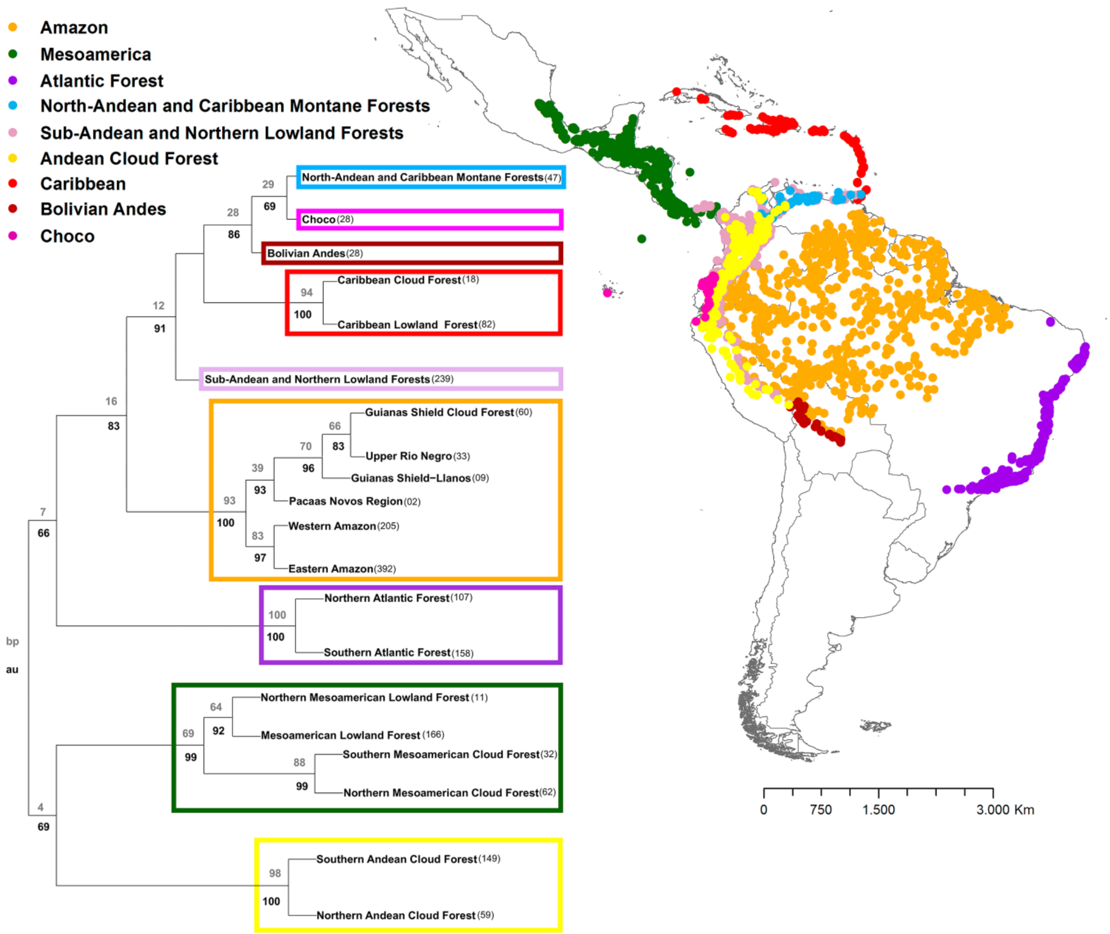

FIGURE 1 Dendrogram obtained with UPGMA cluster analysis showing the location of 1,885 sites classified in nine floristic groups of Neotropical Non-Flooded Evergreen Forests. Support values for dendrogram groups are represented by bootstrap probability (bp; above branches) and approximated unbiased p-value (au; below branches) computed by multiscale bootstrap resampling.

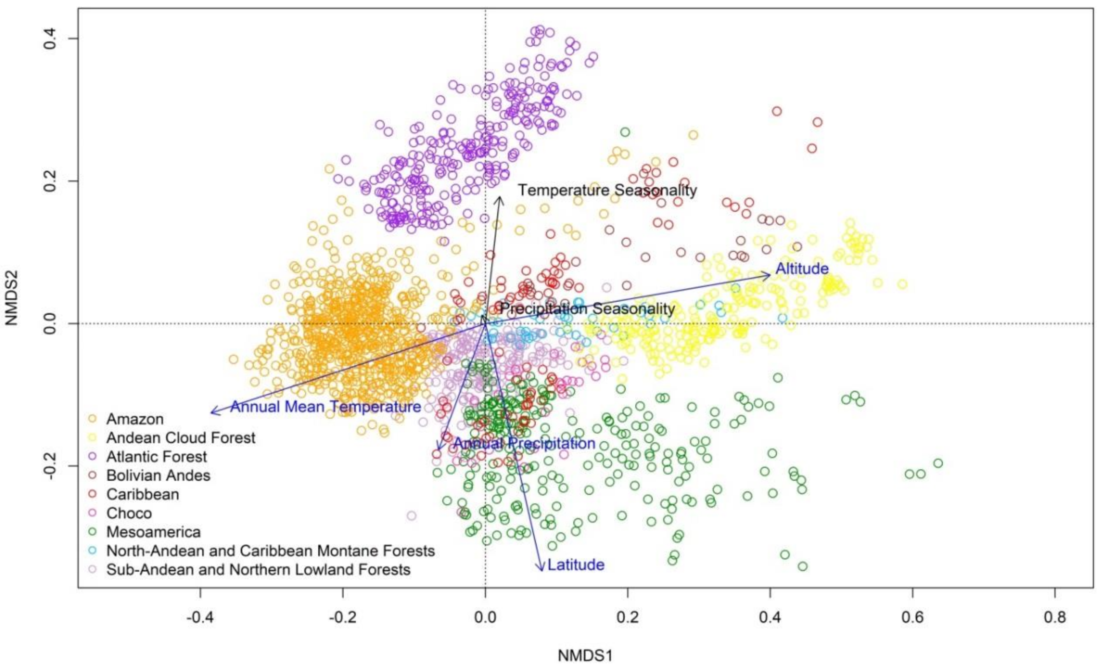

FIGURE 2 Non-Metric Multidimensional Scaling ordination of 1,885 sites demonstrating the affinity of the nine floristic groups obtained in the UPGMA cluster analysis. Blue vectors represent significant correlations of NMS scores with environmental variables.

(ii) How many species, genera and families are shared between floristic groups and what are the unique and indicator species of each one?

Among the nine groups, the greatest number of shared of species, genera and families occurred between Amazon and SANLF and between SANLF and Mesoamerica (Figure 3; Appendix S9; Appendix S10). The group with highest percentage of exclusive species was the Atlantic Forest, followed by Mesoamerica, Amazon, Caribbean and Andean Cloud Forest (Figure 3; Appendix S11). The two groups that comprised more than one geographic unit (SANLF and NACMF) presented a smaller proportion of exclusive species (Appendix S11).

Atlantic Forest had the highest number of indicator species (265 spp.), followed by Bolivian Andes (150) and Choco (139) while NACMF (25) and SANLF (7) presented the lowest number of indicator species (Appendix S6; Appendix S12). The families with the highest number of indicator species were Fabaceae (72 spp.), Rubiaceae (52) and Melastomataceae (50) (Appendix

S12). The genera with the highest number of indicator species were *Solanum* (28 spp.), *Miconia* (26) and *Inga* (18) (Appendix S12). The species with the highest indicator value of each group were: *Licania heteromorpha* (0.761; Amazon), *Hedyosmum cuatrecazanum* (0.706; Andean Cloud Forest), *Myrcia splendens* (0.897; Atlantic Forest), *Miconia cyanocarpa* (0.945; Bolivian Andes), *Cyathea arborea* (0.861; Caribbean), *Aegiphila alba* (0.845; Choco), *Conostegia xalapensis* (0.816; Mesoamerica), *Meriania longifolia* (0.744; NACMF), and *Cordia panamensis* (0.529; SANLF; Appendix S12).

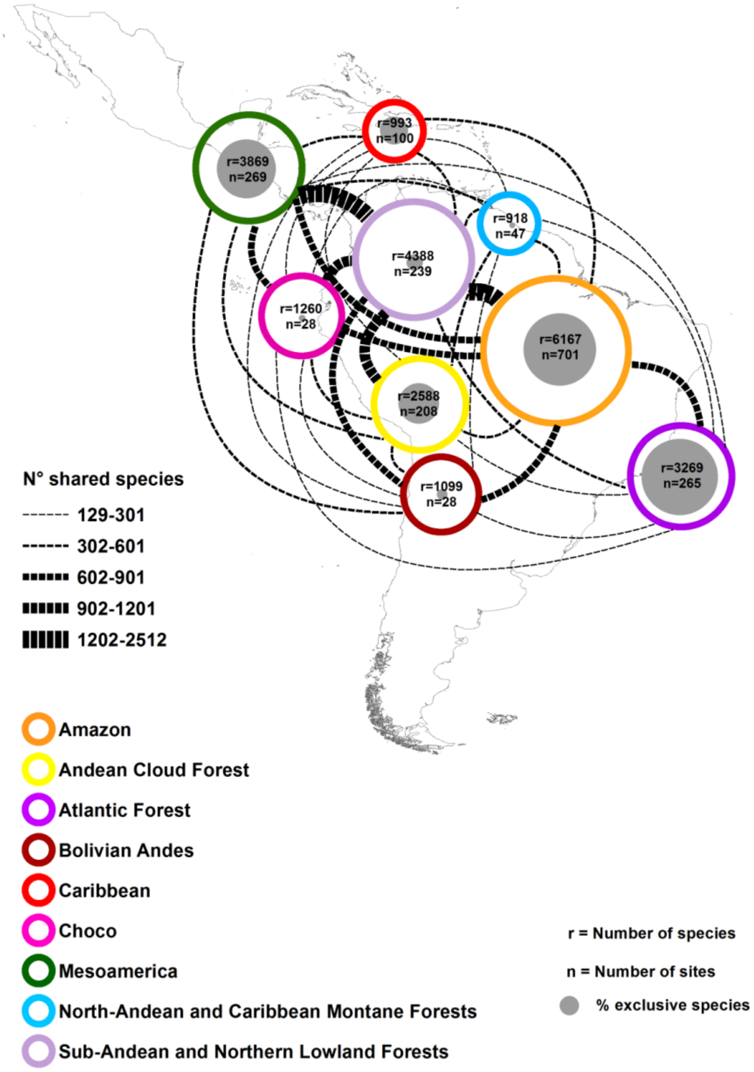

FIGURE 3 Shared species among nine floristic groups of Neotropical Non-Flooded Evergreen Forests. The size of each circle is proportional to the number of species within each group.

(iii) How does species richness vary throughout the Neotropical Non-Flooded Evergreen Forest?

The decreasing order of estimated species richness for the floristic groups was: Amazon (6,590 species), SANLF (4,855), Mesoamerica (4,218), Atlantic Forest (3,447), Andean Cloud Forest (2,904), Choco (1,309), Bolivian Andes (1,210), Caribbean (1,095) and NACMF (1,049; Figure 4A; Appendix S13). Considering all NEF sites together there would be a projected increase of only 6.6% more species than the number observed (15,134) if we had twice the number of sites sampled (Figure 4B Appendix S13). When we consider all the floristic groups, the greatest increase of species richness with projected increased sampling was observed in NACMF (12.6%). However, for the groups with the lowest number of sites (Andean Cloud Forest, Caribbean, NACMF, Bolivian Andes and Choco) there was no stabilization in the interpolation/extrapolation curve, thus indicating that it would be necessary to increase the sampling in these groups so that richness estimates become more robust (Figure 4A; Appendix S13).

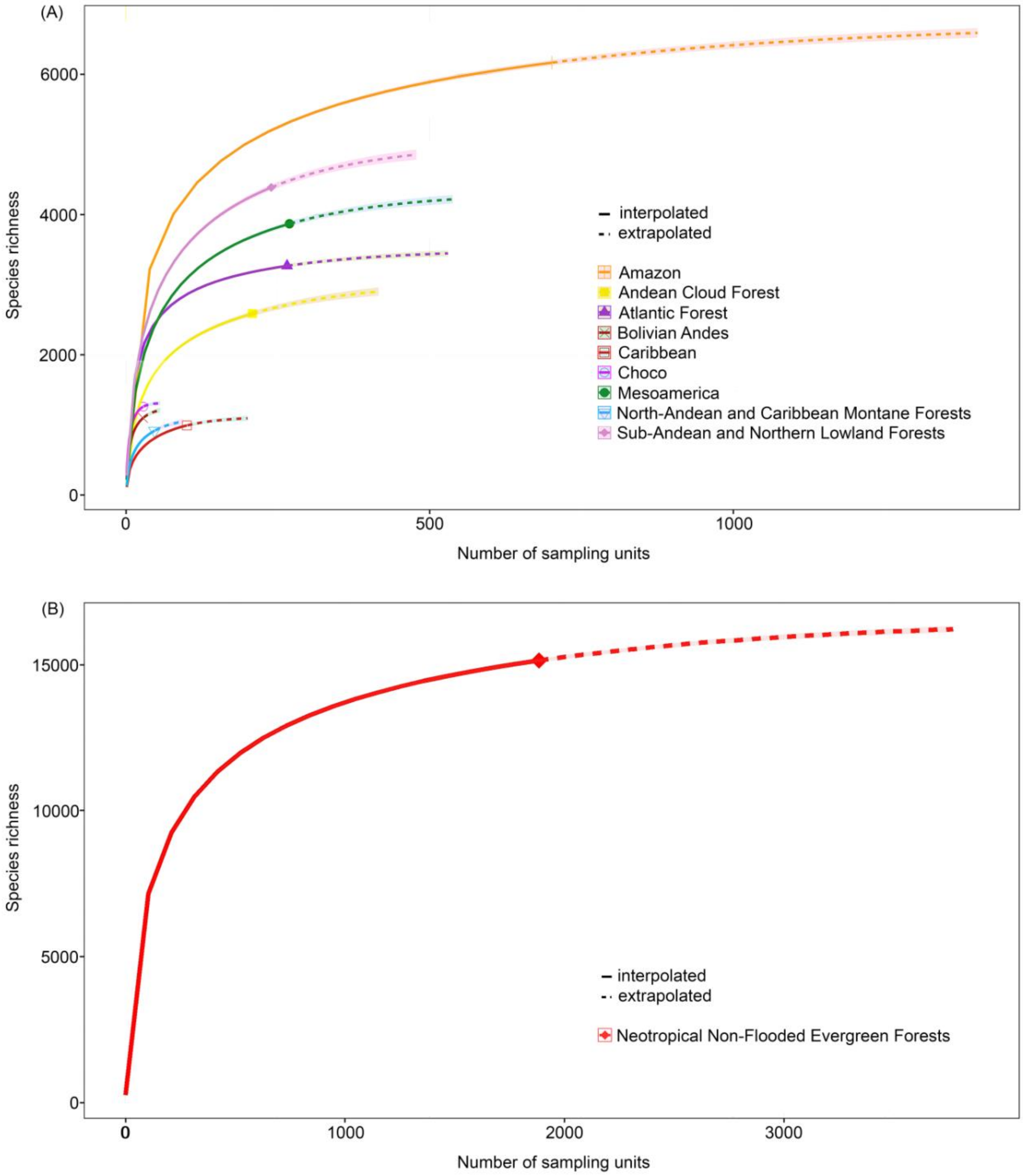

FIGURE 4 (A) Species richness interpolated and extrapolated for nine floristic groups of Neotropical Non-Flooded Evergreen Forests, considering twice the number of sampled sites; (B) Species richness interpolated and extrapolated for 1,885 Neotropical Non-Flooded Evergreen Forest sites, considering twice the number of sampled sites.

4 DISCUSSION

Our occurrence data indicate the high frequency of Fabaceae and Rubiaceae as well as of the genera *Miconia*, *Eugenia* and *Inga* in NEF. Fabaceae and Rubiaceae were the richest families in number of species and genera and presented the highest number of occurrences in the NEF. The preponderance of these botanical families in the neotropical flora has already been demonstrated in several studies (Stehmann et al., 2009; ter Steege et al., 2016; Cardoso et al., 2017; Ulloa-Ulloa et al., 2017). The genera *Eugenia* and *Miconia* were the richest in species along the NEF. *Eugenia* is the species-richest neotropical genus of Myrtaceae (WCSP, 2019). While most genera occurring in the Americas have fewer than 100 species, *Miconia* is among the five genera with more than 1,000 species (Ulloa-Ulloa et al., 2017). *Miconia* was also the genus with the highest number of occurrences in NEF followed by *Inga*, another genus of great representativeness in the Amazon and Atlantic floras (Stehmann et al., 2009; ter Steege et al., 2016; Cardoso et al., 2017).

Our analyzes recovered different floristic groups along NEF. We confirmed, at the species level, the floristic identity of nine major blocks of NEF, which were largely supported by different analytical approaches. We were unable to distinguish NEF groups using genera or family occurrence data. These results suggest that the floristic distinction between the NEF blocks is probably recent (from the Miocene onwards) and related to the uplift of the Andes (Hoorn et al., 2010) and expansion of dry and open habitats in the neotropics (Prado & Gibbs, 1993; Jaramillo et al., 2010). In addition, there is evidence that biotic exchange in the neotropical region has been occurring for more than 60 million years, but has increased towards to the present time (Antonelli et al., 2018).

Most NEF groups identified here broadly correspond to floristic provinces previously reported in the biogeographic literature such as the Andean Cloud Forest, Amazon, Atlantic Forest, Caribbean, Choco and Mesoamerica (Udvardy & Udvardy, 1975; Gentry, 1982b; Takhtajan, 1986; Stadtmüller, 1987 and references therein; Myers et al., 2000; Morrone, 2014). The level of distinctiveness of the tree flora of each NEF block is represented here by a suite of exclusive and indicator species. We were able to corroborate the floristic identify of these groups by using a comprehensive dataset of tree species occurrence, enhancing the support for floristic discontinuities within NEF. NEF groups showed different degrees of similarity reflecting their degree of geographical distance to each other. In addition, the latitudinal gradient found across the NEF may be reflecting the effects of environmental factors such as temperature and precipitation, as well as geographic distance (Whittaker, Willis, & Field, 2001). Along NEF there is a great variation in altitude and annual mean temperature. These variables were associated with a floristic gradient from Amazon to Andean Cloud Forest. Here, altitude, in addition to being correlated with annual mean temperature, can be associated with other environmental factors, such as precipitation, solar radiation, and atmospheric pressure (Korner, 2007). NEF (except seasonal, mountain and nebular forests, which represent the minority of the sites investigated in our study) occur in regions with a low degree of seasonality of precipitation and temperature (e.g., Burnham & Johnson, 2004; Leigh-Jr, 2008; Bruijnzeel et al., 2011). This fact may justify why the correlations with variables of seasonality were not significant. We highlight that these are initial exploratory analyses, and a more comprehensive evaluation including a larger number of variables and modelling is required to provide a detailed assessment of the influence of environmental predictors on floristic variation across NEF.

Andean Cloud Forest and Bolivian Andes

The Andean Cloud Forest, one of the new environments that originated after the Andean uplift, is among the world's species-richest forests (Gentry 1995; Myers et al., 2000; Bruijnzeel, 2004), and according to our analyzes, represent an independent floristic group. Evidence indicates that plant lineages from northern and center Andean cloud forests have a more recent origin than the lineages of the south, reflecting the tendency that the Andean uplift has progressed from the south to the north (*e.g.*, Luebert & Weigend, 2014). In this sense, another group within of the Andean flora, called Bolivian Andes, located to the south of the Tropical Andes, reinforces the role of the differential uplift of the region in the diversification of its lineages. This group is located in a peculiar region of the Andes called "elbow of the Andes". The "elbow of the Andes" comprises a region of the central Andes with relief corresponding to a curving arc with a face encompassing a smaller angle than other faces of the Andes; such a face with a tight angle captures winds that come from the Amazon basin, which increases precipitation on the lower and humid slopes (Killeen, Douglas, Consiglio, Jørgensen, & Mejia, 2007). Such wetter conditions may have persisted during the dry intervals of the Upper Cenozoic and provided the region with a refuge for rainforest taxa (Graham, 2009). This evidence seems to support, as we have shown, the occurrence of a distinct flora in this region.

Mesoamerica

The closure of the Isthmus of Panama, which according to the most accepted evidence occurred about 2.8 million years ago, allowed a terrestrial connection between South and Central America (O'dea et al., 2016). Although this event may have facilitated the dispersal of some lineages from South to Central America (Gentry, 1982a; Burnham & Graham, 1999), molecular phylogenies indicate that the floristic interchange between the flora of Mesoamerica and the Andes, for example, already occurred long before this closure (Cody, Richardson, Rull, Ellis, & Pennington, 2010; Luebert & Weigend, 2014), thus suggesting limited importance of this event as a connection between the NEF blocks of both continents. We thus corroborate the hypothesis that the rich and distinct flora of the Mesoamerican block is composed of multiple-origin lineages (Burnham & Graham, 1999) rather than a result of migrations from South America after the closure of the Panama Isthmus. In fact, Mesoamerica is the region that received the most lineages of angiosperms from other neotropical regions, and is also the second region to supply lineages of angiosperms (Antonelli et al., 2018).

We observed a high species sharing between Mesoamerica and a contact group of floras called Sub-Andean and Northern Lowland Forests (SANLF; see below), as well as high sharing values with the Amazon and Choco. This evidence leads to similar conclusions as those of recent studies that pointed out a high frequency of dispersal events of Amazon plant lineages to Mesoamerica (~442 lineages; Antonelli et al., 2018). In fact, although the northern Andes region and adjacent savannas represent a barrier to dispersion between Amazon and Mesoamerica, species with broad environmental tolerances (capable of inhabiting high elevations and areas of low annual average precipitation) seem to mediate the process of biogeographical filtering responsible for significant floristic exchange between these regions (Bemmels et al., 2018).

Caribbean

The floristic distinction of the Caribbean block evidenced in this study can be explained by the complex geological history of the region and its geographical distance from the American continent (Graham, 2009; Nieto-Blázquez, Antonelli, & Roncal, 2017). The high altitudinal variation, temperature and precipitation regime, and geological diversity of the region result in mosaics of habitats within the same island, which resulted in the occurrence of plant species with different ecological requirements and tolerances (Santiago-Valentin & Olmstead, 2004). In this sense, plant diversity of the Caribbean islands is quite peculiar, which allows its recognition as a distinct phytogeographic unit within the Neotropics (Gentry, 1982a and confirmed by our study) and one of the most important regions for conservation in the world (Myers et al., 2000). The Caribbean region is home to about 13,000 species of vascular plants (Acevedo-Rodríguez & Strong, 2008). More than 50% (8,000 spp.) of these species are endemic to the region and represent 2% of all vascular plants on Earth (Myers et al., 2000; Acevedo-Rodríguez & Strong, 2008; Ulloa-Ulloa et al., 2017). The peculiarity of the Caribbean flora could be evidenced in our study, since we recorded a high proportion (48.5%) of exclusive species.

Choco

The Choco region, which comprehends areas along the Pacific coast of western Ecuador and Colombia bounded on the east by the Andes, was recognized as a distinct floristic group in our study, despite its low proportion of exclusive species. This region presents unique ecological and biogeographic characteristics due to its high geomorphological, ecosystemic and floristic variability (Malagón, Pulido, Llinas, Chamorro, & Fernández, 1995; Rangel, 2004). Choco presents high annual precipitation (up to 13,000 mm), being recognized as one of the most biodiverse regions in the world, with about 4,500 species of spermatophytes (Poveda, Rojas, Rudas, & Rangel, et al 2004).

Choco is bordered by the Andean mountains to the east, and is also isolated to the west by the Pacific Ocean and to the south by seasonally dry tropical forests (Gentry, 1982b). To the north, Chocoan forests have a geographic connection with Mesoamerica along the Isthmus of Panama. The greatest share of species, genera and families of Choco region occurred with the SANLF, Amazon and Mesoamerica groups (see details on these groups below), respectively. The Chocoan flora derives predominantly from Andean immigrants, and has been an accessible region and not totally isolated from adjacent or more distant biogeographic areas (Pérez-Escobar et al., 2019 and references therein).

Amazon

The Amazon constituted the largest (more sites) and species-richest floristic group in our study. This biogeographic unit, as well as being the most diverse rainforest block in the world, is also the main source of biological diversity in the Neotropics, providing > 1,500 plant lineages with other neotropical regions (Antonelli et al., 2018). In our study, the Amazon was the group that shared the largest number of genera with other groups and the second group in shared species and families. All the species registered here as indicators of the Amazon NEF are present in the list of hyperdominant species of the Amazon (ter Steege et al., 2013), including *Eschweilera coriacea*, *Pseudolmedia laevis*, *Trattinnickia burserifolia* and *Licania heteromorpha*, which appear among the 20 most hyperdominant ones.

The robustness of the Amazon as a cohesive floristic group is facilitated by the migration of plant lineages across the Amazon basin in the absence of major physical/ecological barriers to dispersal or establishment, resulting in lack of geographical phylogenetic structure in Amazonian tree communities (Dexter et al., 2017). Lack of regional floristic identity within the Amazon could explain the fact that attempts to subdivide the Amazon into floristic groups has been challenging (Steege et al., 2013; Tuomisto et al., 2019). However, we were able to further separate the Amazon into floristic subgroups (Eastern Amazon, Western Amazon, Pacaas Novos Region, Upper Rio Negro, Guianas Shield-Llanos and Guianas Shield Cloud Forest; Figure 1). Although these floristic subgroups have similarities with other classifications previously proposed, for example, the subdivision in Western Amazon, Eastern Amazon, Guianas Shield and Upper Rio Negro (Prance, 1977; Tuomisto et al., 2019), the greatest divergence is related to the geographical range of such groups, which do not totally overlap between the different classifications. However, it seems a consensus that in all attempts to subdivide the Amazon into biogeographic units, based on floristic data or not, this conflict is present (Steege et al., 2013; Tuomisto et al., 2019 and references therein). In turn, Pacaas Novos, recognized for the first time according to our knowledge as a floristic subgroup, is composed of only two sites and 346 species.

Atlantic Forest

Another robust floristic group found was the Atlantic Forest, the group with the most unique flora recorded (>75% of exclusive species), which suggests limited floristic interchange with other NEF. The floristic distinctiveness of this group seems to have been apparent already in the Neogene with its isolation of other blocks of NEF by the formation of the “dry diagonal”, an area extending through South America from SW to NE that is dominated by seasonally dry vegetation, which was one of the results of the climatic changes influenced by the Andean elevation (Prado & Gibbs, 1993; Hoorn et al., 2010). In addition, it was possible to corroborate two widely recognized floristic subgroups (Oliveira-Filho & Fontes, 2000; Oliveira-Filho et al., 2005) along the Atlantic Forest: Northern and Southern Atlantic Forest. Recent findings support the floristic distinction between the Amazon and Atlantic rainforest (Miranda et al., 2018). However, possible routes for maintaining floristic interchange between Atlantic forest and Amazon have been suggested (*e.g.*, Ledo & Guarino, 2017). Our results support the presence of these routes when we registered 757 species shared between the two blocks.

Sub-Andean and Northern Lowland Forests (SANLF)

Besides the floristic identity of the seven blocks discussed above, we found two other groups that represent mixtures between floras (SANLF, and NACMF). The SANLF contact group encompasses the confluence of Ecuadorian, Peruvian and Colombian sub-Andean forest sites adjacent to the Amazon, part of the Andean rainforests of Colombia, the sub-Andean Llanos of Colombia and Venezuela, part of the Venezuelan Caribbean, as well as

Colombian and Mesoamerican sites (sub-region Choco-Darien). This extensive and complex group does not have a clear altitudinal, geographic or ecological distinction, and was the one that most shared species with other groups, mainly with Amazon and Mesoamerica, which probably reflects the different origins of the species that compose it. Results as this are expected when we consider the wide scale as adopted here in regions with a complex biogeographic history.

North Andean and Caribbean Montane Forests (NACMF)

The NACMF group showed an even proportion proportion of species sharing with the other groups and the lowest number of exclusive species. The NACMF also represents a meeting of floras (Andean and Caribbean), however to a lesser extent and complexity when compared to the SANLF group. NACMF are located in northeastern South America, being composed mostly of montane forest sites of the Eastern Cordillera of the Venezuelan Andes and Colombian Equatorial Caribbean. The low-differentiation between the Caribbean flora and the NACMF flora (more than 25% of shared species) could be explained by the geographical proximity between the two groups.

Perspectives

The floristic differentiation based on tree species composition detected among the nine NEF groups was corroborated by the high proportion of exclusive species in most groups, as well as by the variation in the number of indicator species and species richness. Although each group is likely to be essentially derived from the same set of ancestral lineages that make up the neotropical flora (Antonelli et al., 2018), the variation in species richness may be related to different regional processes that regulate the floristic composition at the species level (Miranda et al., 2018), since there is remarkable environmental heterogeneity between groups (Stadtmüller, 1987; Oliveira-Filho & Fontes, 2000; Rangel, 2004; Santiago-Valentin & Olmstead, 2004; Marshall, 2007). Thus, environmental heterogeneity could be a relevant factor to influence the species richness. However, we emphasize that despite the fact that most species richness estimates appear to be sound, the number of sampled sites in some groups was too low to provide reliable estimates, such as verified, for instance, in Choco and Bolivian Andes. Considering that our analyzes took into account only incidence data of individuals of tree size along the NEF, comparisons with other estimates of species richness for other regions that considered all vegetation types and/or abundance and/or other life habits should be avoided.

We emphasize that the floristic distinction found in NEF blocks portrays the singular diversity of species of these groups, which reinforces the importance of preserving their unique species assemblages. Detailed investigations on the variation of phylogenetic diversity among these groups are urgent because, although our study apparently did not capture ancient floristic differentiation among the lineages that compose them, only a more accurate analysis will be able to elucidate which lineages most contribute to the diversity of each of these groups.

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AUTHOR CONTRIBUTIONS

MACE and MFS conceived and designed the study; ATOF prepared the database; MACE analysed the data and led the writing of the manuscript; and all authors contributed critically to the writing and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Floristic data prior to our taxonomic review is publicly available in http://www.neotroptree.info/

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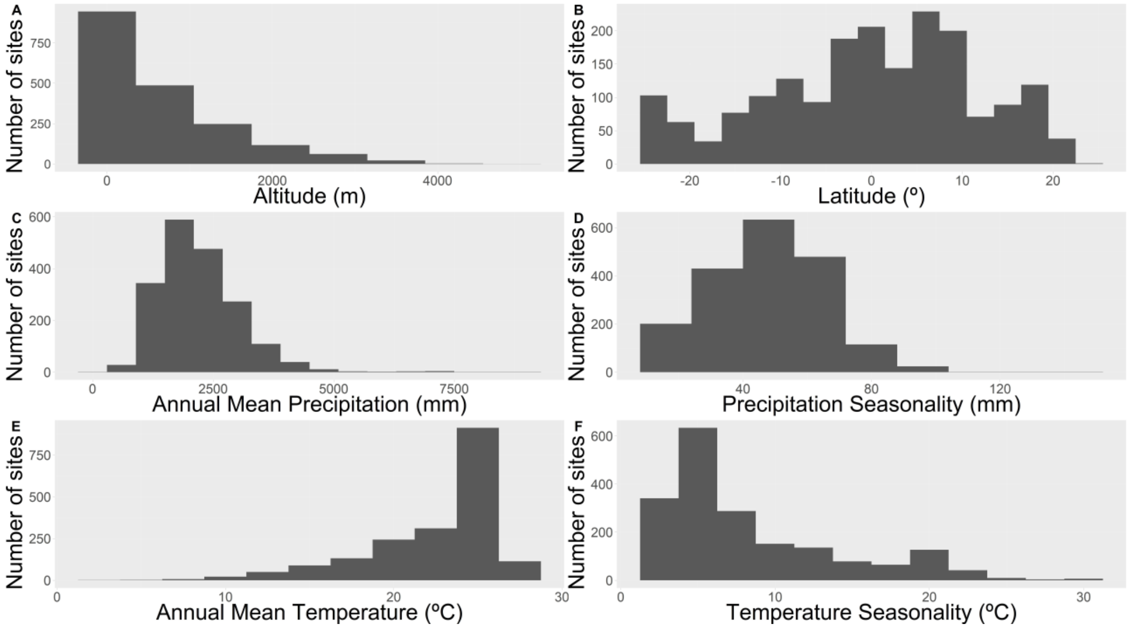
SUPPLEMENTARY MATERIAL

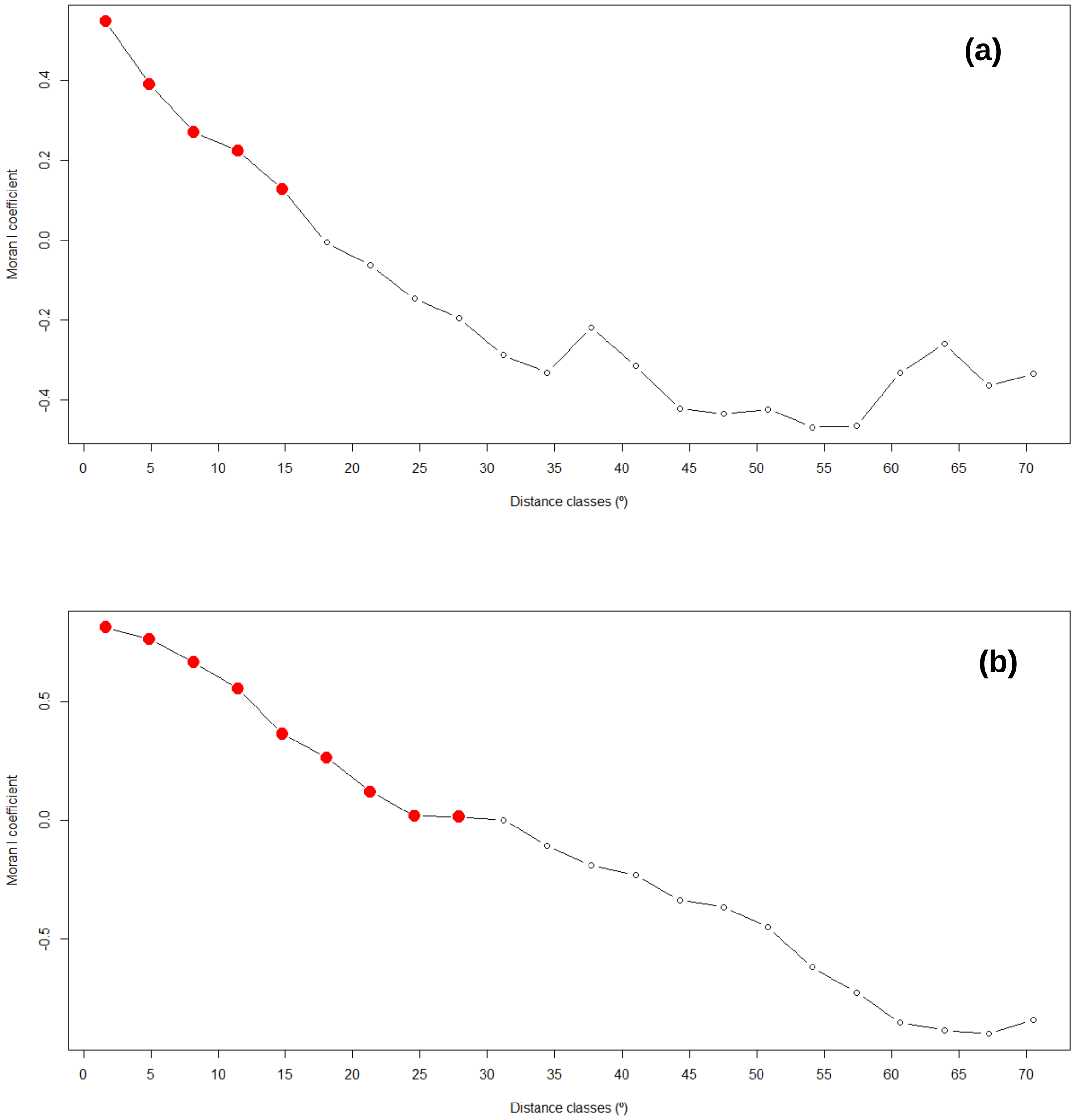
APPENDIX S1. Variation of environmental and spatial attributes of 1,885 sites of Neotropical Non-Flooded Evergreen Forests sampled in this study. Environmental attributes were obtained from CHELSA database (Karger et al., 2017).



APPENDIX S2 Description of 1,885 sites of Neotropical Non-Flooded Evergreen Forests including geographic coordinates (central point), vegetation type and species richness.

Available in: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Favsc.12522&file=avsc12522-sup-0002-AppendixS2.pdf

APPENDIX S3 Moran's I correlograms showing significant spatial autocorrelation in (a) Axis 1 and (b) Axis 2 of Non-metric Multidimensional Scaling (NMS) ordination. Correlograms were prepared in the 'pgirmess' package (Giraudoux, 2018) of R.



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Appendix S4. Ten families, ten genera and a hundred species with the highest number of occurrences recorded in 1,885 sites of Neotropical Non-Flooded Evergreen Forests.

Family	**N° of occurrence records**
Fabaceae	543,56
Rubiaceae	38,261
Melastomataceae	31,445
Lauraceae	23,359
Moraceae	22,449
Myrtaceae	20,273
Annonaceae	16,664
Euphorbiaceae	16,136
Arecaceae	15,729
Sapotaceae	14,094

Genera	**N° of occurrence records**
Miconia Ruiz & Pav.	19,672
Inga Mill.	15,627
Ficus L.	9,226
Ocotea Aubl.	9,204
Eugenia L.	7,698
Protium Burm.f.	7,166
Pouteria Aubl.	7,090
Solanum L.	6,789
Piper L.	6,361
Psychotria L.	6,218

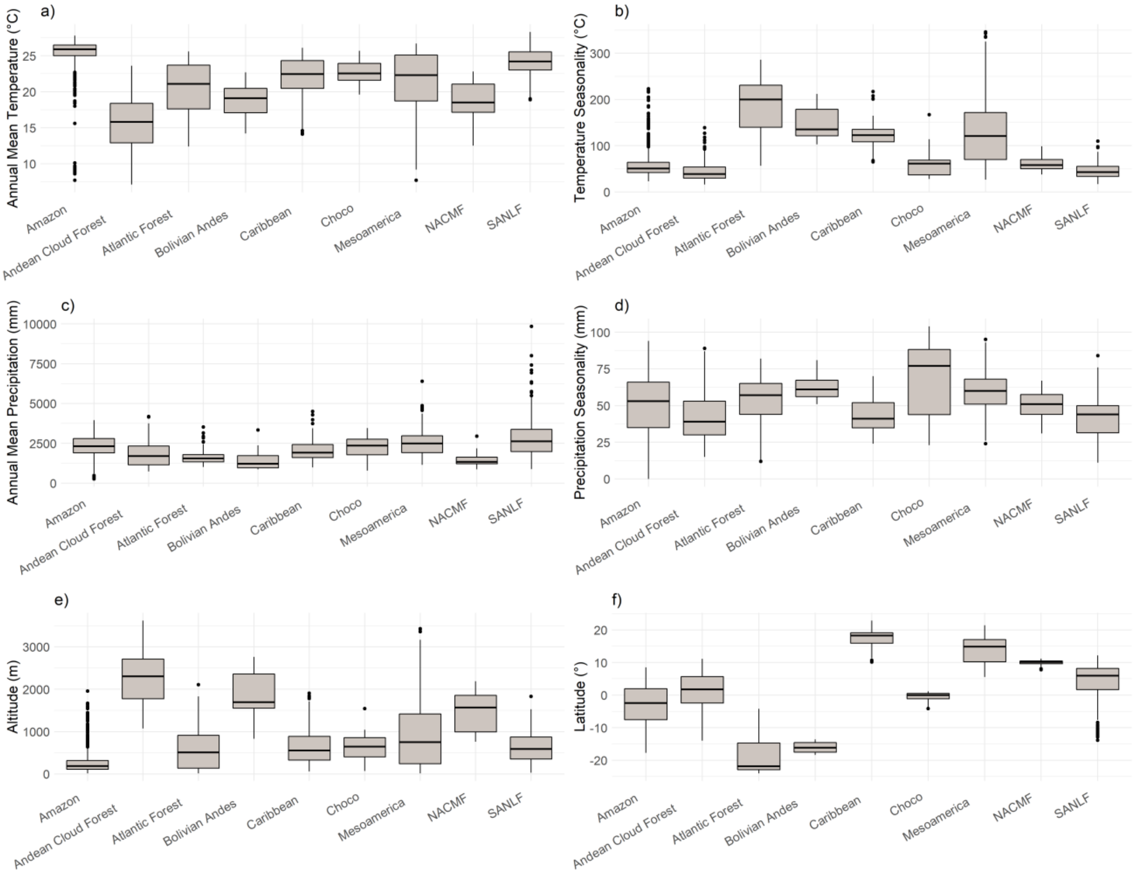
Species	**N° of occurrence records**
Tapirira guianensis Aubl.	1,117
Miconia prasina (Sw.) DC.	1,053
Piper arboreum Aubl.	1,028
Piper aduncum L.	1,002
Trema micrantha (L.) Blume	945
Simarouba amara Aubl.	842
Hieronyma alchorneoides Allemão	841

Species	**N° of occurrence records**
Guarea kunthiana A.Juss.	839
Lacistema aggregatum (P.J.Bergius) Rusby	829
Inga thibaudiana DC.	816
Siparuna guianensis Aubl.	800
Ficus americana Aubl.	796
Trichilia pallida Sw.	787
Palicourea guianensis Aubl.	785
Piper hispidum Sw.	785
Inga edulis Mart.	771
Inga nobilis Willd.	761
Ocotea leptobotra Mez.	755
Cedrela odorata L.	743
Posoqueria latifolia (Rudge) Schult.	742
Hymenaea courbaril L.	738
Psychotria deflexa DC.	735
Casearia arborea (Rich.) Urb.	730
Aparisthmium cordatum (A.Juss.) Baill.	729
Schefflera morototoni (Aubl.) Maguire et al.	724
Cordia nodosa Lam.	721
Dialium guianense (Aubl.) Sandwith	715
Margaritaria nobilis L.f.	707
Ficus pertusa L.f.	705
Symphonia globulifera L.f.	701
Guarea macrophylla Vahl	695
Brosimum guianense Huber ex Ducke	690
Jacaranda copaia (Aubl.) D.Don	685
Calophyllum brasiliense Cambess.	666
Psychotria carthagenensis Jacq.	663
Tococa guianensis Aubl.	663
Inga punctata Willd.	655
Cestrum schlechtendalii G.Don	650
Miconia minutiflora DC.	649

Species	**N° of occurrence records**
Helicostylis tomentosa (Poepp. & Endl.) Rusby	647
Erythroxylum macrophyllum Cav.	644
Dendropanax arboreus (L.) Decne. & Planch.	638
Urera baccifera (L.) Gaudich. ex Wedd.	621
Faramea multiflora A.Rich. ex DC.	619
Chamaedorea pinnatifrons (Jacq.) Oerst.	618
Pouteria caimito (Ruiz & Pav.) Radlk.	617
Guarea guidonia (L.) Sleumer	615
Micropholis guyanensis (A.DC.) Pierre	615
Erythroxylum citrifolium A.St.-Hil.	614
Socratea exorrhiza (Mart.) H.Wendl.	614
Eugenia florida DC.	613
Bixa orellana L.	612
Inga alba (Sw.) Willd.	610
Ocotea aciphylla (Nees & Mart.) Mez	610
Inga capitata Desv.	608
Turpinia occidentalis (Sw.) G.Don	606
Terminalia amazonia (J.F.Gmel.) Exell	603
Pourouma guianensis Aubl.	602
Geonoma deversa (Poit.) Kunth	601
Euterpe precatoria Mart.	590
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	587
Aegiphila integrifolia (Jacq.) Moldenke	578
Bellucia grossularioides (L.) Triana	574
Zanthoxylum rhoifolium Lam.	570
Cheiloclinium cognatum (Miers) A.C.Sm.	562
Miconia tomentosa (Rich.) D.Don	559
Roupala montana Aubl.	554
Cordia alliodora (Ruiz & Pav.) Cham.	552
Sloanea guianensis (Aubl.) Benth.	552
Protium heptaphyllum (Aubl.) Marchand	550
Brosimum lactescens (S.Moore) C.C.Berg	548

Species	**N° of occurrence records**
Acalypha macrostachya Jacq.	544
Ficus citrifolia Mill.	541
Protium aracouchini (Aubl.) Marchand	540
Hirtella triandra Sw.	535
Ficus insipida Willd.	532
Miconia nervosa (Sm.) Triana	532
Hamelia patens Jacq.	531
Handroanthus serratifolius (Vahl) S.Grose	531
Spondias mombin L.	529
Genipa americana L.	527
Garcinia madruno (Kunth) Hammel	523
Miconia punctata (Desr.) DC.	518
Acalypha diversifolia Jacq.	517
Apeiba tibourbou Aubl.	511
Minquartia guianensis Aubl.	511
Licania heteromorpha Benth.	507
Miconia dodecandra Cogn.	507
Ficus maxima Mill.	506
Abarema jupunba (Willd.) Britton & Killip	505
Banara guianensis Aubl.	504
Himatanthus articulatus (Vahl) Woodson	497
Inga vera Willd.	497
Oreopanax capitatus (Jacq.) Decne. & Planch.	497
Miconia serrulata (DC.) Naudin	491
Guatteria punctata (Aubl.) R.A.Howard	490
Oenocarpus bataua Mart.	490
Andira inermis (W.Wright) DC.	489
Miconia splendens (Sw.) Griseb.	488
Nectandra membranacea (Sw.) Griseb.	487

APPENDIX S5 Variation of environmental attributes of nine floristic groups of Neotropical Non-Flooded Evergreen Forests (NEF) recovered in this study. Environmental attributes were obtained from CHELSA database (Karger et al., 2017).



APPENDIX S6. Summary floristic data of nine groups of Neotropical Non-Flooded Evergreen Forests.

Groups	n° of sites	n° of occurrence records	n° of families	n° of genera	n° of species	n° of exclusive species	n° of indicator species
Amazon	701	240,256	138	838	6,167	3,092 (50.1%)	106 (1.7%)
Andean Cloud Forest	208	36,259	122	435	2,588	1,156 (44.6%)	59 (2.3%)
Atlantic Forest	265	84,912	114	573	3,269	2,477 (75.7%)	265 (8.1%)
Bolivian Andes	28	6,220	114	361	1,099	158 (14.4%)	150 (13.6%)
Caribbean	100	11,507	96	304	993	482 (48.5%)	63 (6.3%)
Choco	28	7,519	104	388	1,260	116 (9.2%)	139 (11.0%)
Mesoamerica	269	58,571	150	772	3,869	2,140 (55.3%)	34 (0.9%)
NACMF	47	6,213	106	323	918	92 (10.0%)	25 (2.7%)
SANLF	239	66,547	131	708	4,388	632 (14.4%)	7 (0.2%)

NACMF: North-Andean and Caribbean Montane Forests; SANLF: Sub-Andean and Northern Lowland Forests

APPENDIX S7 *Post hoc* permutation test for axes 1 (blank) and 2 (gray) obtained with Non-metric Multidimensional Scaling (NMS) for nine Neotropical Non-Flooded Evergreen Forests groups.*Significance results ($p \leq 0.05$).

	Amazon	**Andean Cloud Forest**	**Atlantic Forest**	**Bolivian Andes**	**Caribbean**	**Choco**	**Mesoamerica**	**NACMF**	**SANLF**
Amazon		<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Andean Cloud Forest	<0.0001*		<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Atlantic Forest	<0.0001*	<0.0001*		<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Bolivian Andes	<0.0001*	<0.0001*	<0.0001*		<0.0001*	<0.0001*	0.0010*	0.0021*	<0.0001*
Caribbean	0.0181*	0.1920	<0.0001*	0.0014*		0.8677	0.0184*	0.0698	<0.0001*
Choco	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*		0.1157	0.0666	<0.0001*
Mesoamerica	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*		0.9971	<0.0001*
NACMF	0.0902	0.0236*	<0.0001*	<0.0001*	0.8620	<0.0001*	<0.0001*		<0.0001*
SANLF	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	

NACMF: North-Andean and Caribbean Montane Forests; SANLF: Sub-Andean and Northern Lowland Forests

APPENDIX S8 Correlations between floristic composition and precipitation, temperature, altitude, and latitude in the ordination produced by the NMS, using the *envfit* function of 'vegan' package. Figures are Pearson correlation and determination coefficient (R^2). Values in bold correspond to significant correlations (P>0.05), accounting for spatial autocorrelation using the *modified.ttest* function of 'SpatialPack' package.

Environmental variables	**NMDS1**	**NMDS2**	**R^2**
Annual Mean Temperature	**-0.8077**	-0.2633	0.7217
Temperature Seasonality	0.0421	0.3740	0.1417
Annual Precipitation	-0.1377	**-0.3714**	0.1569
Precipitation Seasonality	-0.0103	0.0250	0.0007
Altitude	**0.8384**	0.1431	0.7234
Latitude	**0.1664**	**-0.7283**	0.5581

APPENDIX S9 Number of species shared among nine groups of Neotropical Non-Flooded Evergreen Forests. Values in the diagonal correspond to the total numbers of species within each group.

	Amazon	**Andean Cloud Forest**	**Atlantic Forest**	**Bolivian Andes**	**Caribbean**	**Choco**	**Mesoamerica**	**NACMF**	**SANLF**
Amazon	**6,167**	541	757	671	410	758	895	473	2,512
Andean Cloud Forest	**2,588**	129	523	130	443	546	494	990	
Atlantic Forest			**3,269**	228	0	170	272	170	416
Bolivian Andes				**1,099**	129	285	312	129	622
Caribbean					**993**	201	336	250	414
Choco						**1,260**	633	288	1,090
Mesoamerica							**3,869**	411	1,527
NACMF								**918**	601
SANLF									**4,388**

NACMF: North-Andean and Caribbean Montane Forests; SANLF: Sub-Andean and Northern Lowland Forests

APPENDIX S10 Number of genera (gray) and families (blank) shared among nine groups of Neotropical Non-Flooded Evergreen Forests. Values in the diagonal correspond to the numbers of genera/families within each group.

	Amazon	**Andean Cloud Forest**	**Atlantic Forest**	**Bolivian Andes**	**Caribbean**	**Choco**	**Mesoamerica**	**NACMF**	**SANLF**
Amazon	**838/138**	327	453	315	271	367	527	298	618
Andean Cloud Forest	108	**435/122**	244	272	190	271	336	258	350
Atlantic Forest	107	96	**573/114**	258	216	251	373	223	390
Bolivian Andes	106	107	96	**361/114**	187	235	299	226	313
Caribbean	91	86	85	86	**304/96**	216	278	190	263
Choco	101	94	90	93	83	**388/104**	362	247	378
Mesoamerica	120	117	105	111	96	101	**772/150**	299	550
NACMF	101	102	93	98	86	89	104	**323/106**	300
SANLF	122	111	105	107	89	103	120	99	**708/131**

NACMF: North-Andean and Caribbean Montane Forests; SANLF: Sub-Andean and Northern Lowland Forests

APPENDIX S11 Exclusive species of each group of Neotropical Non-Flooded Evergreen Forests.

Available in:
https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Favsc.12522&file=avsc12522-sup-0011-AppendixS11.pdf

APPENDIX S12 Indicator species of each group of Neotropical Non-Flooded Evergreen Forests.

Available in:
https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Favsc.12522&file=avsc12522-sup-0012-AppendixS12.pdf

APPENDIX S13 Species richness estimates throughout the Neotropical Non-Flooded Evergreen Forests and nine floristic groups. qD: the diversity estimate of order q; qD.LCL and qD.UCL: the 95% lower and upper confidence limits of diversity, respectively; SC: sample coverage estimate; SC.LCL and SC.UCL: the 95% lower and upper confidence limits of sample coverage, respectively.

Neotropical Non-Flooded Evergreen Forest

	t	**method**	**qD**	**qD.LCL**	**qD.UCL**	**SC**	**SC.LCL**	**SC.UCL**
1	1	interpolated	274.803	274.056	275.551	0.110	0.109	0.111
10	942	interpolated	13552.08	13507.68	13596.48	0.990	0.990	0.990
20	1885	observed	15134	15072.67	15195.33	0.996	0.996	0.996
30	2778	extrapolated	15826.29	15743.05	15909.53	0.998	0.998	0.998
40	3770	extrapolated	16204.84	16095.08	16314.61	0.999	0.999	0.999

Amazon

	t	**method**	**qD**	**qD.LCL**	**qD.UCL**	**SC**	**SC.LCL**	**SC.UCL**
1	1	interpolated	342.733	341.569	343.897	0.219	0.218	0.22
10	350	interpolated	5572.209	5543.177	5601.24	0.992	0.992	0.992
20	701	observed	6167	6122.019	6211.981	0.997	0.997	0.997
30	1033	extrapolated	6437.298	6375.628	6498.968	0.998	0.998	0.999
40	1402	extrapolated	6590.974	6511.294	6670.654	0.999	0.999	0.999

Andean Cloud Forest

	t	method	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	174.322	172.859	175.785	0.236	0.233	0.239
10	104	interpolated	2207.552	2184.283	2230.821	0.969	0.967	0.97
20	208	observed	2588	2553.239	2622.761	0.986	0.984	0.987
30	307	extrapolated	2781.848	2734.505	2829.192	0.992	0.99	0.993
40	416	extrapolated	2904.512	2841.99	2967.035	0.995	0.994	0.996

Atlantic Forest

	t	method	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	320.423	318.449	322.396	0.274	0.272	0.276
10	132	interpolated	2994.267	2977.879	3010.656	0.989	0.989	0.99
20	265	observed	3269	3246.46	3291.54	0.996	0.996	0.996
30	391	extrapolated	3385.073	3354.453	3415.693	0.998	0.998	0.998
40	530	extrapolated	3447.268	3406.506	3488.031	0.999	0.999	0.999

Bolivian Andes

	t	method	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	222.143	217.817	226.469	0.328	0.318	0.337
10	14	interpolated	932.731	918.668	946.794	0.918	0.913	0.922
20	28	observed	1099	1080.604	1117.396	0.967	0.963	0.971
30	41	extrapolated	1170.108	1145.98	1194.235	0.983	0.979	0.987
40	56	extrapolated	1210.09	1178.018	1242.162	0.992	0.989	0.995

Caribbean

	t	method	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	115.07	113.502	116.638	0.328	0.322	0.334
10	50	interpolated	826.639	812.352	840.927	0.957	0.955	0.958
20	100	observed	993	972.815	1013.185	0.982	0.98	0.984
30	147	extrapolated	1061.592	1035.414	1087.77	0.992	0.99	0.993
40	200	extrapolated	1095.16	1062.429	1127.891	0.997	0.995	0.998

Choco

	t	method	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	268.536	263.604	273.468	0.311	0.304	0.318
10	14	interpolated	1115.257	1101.84	1128.673	0.932	0.929	0.935
20	28	observed	1260	1244.216	1275.784	0.982	0.98	0.985
30	41	extrapolated	1297.252	1276.344	1318.161	0.995	0.992	0.997
40	56	extrapolated	1309.159	1281.743	1336.574	0.999	0.997	1

Mesoamerica

	t	method	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	1	interpolated	217.736	216.053	219.419	0.206	0.204	0.209
10	134	interpolated	3341.703	3320.497	3362.91	0.972	0.971	0.972
20	269	observed	3869	3835.387	3902.613	0.989	0.988	0.989
30	396	extrapolated	4096.144	4048.9	4143.388	0.994	0.994	0.995
40	538	extrapolated	4218.983	4157.365	4280.602	0.997	0.997	0.998

North-Andean and Caribbean Montane Forests

	t	**method**	**qD**	**qD.LCL**	**qD.UCL**	**SC**	**SC.LCL**	**SC.UCL**
1	1	interpolated	132.191	129.62	134.763	0.322	0.314	0.331
10	23	interpolated	750.931	735.717	766.144	0.922	0.918	0.927
20	47	observed	918	894.924	941.076	0.964	0.96	0.968
30	69	extrapolated	998.739	967.588	1029.891	0.979	0.975	0.984
40	94	extrapolated	1049.95	1008.725	1091.175	0.989	0.985	0.993

Sub-Andean and Northern Lowland Forests

	t	**method**	**qD**	**qD.LCL**	**qD.UCL**	**SC**	**SC.LCL**	**SC.UCL**
1	1	interpolated	278.439	276.638	280.241	0.258	0.255	0.26
10	119	interpolated	3739.922	3703.514	3776.33	0.97	0.97	0.971
20	239	observed	4388	4342.278	4433.722	0.987	0.986	0.988
30	352	extrapolated	4685.866	4628.696	4743.037	0.993	0.992	0.994
40	478	extrapolated	4855.539	4781.898	4929.181	0.997	0.996	0.997

CAPÍTULO II

Environmental variables and dispersal barriers explain broad-scale variation in tree species composition across Neotropical Non-Flooded Evergreen Forests

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ABSTRACT

Questions: We examined the drivers of tree species variation across Neotropical Non-Flooded Evergreen Forests (NEF) to answer the following questions: Can NEF blocks be differentiated based on environmental predictors? How do bioclimatic, topographic, edaphic predictors and dispersal barriers contribute to explain the floristic variation throughout NEF?

Location: Neotropical region.

Material and Methods: Based on 1,843 sites, 15,072 species and 509,793 occurrence records of trees, as well as on 59 environmental variables and dispersal barriers (based on ecological and geographical dispersal suitability), we tested whether environmental predictive variables can discriminate NEF blocks, and built canonical models and variation partitioning to assess which variables contributed most to the floristic variation.

Results: Despite extensive overlap in predictive variables between NEF blocks, Amazon and Atlantic Forest were the most differentiated among NEF groups. Floristic variation along NEF was mainly determined by environmental factors (54.1%; $p = 0.001$), with topographic and edaphic variables representing the most important predictors. Dispersal barriers also contributed significantly to our model (3.7%; $p = 0.001$).

Conclusion: The broad environmental variation between NEF blocks is largely responsible for the distinctive species composition found in these highly diverse areas. In addition, dispersal barriers do not seem to have prevented floristic exchanges between most NEF groups, except in the Atlantic Forest.

KEYWORDS
ecological barriers, environmental drivers, floristic variation, NeoTropTree database, Tropical Forest

1 INTRODUCTION

Investigating broad-scale environmental and spatial factors that structure species composition across highly diverse regions can help us to understand how deterministic and evolutionary processes influenced present-day plant assemblages. The evolution of niches, trait filtering and long-distance dispersal have played a significant role in the assembly of Neotropical forest communities (Coronado *et al.,* 2014; Dick *et al.,* 2013; Dick and Pennington, 2019). In addition, it has been shown that biogeographic filtering along dispersal barriers, based mainly on differential environmental tolerances and dispersal/colonization abilities between species, has mediated the floristic assembly in the Neotropics (Bemmels *et al*., 2018).

Neotropical Non-Flooded Evergreen Forests (NEF) comprise one of the richest ecosystems in the world (Wilson, 1988; Myers *et al*., 2000; Corlett and Primack, 2011). NEF extend from southern Mexico to Central America and the Caribbean, the Amazon basin and coastal Brazil (Kappelle, 2004; Corllet and Primack, 2011). NEF comprise the (i) neotropical rainforests, which can be defined by closed, evergreen canopies that occur in lowland regions with warm and wet climates (generally >2000 mm annual rainfall) that normally do not experience a pronounced dry season (Corllet and Primack, 2011) and (ii) tropical montane forests, which occurs predominantly between 1,200 and 2,800 m a.s.l., with small areas occurring in regions over 4,000 m in the Andes (Kappelle, 2004). Thus, NEF experience wide latitudinal, altitudinal and longitudinal gradients, implying considerable environmental and spatial variations across its range (*e.g*., Cupertino-Eisenlohr *et al*., 2020). Floristic variation along these environmental gradients can be seen along disjoint NEF blocks such as the Atlantic, Amazon, Tropical Andes, Choco, Mesoamerica and Caribbean (Asprey, 1959; Gentry, 1982a; Henderson *et al*., 1991; Miranda *et al*., 2018). A study based on a large dataset spanning the whole extension of NEF has confirmed previous works by demonstrating that those disjoint blocks represent distinct floristic groups (Cupertino-Eisenlohr *et al.*, 2020).

The structuring of floristic patterns along NEF blocks has been correlated with bioclimatic, edaphic and topographic variables (Coronado *et al*., 2009; Quesada *et al*., 2012; Eisenlohr and Oliveira-Filho, 2015; Arruda *et al*., 2017;

Miranda *et al*., 2018), but such analyses have been restricted to few blocks. Preliminary correlations between floristic composition and a limited number of environmental variables have been carried out for the NEF (Cupertino-Eisenlohr *et al*., 2020), but more comprehensive analyses are required to understand the drivers throughout the whole extension of such forests. In addition to variation in environmental variables, blocks of NEF display different degrees of geographical and ecological isolation, which have varied in space and time (*e.g*., Dick and Pennington, 2019). Currently, floristic interchanges between blocks of NEF is prevented by different types of barriers such as the sea (isolating the Caribbean from continental America), high elevation mountain ranges (*e.g.* the Amazon basin is separated from the Choco and Mesoamerican forests by the Andes), and expanses of land dominated by unsuitable seasonally dry climates (Gentry, 1982b; Prado and Gibbs, 1993; Hoorn *et al*., 2010; Jaramillo *et al*., 2010; Nieto-Blázquez *et al*., 2017; Bemmls *et al*., 2018). In fact, due to the disjoint occurrence of NEF floristic groups (Cupertino-Eisenlohr *et al*., 2020), geographic barriers are expected to play an important role in plant species assembly.

The relevance for investigating floristic drivers becomes even more urgent in ecosystems that have a combination of high rates of species richness and endemism and accelerated habitat loss, as is the case of the five biodiversity hotspots within NEF: Mesoamerica, Caribbean, Choco, Tropical Andes and Atlantic Forest (Myers *et al*., 2000; Zachos and Habel, 2011). In addition, understanding the association between environmental variables (temperature, rainfall) and vegetation are critical to predict the future of NEF blocks in face of ongoing global climate change (*e.g.* Sullivan *et al*., 2020).

Here we investigate the predictors of broad-scale floristic variation throughout NEF based on environmental variables, dispersal barriers and a dataset of more than 500,000 occurrence records of tree species available for 1,843 sites distributed across all NEF blocks. Specifically, we addressed: (i) Can NEF blocks, which were defined a priori based on floristic similarities (Cupertino-Eisenlohr *et al*., 2020), be discriminated based on environmental predictors? We expect that environmental predictors would be useful in discriminating floristic groups since variation in species composition would be driven by environmental predictors. Here we also evaluated the environmental variation among such NEF blocks; (ii) What are the main environmental predictors of tree composition patterns? How do bioclimatic, topographic and edaphic factors contribute to explain floristic variation over NEF? We expected that among environmental variables bioclimatic factors are the most important to explain floristic variation, as these predictors act more strongly at broader scales. (iii) In addition to environmental factors, are dispersal barriers good predictors of floristic variation throughout NEF? We expect that the dispersal barriers would greatly impact tree composition, since geographic and ecological isolation can limit species dispersal between NEF blocks, preventing floristic exchange and influencing floristic patterns.

2 METHODS

2.1 Study area

The delimitation of Neotropical Non-Flooded Evergreen Forests (Cupertino-Eisenlohr *et al*., 2020) was based on the Neotropical Vegetation Classification System of Oliveira-Filho (2009; 2015), who defined NEF based on a perennial leaf renewal regime. This regime occurs in the equatorial and tropical thermal domains and under the pluvial, seasonally dry and cloud climatic regimes (Oliveira-Filho, 2017).

2.2 Floristic composition data

We obtained occurrence data of tree and tree-like species (plants with free stems, that is, without relying on other plants, at least 3 m high) from the NeoTropTree (NTT) database (http://www.neotroptree.info; Oliveira-Filho, 2017). This database presents lists of tree species composition for sites compiled between the years 1992-2017 based on floristic surveys, checklists, herbarium records from online platforms (e.g., speciesLink) and taxonomic monographs for the entire Neotropical region. NTT's floristic lists are georeferenced and organized in sites with a spatial resolution of 10 km in diameter. A NTT site is defined by a single vegetation type (*sensu* Oliveira-Filho, 2015); when two or more vegetation types are superimposed on the same site in the NTT, each will represent a distinct habitat. Although floristic data in

NTT sites were obtained by different methodologies with unequal sampling effort, species composition in NTT sites generally reflects large-scale patterns of floristic variation (Neves *et al*., 2017; Miranda *et al*., 2018; Cupertino-Eisenlohr *et al*., 2020).

Taxonomic and geographic circumscriptions of all species included in the NTT were based on information the following projects: Flora do Brasil online, Catalog of Vascular Plants of Ecuador, Peru Checklist, Catalog of Bolivia (available at http://floradobrasil.jbrj.gov.br/, http://www.tropicos.org/Project/CE/, http://www.tropicos.org/Project/PEC and http://www.tropicos.org/Project/BC/, respectively) and published floras (Boggan *et al*., 1997; Steyermark *et al*., 1995-2005; Bernal et *al*., 2016). In addition, we carried out additional checks using the floristic list of Cardoso *et al*., (2017) and Vascular Plants of Americas (Ulloa-Ulloa *et al*., 2018 onwards). By accessing the Flora do Brasil 2020 under construction (http://floradobrasil.jbrj.gov.br/), The Plant List (http://www.theplantlist.org/), IPNI (https://www.ipni.org/), TROPICOS (http://www.tropicos.org/), PLANTMINER (http://www.plantminer.com/) and iPlantCollaborative - Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/TNRSapp.html) databases, we checked for correct spelling and possible synonyms present in the occurrence data. We eliminated 42 sites due to the unavailability of some environmental variables to be used in the models (see below) and, after these steps, our database had 1,843 sites / checklists, 15,072 species and 509,793 occurrence records representing the whole extension of NEF.

Before analysis, we excluded species that only occurred once (unicates) to avoid noise in the analysis, totaling 13,054 species. We built a floristic matrix using the Simpson's distance coefficient, which allows us to investigate composition patterns in ecological communities when there is great variation in species richness between sampling units (Baselga *et al*., 2007). We then reduced the dimensionality of the floristic matrix using PCoA (Principal Coordinate Analysis) axes, a method that preserves the original distances from the floristic matrix (Gower, 1966; Legendre and Legendre, 2012). To access the main patterns of variation in species composition, we selected only the significant axes of the PCoA based on the Broken Stick model, that is, the axes whose PCoA eigenvalues were superior to the eigenvalues generated by a

PCoA obtained from a null model (Appendix S1). For this, we used the routine provided by Borcard *et al*., (2011). Thus, the floristic matrix (*matrix i*) was constituted by the significant axes of PCoA. The patterns of floristic variation along NEF were investigated based on nine floristic groups proposed by Cupertino-Eisenlohr *et al*., 2020. The number of sites and species for each floristic group is available in Table 01.

TABLE 1 Number of sites and species in the nine floristic groups of Neotropical Non-Flooded Evergreen Forests proposed by Cupertino-Eisenlohr et al. (2020) that comprised the dataset used in the present study.

Floristic group	**N° of sites**	**N° of species**
Amazon	698	6,167
Andean Cloud Forest	208	2,588
Atlantic Forest	258	3,266
Bolivian Andes	28	1,099
Caribbean	84	981
Choco	28	1,260
Mesoamerica	259	3,797
North-Andean and Caribbean Montane Forests	46	904
Sub-Andean and Northern Lowland Forests	234	4,340

2.3 Environmental data

We obtained 59 environmental variables for 1,843 NEF sites. We used a spatial resolution of ~ 10 km because it is equivalent to the size of NTT sites. When the variable was only available at a finer resolution (<10 km), we applied the resample function of the ‘raster’ package to resample variables to the resolution used here. The 59 variables (Appendix S2) comprise: a) 19 bioclimatic layers of temperature and precipitation from the 'CHELSA' database (Karger *et al*., 2017); b) six variables of relative humidity of the ‘CliMond’

(Kriticos *et al*., 2012); c) three solar radiation variables, three water vapor pressure variables and three wind speed variables from ‘WorldClim 2.0’ (Fick and Hijmans, 2017); d) four topographic and relief variables, which were: topographic moisture index and rockiness index, obtained through 'ENVIREM' (Title and Bemmels, 2018); global relief model, which combines land topography with ocean bathymetry, obtained from 'UNEP/GEODATA' (http://geodata.grid.unep.ch/results.php); elevation, obtained from the NASA Shuttle Radar Topographic Mission (SRTM; https://lpdaac.usgs.gov/products/srtmgl1v003/); e) seven evapotranspiration variables and six potential evapotranspiration variables (PET) obtained from the 'Global Aridity and PET Database' database (Trabucco and Zomer, 2019a) and from 'ENVIREM', and one actual evapotranspiration variable (AET) obtained from the 'Global High-Resolution Soil-Water Balance' (Trabucco and Zomer, 2019b); f) aridity index, from the ‘Global Aridity and PET Database’; g) 13 soil variables, of which ten (apparent density, coarse particles, clay, sand, and silt content, depth to horizon R, probability of occurrence of horizon R, carbon content, pH in water and cation exchange capacity) obtained from 'SoilGrids' (Hengl *et al*., 2014), and the others (maximum, medium and minimum soil water stress) from the 'Global High-Resolution Soil-Water Balance'. Means and standard deviations for these variables by floristic group are presented in Appendix S3.

2.4 Dispersal barriers

In addition to environmental predictors, spatial parameters are expected to play a role in floristic variation between NEF sites. Most NEF blocks occur isolated from each other, either separated by the sea, mountain ranges, unsuitable habitats or large geographic distance. Such dispersal barriers can reduce species exchange between NEF blocks, influencing tree species their tree species composition. To include this aspect in our analyses, we developed a dispersal barrier model that takes into account not only the geographic distance between sites, but the cost of dispersal between them, by considering different dispersal barriers for NEF species.

For the dispersal barrier model we calculated weighted pairwise distances between sites that incorporate the difficulties of a species cross a geographical or ecological barrier. For this, we built cost surfaces for three main barriers to species dispersal: (i) altitudinal gradient, (ii) ocean and (iii) biomes. We assigned weights to each class of barriers according to the dispersal limitation they impose.

In order to implement an altitudinal gradient barrier, we considered that NEF occurs from lowland to over 3,000 m in altitude, so that the plain can act as a barrier to the limitation of species in the cloud forests and vice versa. To incorporate this trend into our analysis, we divided the NEF sites into eight altitudinal classes (Appendix S4) according to the classification system of Oliveira-Filho (2009; 2015). For each of these eight sets of sites we built a cost surface. The elevation data used here were obtained from the SRTM database. Weight 1 was given to the elevation where the sites of each set occur, gradually increasing to the most distant elevation (Weight 9; Appendix S4). On each of these eight elevation cost surfaces, we assumed the ocean as all cells that do not overlap the Earth's surface, and we assigned a penalty weight (9) to this barrier.

The cost surface for the different biomes in the Neotropical region followed the classification of biomes by Olson *et al*. (2001). We chose this classification because it reflects the distribution of NEF, as well as and open, seasonally dry unsuitable habitats that act as limiting factors for the dispersal of NEF species. We assigned weight 1 to the Tropical & Subtropical Moist Broadleaf Forests, a biome that broadly overlaps with the occurrence of NEF, and increasing weights to more unsuitable biomes (Appendix S4; for the weights assigned to the other biomes).

We built all the rasters in 10 km resolution, which corresponds to the resolution of the NTT sites, and used the ‘Reclassify’ tool from ArcMap 10.8 (Esri 2020) to reclassify the rasters according to the classes and weights described above. To generate the eight cost surfaces, we added each elevation raster with the biome raster. From each of the cost surfaces we generated a transition matrix based on the neighborhood eight-way (or Moore neighborhood algorithm) using the *transition* function of the package 'gdistance' (van Etten, 2017). By default, the *transition* function works on a conductance matrix. Here we worked with a matrix of resistance (1/conductance). Based on the eight transition matrices we calculated the least cost paths for each pair of sites separated by altitudinal dimensions, using the *shortestPath* function of the 'gdistance' package. Finally, based on all the least cost path pairs, we obtained the weighted ecological distance using the *spTransform* function of the ‘sp’ package (Pebesma *et al*., 2016) and built a weighted ecological distance matrix.

We then reduced the dimensionality of the weighted ecological distance matrix by using a Principal Coordinate Analysis (PCoA) based on the Euclidean distance (Gower, 1966; Legendre and Legendre, 2012). When PCoA is performed in this way, it is equivalent to a Principal Component Analysis (PCA). We selected the significant axes of the PCoA based on the Broken Stick null model (Appendix S5). Only the first axis was significant, and the respective scores were used in subsequent analyses.

2.5 Environmental discrimination of NEF blocks

To check if NEF defined a priori by Cupertino-Eisenlohr *et al*. (2020) could be separated by their environmental attributes (matrix ii; see section 2.7), we performed a Flexible Discriminant Analysis (FDA), on which we applied the multivariate adaptive regression splines (MARS) (Hastie *et al*., 1994). For this, we used the *fda* function of the ‘mda’ package (Hastie and Tibshirani, 2017). We used the *envfit* function of ‘vegan’ package (Oksanen *et al*., 2019) to examine the influence of each environmental variable to the FDA model.

2.6 Main patterns of environmental variation

Based on *matrix ii*, composed of 17 selected environmental variables (see section 2.7 below), we performed Principal Component Analyzes (PCAs) to assess the variation of environmental data among NEF floristic groups. Based on this set of variables, we obtained significant PCA axes according to the Broken Stick criterion. From the scores of significant PCA axes, we performed ANOVAs with permutations to test the difference between the nine NEF groups using the *IndependenceTest* function of the 'coin' package (Hothorn *et al*., 2008). To discount the effects of spatial autocorrelation and avoid inflation of type I errors, we included spatial filters (Moran’s Eigenvector Maps; MEMs, obtained from latitude and longitude) as covariates. We optimized the selection of the best spatial weighted matrix (SWM) by minimizing spatial autocorrelation in the ANOVA residuals (Bauman *et al*., 2018). We applied *a* *posteriori test* with permutations based on the *pairwisePermutationMatrix* function of the 'rcompanion' package (Mangiafico, 2019). To avoid inflation of the type I error rate due to multiple comparisons, we used an adjusted p-value (Mangiafico, 2019). We correlated the environmental variables to PCA axes by using the *envfit* function of ‘vegan’ package.

2.7 Influence of environmental variables and dispersal barriers on floristic variation along NEF

We built canonical models to explain the main patterns of floristic variation throughout NEF. Initially, we standardized the scale of the 59 environmental variables using the *decostand* function of the ‘vegan’ package. Considering that an important assumption of multiple statistical models is the absence of multicollinearities (Borcard *et al*., 2011), we checked for redundancies among environmental variables by calculating the Variance Inflation Factor (VIF). When the VIF was greater than 10 (*e.g*., Borcard *et al*., 2011) we progressively eliminated collinear variables using the *vifcor* function of the ‘usdm’ package (Naimi, 2014). In this function, we adopted a correlation threshold of 0.8, which means that, in all pairs of variables with maximum correlation with each other ≥ 0.8, one of the variables - the one with the highest VIF - was excluded (Naimi, 2014). When the VIF remained above 10, the threshold was lowered until we were successful in removing the collinearities.

We then conducted a forward selection procedure (*forward.sel* function of the ‘adespatial’ package; Dray *et al*., 2020) to obtain, from these non-collinear variables, the most adjusted subset to the species composition data (matrix i). We only performed this selection when the global model (i.e., containing all non-collinear variables) was significant (Blanchet *et al*., 2008). During this selection we used the double stop criterion of Blanchet *et al*. (2008), which consists of: (i) the candidate variable must have a significant effect on the model ($p \leq 0.05$) and (ii) the adjusted R^2 of the explanation of the set of selected variables must not be higher than the adjusted R^2 of the global model. Additionally, we incorporated a third stopping criterion related to the variance of the adjusted R^2 of the variable to be added to the model ('R2 more criterion'), which consists of interrupting the progressive selection in case the difference of the R^2 of the model in relation to the previous stage of construction of this model is less than a cut-off threshold (we used 0.001 here). The subset of 17 selected environmental variables comprised *matrix ii*.

As the dispersal barrier data were comprised by only one variable, named, the scores of the first axis of a PCoA derived from the cost surface analysis (see section 2.4 above), we just confirmed the significance of this variable and used it to compose a dispersal barrier matrix (*matrix iii*).

We modeled the relationships between tree species composition (*matrix i*) and the selected environmental and dispersal barrier variables (*matrices ii and iii*) using Canonical Redundancy Analysis (RDAs) in the ‘vegan’ package. Despite the established use of Canonical Correspondence Analysis (CCA) in Ecology (McCune and Grace, 2002), this method should be avoided when there are strong variations in the frequency of species occurrence (Legendre and Gallagher, 2001). The RDA, when based on data transformation, avoids the classic biases of Euclidean distance and, therefore, presents advantages in relation to CCA (Legendre and Gallagher, 2001).

We partitioned the floristic variation (*matrix 1*) of the sites according to the fractions: [a] only environmental variables, [b] fraction shared between environment and dispersal barriers; [c] only dispersal barrier variables; and [d] residuals. We used the function *varipart* (package 'ade4'; Dray and Dufour, 2007). We tested the [a] and [c] fractions based on ANOVA with permutations. To prevent inflation of type I errors in ANOVAs, we controlled spatial autocorrelation by using MEMs (see topic 2.6, above). The best SWM used to build MEMs was the one that provided the most fitted set of eigenvectors after a forward selection procedure (Bauman *et al*., 2018).

Finally, we hierarchized the predictor variables according to the intraset and interset correlations with the main axes of the RDA and extracted the means yielded by each component (bioclimatic, soils and topographic variables). All analyses were performed using R software (R Development Core Team, 2019).

3 RESULTS

3.1 Environmental discrimination of NEF blocks

Discriminant analysis was able to effectively assign sites to their corresponding NEF group based on a selection of 17 environmental predictors (Figure 01; Table 02). The rate of sites incorrectly classified was 11.2%. Atlantic Forest, Caribbean, Amazon and Mesoamerica were the groups best predicted by selected environmental variables (>90% correctly assigned), while Choco, NAFMC, Andean Cloud Forest, and SANFL groups were poorly defined (<80% correctly assigned) because of substantial overlap in environmental predictors. The most important variables to explain the FDA model was pH (Appendix S6).

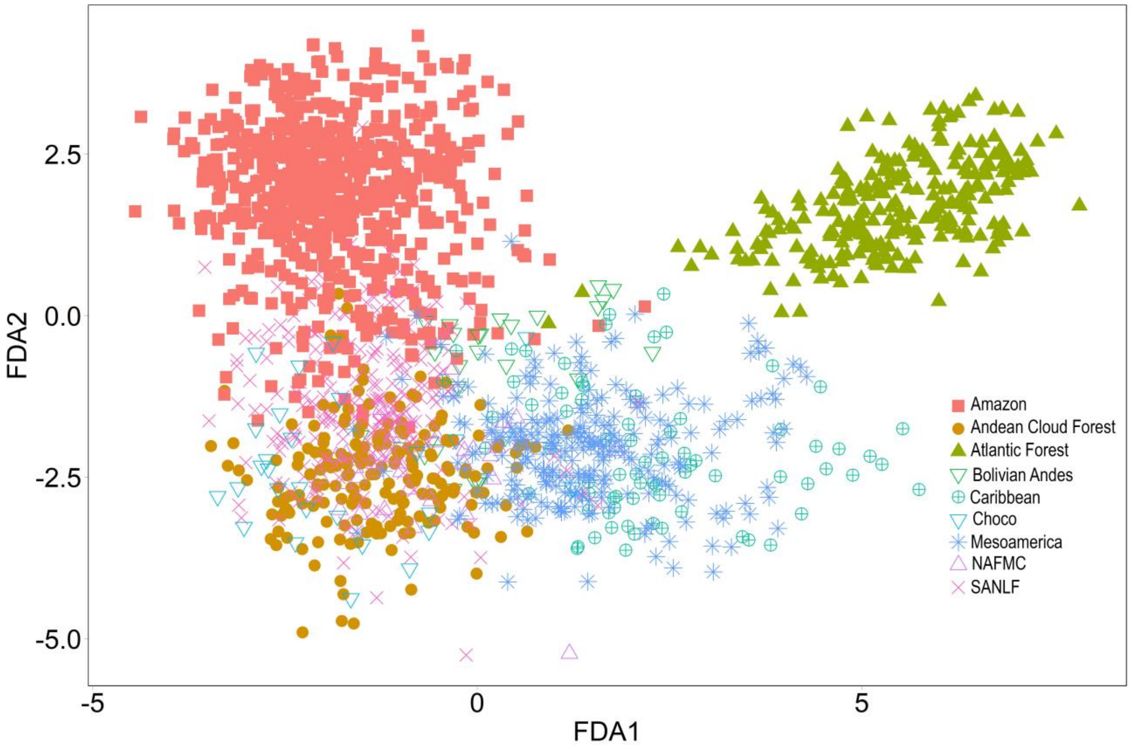

FIGURE 1 Flexible Discriminant Analysis for nine groups of Neotropical Non-Flooded Evergreen Forests based on 17 selected environmental variables showed in table 04. NAFMC: North-Andean and Caribbean Montane Forests; SANFL: Sub-Andean and Northern Lowland Forests.

TABLE 2 Site discrimination among nine floristic groups of Neotropical Non-Flooded Evergreen Forests based on 17 environmental variables derived from a Flexible Discriminant Analysis (FDA). Diagonal shows the number of sites correctly assigned / total sites for each floristic group. NAFMC: North-Andean and Caribbean Montane Forests; SANFL: Sub-Andean and Northern Lowland Forests.

	Amazon	**Andean Cloud Forest**	**Atlantic Forest**	**Bolivian Andes**	**Caribbean**	**Choco**	**Mesoamerica**	**NAFMC**	**SANLF**
Amazon	650 /698	1	0	1	0	0	1	0	12
Andean Cloud Forest	5	151/208	0	0	0	5	6	6	10
Atlantic Forest	1	0	256/258	0	0	0	2	0	0
Bolivian Andes	1	8	0	26/28	0	0	3	0	0
Caribbean	0	0	0	0	79/84	1	2	2	3
Choco	0	8	0	0	0	19/28	0	0	2
Mesoamerica	2	0	0	0	5	0	241/259	0	5
NAFMC	1	10	0	0	0	1	2	33/46	20
SANLF	38	30	2	1	0	2	2	5	182/234

3.2 Main patterns of environmental variation

We recorded significant environmental variation between NEF floristic groups (Table 03). Axis 1 of the PCA was responsible for 26.94% of the variation in environmental predictors (Figure 02). On this axis, the separation of Amazon in relation to the other groups was mainly correlated with topographic wetness index and edaphic predictors (Figure 02; Appendix S6). Also on axis 1 there was a gradient of environmental variation from Amazon to Andean Cloud Forest, mainly associated with topographic and edaphic variables, with Andean Cloud Forest exhibiting higher values of soil carbon, silt content and coarse fragments. Axis 2 of the PCA explained 17.5% of the variation of the predictors; in this axis, isothermality and clay content were the most important predictors and were mainly associated with the separation of Atlantic Forest from other groups (Figure 02; Appendix S7).

TABLE 3 Analysis of variance comparing the averages of Principal Component Analysis (PCA) scores between nine groups of Neotropical Non-Flooded Evergreen Forests. Average scores shown for three significant axes were obtained in a PCA based on 17 environmental variables from 1,843 sites. Different letters in the same column correspond to group averages that differed from each other ($p \leq 0.05$) by an *a posteriori* test with permutations. NAFMC: North-Andean and Caribbean Montane Forests; SANFL: Sub-Andean and Northern Lowland Forests.

Floristic group	**PCA1**	**PCA2**	**PCA3**
Amazon	-0.1535^{a}	0.0270^{a}	-0.0104^{a}
Andean Cloud Forest	0.2022^{b}	0.1481^{b}	0.0586^{b}
Atlantic Forest	-0.0129^{c}	-0.1325^{c}	0.1126^{c}
Bolivian Andes	0.2067^{b}	-0.0414^{de}	0.1866^{d}
Caribbean	0.1414^{d}	-0.1582^{f}	-0.0663^{ef}
Choco	0.0599^{e}	0.1196^{b}	0.0823^{bc}

Floristic group	PCA1	PCA2	PCA3
Mesoamerica	0.1260^{d}	-0.0664^{d}	-0.0849^{e}
NAFMC	0.1832^{b}	-0.0332^{e}	-0.0561^{ef}
SANFL	0.0343^{e}	0.0613^{g}	-0.0484^{f}

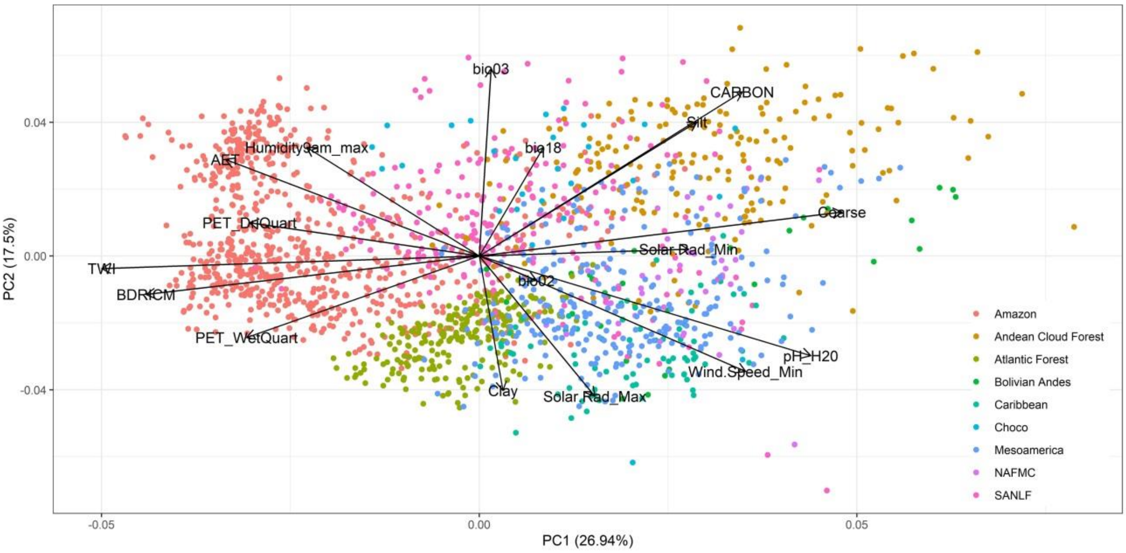

FIGURE 2 Principal Component Analyzes (PCA) for 1,843 sites belonging to nine floristic groups of Neotropical Non-Flooded Evergreen Forests based on a set of 17 selected environmental variables. NAFMC: North-Andean and Caribbean Montane Forests; SANFL: Sub-Andean and Northern Lowland Forests.

3.3 Influence of environmental variables and dispersal barriers on floristic variation along NEF

The main patterns of floristic variation emerged from the model containing 17 environmental variables and one dispersal barrier variable were mostly determined by the pure environmental fraction (fraction [a]; 54.1% (p-value = 0.001) followed by a combination of environmental and barrier factors (fraction [b]; 22.7%). The pure dispersal barrier fraction (fraction [c]) was responsible for 3.7% (p-value = 0.001) of the explanation of the floristic variation along NEF. Residuals accounted for 19.5% of the model explanation.

Axis 1 of the RDA explained 36.8% of the main patterns of floristic variation along NEF (Figure 03). On this axis, on average, topographic variables played the greatest role over floristic variation with highest correlation with axis 1 scores (Table 04). The most important environmental variables on this axis were topographic wetness index and pH (Figure 03). These variables seem to determine the separation of the Amazon from other groups (Figure 03). Another evident pattern along axis 1 was the occurrence of a species composition gradient starting in the Amazon, at the extreme left of the diagram, and culminating in the Andean Cloud Forest, at the extreme right (Figure 03).

Axis 2 of the RDA explained 28.1% of the floristic variation, with dispersal barriers and potential evapotranspiration of the driest quarter as the most important environmental predictors, which influenced the dissociation of the Atlantic Forest in relation to other NEF groups (Figure 03; Table 04).

Axis 3 was responsible for 15.9% of the floristic variation and was more strongly associated with maximum solar radiation and clay content , with Andean Cloud Forest appearing separated from other groups (Figure 04; Table 04).

TABLE 4 Interset | intraset correlations between 17 selected environmental variables and dispersal barrier, and the scores of three main axes from an environmental-spatial RDA (Redundancy Analysis). In bold, the two variables with highest correlation with the respective axis.

Environmental and dispersal barrier variables	RDA1	RDA2	RDA3
Topographic wetness index	**-0.7742|-0.8463**	0.0051|0.0054	0.1067|0.1326
Mean diurnal temperature range	0.1917|0.2096	-0.1674|-0.1774	-0.2424|-0.3013
Isothermality	0.0297|0.0324	0.4987|0.5287	-0.3818|-0.4746
Precipitation of warmest quarter	0.2416|0.2641	0.0831|0.088	0.0856|0.1065
Solar radiation (max)	0.1196|0.1307	-0.0694|-0.0736	**0.5070|0.6302**
Solar radiation (min)	0.3229|0.3529	0.4791|0.5079	0.2427|0.3016
Wind speed (min)	0.411|0.4493	-0.2192|-0.2323	0.2288|0.2844
Potential evapotranspiration of the driest quarter	-0.562|-0.6144	**0.5803|0.6151**	0.1146|0.1424
Potential evapotranspiration of the	-0.3659|-0.3999	-0.0462|-0.049	0.2728|0.339

Environmental and dispersal barrier variables	RDA1	RDA2	RDA3
wettest quarter			
Mean annual actual evapotranspiration	-0.4566|-0.4991	0.4603|0.4879	0.1308|0.1626
Relative humidity data for 9 am (max)	-0.2734|-0.2988	0.0615|0.0652	-0.1325|-0.1646
Clay content	0.0836|0.0913	-0.0415|-0.044	**0.4342|0.5397**
Coarse fragments	0.5991|0.6549	0.2862|0.3033	0.0315|0.0391
Silt content	0.4043|0.442	0.5151|0.546	-0.2486|-0.3091
Depth to bedrock (up to 200 cm)	-0.5974|-0.6531	-0.0481|-0.051	0.1857|0.2308
Soil organic carbon stock	0.5542|0.6058	0.2129|0.2256	-0.3193|-0.3969
pH index (H2O solution)	**0.6729|0.7356**	-0.0265|-0.0281	0.3793|0.4715
Dispersal barrier	0.4041|0.4417	**0.7736|0.8201**	0.1299|0.1615

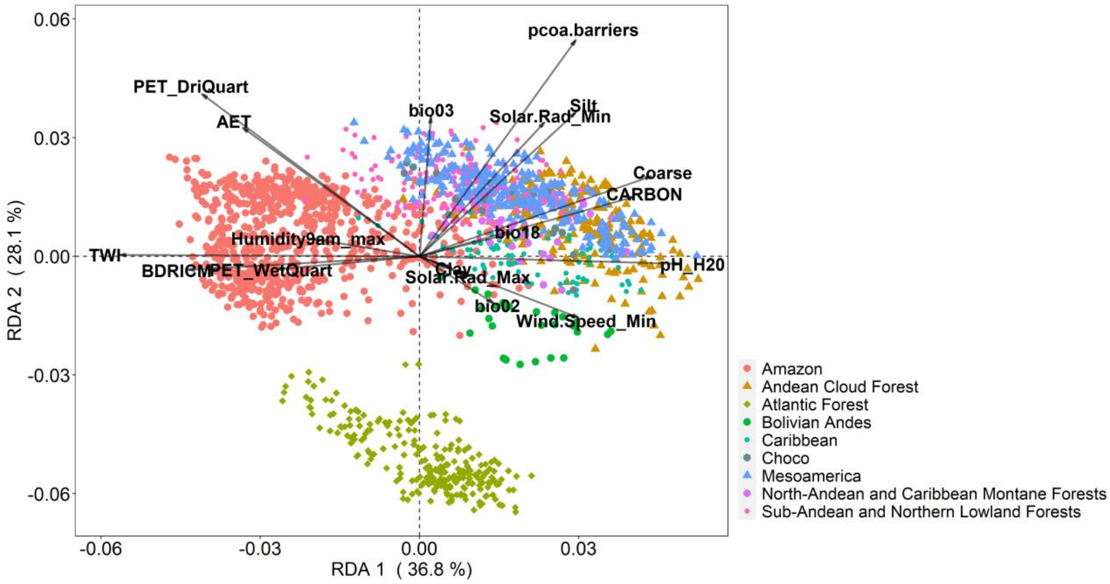

FIGURE 3 Diagram resulting from the Canonical Redundancy Analysis of tree species composition and environmental and dispersal barrier variables of 1,843 sites of Neotropical Non-Flooded Evergreen Forests. Axes 1 and 2 are shown.

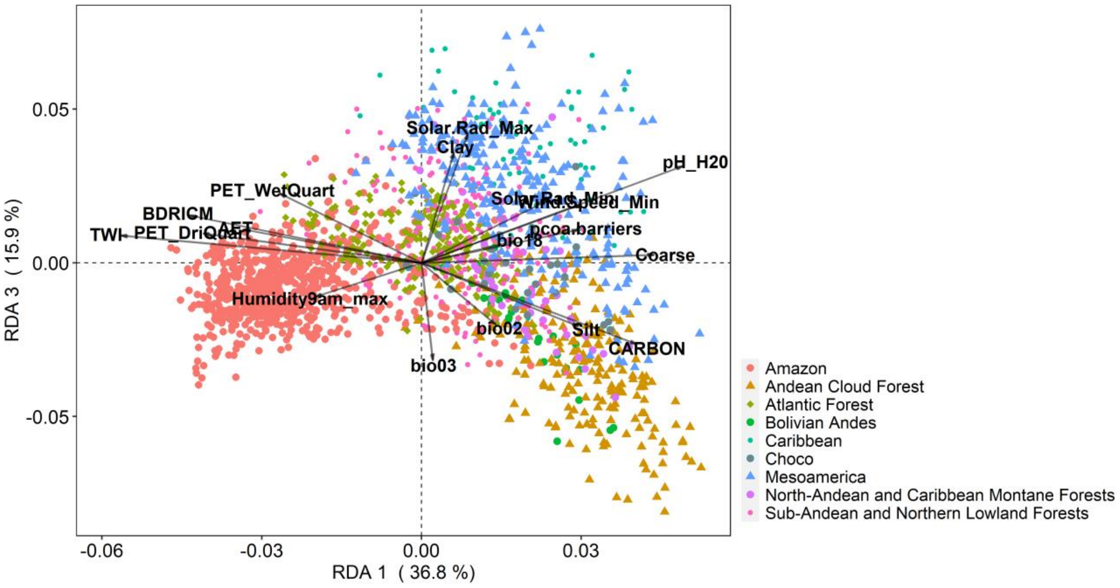

FIGURE 4 Diagram resulting from the Canonical Redundancy Analysis of tree species composition and environmental and dispersal barrier variables of 1,843 sites of Neotropical Non-Flooded Evergreen Forests. Axes 1 and 3 are shown.

We found high correlation values between species composition (denoted by RDA scores) and predictors, especially when we examined the model composed of both environmental and barrier variables. Here, there was a 91.48% correlation on the first axis of the RDA, 93.33% on the second axis and 80.46% on the third axis (Table 04).

4 DISCUSSION

4.1 NEF blocks can be discriminated based on environmental predictors

We were able to confirm that NEF can be subdivided into broad-scale discrete groups based on tree species composition, and that such groups can be largely differentiated by environmental and dispersal barriers.

Environmental variables used in the discriminant analysis allowed the correct assignment of 88.8% sites to their respective NEF groups, which were defined *a priori* (Cupertino-Eisenlohr *et al*., 2020). Poorly discriminated NEF blocks included NACMF and SANFL, groups that include multiple geographic regions and mixed floras. Overall, the results from discriminant analysis were reinforced in the PCA on environmental data that showed statistical differences in average PCA axes scores between blocks. Despite some physiognomic similarity, environmental heterogeneity is indeed a characteristic of NEF (Stadtmüller, 1987; Rangel, 2004; Santiago-Valentin and Olmstead, 2004; Marshall, 2007; Eisenlohr and Oliveira-Filho, 2015) and an important driver of floristic variation. Among the environmental predictors considered in our analyses, topographic wetness index and edaphic predictors were the variables that most varied along the NEF and the most important to explain its floristic variation. Topographic wetness index, which is an index based on topographic variation that is highly correlated with soil moisture, proved to be important for predicting vegetation types (*e.g*., Taverna *et al*., 2005; Dobrowski *et al*., 2008), which is supported by the high predictive power of this variable in our discriminant analysis.

Several studies have pointed to the effects of topographic and edaphic variables on variation in tree species distribution within individual NEF blocks. These studies have shown that tree diversity and distribution can be determined by topographic heterogeneity in the Atlantic Forest (Eisenlohr and Oliveira-Filho, 2015); soil fertility gradients in the Amazon (Phillips *et al*., 2003; ter Steege *et al*., 2006; Bohlman *et al*., 2008; Coronado *et al*., 2009; Higgins *et al*., 2011; Pansonato *et al*., 2013); altitude and interaction between wind and topography in the Andean forest (Stadtmuller, 1987; Killeen *et al*., 2007); geomorphology and soil fertility in the Choco (Gentry, 1986; Faber-Langendoen and Gentry, 1991; Mosquera and Hurtado, 2014; Copete *et al*., 2019);

topographic heterogeneity, geological gradients, and soil texture in Mesoamerica (Pyke *et al*., 2001; Sesnie *et al*., 2009; Chain-Guadarrama *et al*., 2012; Morera-Beita *et al*., 2019); and geology, soil type and altitudinal variation in the Caribbean (Graham, 2003; Santiago-Valentin and Olmstead, 2004; Maunder *et al*., 2008; Ortiz *et al*., 2019).

4.2 Edaphic and topographic variables predict the main floristic gradient of NEF

For the whole extension of NEF, we would expect a major contribution of bioclimatic variables to explain the primary gradients of floristic variation. However, this was not confirmed by our analyses, since edaphic and topographic variables were the most important predictors. Only in the secondary gradients, bioclimatic variables, along with dispersal barriers, appeared as relevant predictors. Bioclimatic variables are more important than edaphic variables to distinguish multiple biogeographic units and biomes at continental scales. Because our analysis is restricted to sites belonging to a single vegetation type (NEF) with similar environmental requirements, climatic variables tended to have a lower power in explaining variation in tree species composition.

Although there is an important sharing of species (Cupertino-Eisenlohr *et al*., 2020) and contribution of plant lineages (Antonelli *et al*., 2018) between the Amazon and other Neotropical regions, the separation of Amazon from other NEF groups was evidenced in the main trend of our model (axis 1 of the RDA). This separation was mainly explained by, once again, topographic wetness index and soil pH. Topographic wetness index quantifies how soil moisture is affected by topography (Radula *et al*., 2018), and it has been demonstrated as a strong predictor for vegetation variation along environmental gradients (Kopecký and Čížková, 2010), in addition to identifying areas with high species richness and rarity of vascular plants (Zinko *et al*., 2005). Amazon presented the highest topographic wetness index values in relation to other NEF groups, a fact that can be explained by a combination of high humidity and flat relief. We also found that the sites with lowest pH values are located in the Amazon. Amazon soils are generally known to be weathered, nutrient-poor and acidic (Laurance *et al*., 1999), showing little pH variation (Myster *et al*., 2017 and references therein). This characteristic seems to be important to distinguish Amazon from other NEF blocks. In fact, it has been shown that the distribution of plant species in the Amazon is strongly affected by edaphic characteristics (Gentry, 1988; Tuomisto and Poulsen, 1996; Figueiredo *et al*., 2018). The correlation we found between the effects of topographic wetness index and pH on vegetation is expected, since it has been shown that the proportion of species inhabiting soils with lower pH would increase with increasing topographic wetness index (Zinko *et al*., 2005).

As a main trend of our model, we also registered a gradient of species turnover from the Amazon lowland to the Andean Cloud Forest, which is a typical altitudinal pattern recorded in moist tropical forests (Gentry, 1988; Corlett and Primack, 2011). However, along this floristic gradient, we found little separation between other floristic groups, indicating some degree of overlap. This suggests that although the extremes of the Amazon-Andes gradient allow the ecological distinction between lowland and mountain NEF, this variation does not seem capable of separating other NEF groups located along this gradient, unlike the floristic variation *per se*, which allowed differentiating floristic groups (Cupertino-Eisenlohr *et al*., 2020). Situated at the extreme of the floristic gradient in the PCoA, Andean Cloud Forest sites also appeared as well differentiated in terms of environmental characteristics, particularly those associated to soil parameters such as high carbon, silt content and coarse fragments, as well as lower solar radiation (Figs. 2, 4). Reduced solar radiation in cloudy environments is considered an important factor in structuring the vegetation in cloud forests (Grubb, 1977). In addition, with the increase in altitude, a decrease in the proportion of clay in the soil is also expected (Wilcke *et al*., 2008).

4.3 Dispersal barriers also predict floristic variation throughout NEF

The Atlantic Forest separated from other NEF groups in a secondary trend (axis 2 of the RDA). This separation was mainly influenced by dispersal barriers. Considering geographic barriers, one should note that the Atlantic Forest is one of the most isolated blocks of the NEF, since the formation of the so called South America dry diagonal currently occupied by seasonally dry biomes (Chaco-Cerrado-Caatinga) during the Neogene (ca. 23 Ma) has culminated in the separation of Atlantic Forest from other blocks of humid forest in the Neotropics (Prado and Gibbs, 1993). Despite the establishment of several putative connections between the Amazon and Atlantic Forests during the Pleistocene (ca. 1.8 Ma) (Ledo and Colli, 2017), such past contacts did not result in substantial migration and floristic interchange between these blocks.

To account for differential dispersal limitation across the study area, we implemented a weighted matrix in the study area that incorporated different barriers for dispersal between NEF sites. Surprisingly, dispersal barriers do not seem to have prevented floristic exchanges between most NEF groups, except in the aforementioned Atlantic Forest. We expected that the high elevations of the Andes (an altitudinal barrier between the Amazon and Mesoamerica) and the sea (isolating sites in the Caribbean) would have played a more prominent role in explaining variation in tree species composition. Contrary to our expectations, such barriers did not represent major obstacles for plant dispersal between NEF blocks. Our analyses suggest that in most cases the effects of dispersal limitation were overshadowed by the influence environmental variables on species composition. In fact, the fraction of variation explained by dispersal barriers alone (3.7%) was much lower compared to the influence of the environment (54.1%).

4.4 Conclusions

We found a clear distinction between the Amazon, Atlantic Forest, and to a lesser degree the Andean Cloud Forest from other NEF groups, which highlights the floristic and environmental uniqueness of these blocks. Biotic and environmental differentiation of Amazon and Atlantic Forest has been evidenced in recent studies (Sobral-Souza *et al*., 2015; Miranda *et al*., 2018; Ledo and Colli, 2017). We also found relevant contribution of soil variables and dispersal barriers to floristic differentiation of NEF groups, which was not reported by most studies. Overall, the occurrence of NEF seems to be associated with a relatively broad environmental envelope, since climate, topography and soils showed significant variation along its range. Variation in tree species composition is largely influenced by environmental predictors, mainly topographic wetness index and pH, as well as dispersal barriers. Our results, which were based on comprehensive analyses that included a large number of explanatory variables, represent an improvement compared to the environmental associations showed in the preliminary assessment of NEF. Finally, we emphasize that the distinction of floristic groups throughout NEF points to the diversity of tree species that this forest holds, and the environmental variation indicates that the occurrence of this diversity is structured by several factors. The occurrence of relatively restricted edaphic and topographic niches throughout the NEF indicates that habitats of a certain floristic group (e.g., Amazon) do not replace the conditions of any of the others. Thus, conservation strategies should not be generalized for the entire NEF. Therefore, it is likely that the forecasted changes in global climate will affect each NEF blocks differently, with more severe impacts on regions that hold biotas more sensitive to increasing temperatures such as the Andean Cloud Forest and Bolivian Andes.

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SUPPLEMENTARY MATERIAL

APPENDIX S1 Reduction of the dimensionality of the floristic matrix through Principal Coordinate Analysis and selection of significant axes according to the Broken Stick null model.

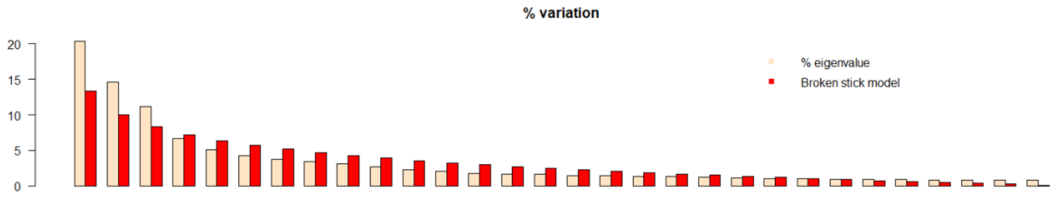


Figure 01: Significant axes of Principal Coordinate Analysis based on the Broken Stick null model.

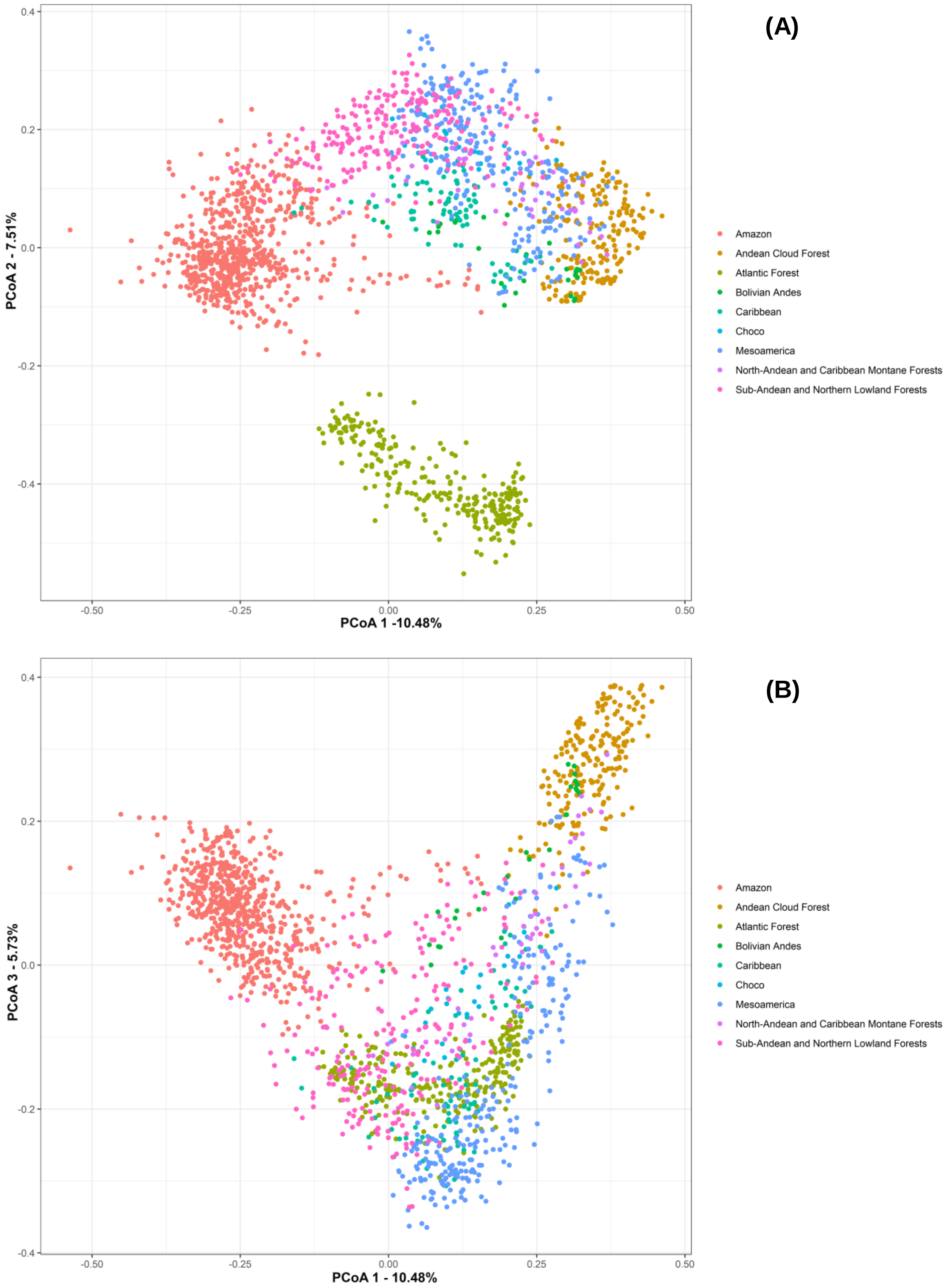


Figure 02: Significant axes of Principal Coordinate Analysis based on the Broken Stick null model.

APPENDIX S2 Environmental variables obtained for 1,843 sites of the Neotropical Non-Flooded Evergreen Forests.

Environmental variables	Code	Source
Bioclimatic variables		
Annual Mean Temperature	bio 01	CHELSA (KARGER et al., 2017)
Mean Diurnal Temperature Range	bio 02	CHELSA (KARGER et al., 2017)
Isothermality	bio 03	CHELSA (KARGER et al., 2017)
Temperature Seasonality	bio 04	CHELSA (KARGER et al., 2017)
Max Temperature of Warmest Month	bio 05	CHELSA (KARGER et al., 2017)
Min Temperature of Coldest Month	bio 06	CHELSA (KARGER et al., 2017)
Temperature Annual Range	bio 07	CHELSA (KARGER et al., 2017)
Mean Temperature of Wettest Quarter	bio 08	CHELSA (KARGER et al., 2017)
Mean Temperature of Driest Quarter	bio 09	CHELSA (KARGER et al., 2017)
Mean Temperature of Warmest Quarter	bio 10	CHELSA (KARGER et al., 2017)
Mean Temperature of Coldest Quarter	bio 11	CHELSA (KARGER et al., 2017)
Annual Precipitation	bio 12	CHELSA (KARGER et al., 2017)
Precipitation of Wettest Month	bio 13	CHELSA (KARGER et al., 2017)
Precipitation of Driest Month	bio 14	CHELSA (KARGER et al., 2017)
Precipitation Seasonality	bio 15	CHELSA (KARGER et al., 2017)
Precipitation of Wettest Quarter	bio 16	CHELSA (KARGER et al., 2017)
Precipitation of Driest Quarter	bio 17	CHELSA (KARGER et al., 2017)
Precipitation of Warmest Quarter	bio 18	CHELSA (KARGER et al., 2017)
Precipitation of Coldest Quarter	bio 19	CHELSA (KARGER et al., 2017)
Solar radiation (mean)	Solar.Rad_Mean	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)

Environmental variables	Code	Source
Solar radiation (max)	Solar.Rad_Max	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Solar radiation (min)	Solar.Rad_Min	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Water vapor pressure (mean)	Water.Vapor.Press_Mean	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Water vapor pressure (max)	Water.Vapor.Press_Max	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Water vapor pressure (min)	Water.Vapor.Press_Min	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Wind speed (mean)	Wind.Speed_Mean	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Wind speed (max)	Wind.Speed_Max	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Wind speed (min)	Wind.Speed_Min	WORLDCLIM 2.0 (FICK & HIJMANS, 2017)
Annual mean potential evapotranspiration	Annual.PET	Global Aridity and Pet Database (CGIAR 2006b)
Potential evapotranspiration of the coldest quarter	PET_ColdQuart	Global Aridity and Pet Database (CGIAR 2006b)
Potential evapotranspiration of the driest quarter	PET_DriQuart	Global Aridity and Pet Database (CGIAR 2006b)
Potential evapotranspiration of the warmest quarter	PET_WarmQuart	Global Aridity and Pet Database (CGIAR 2006b)
Potential evapotranspiration of the wettest quarter	PET_WetQuart	Global Aridity and Pet Database (CGIAR 2006b)
Seasonal potential evapotranspiration	PET_Seas	Global Aridity and Pet Database (CGIAR 2006b)
Aridity index	Aridity	Global Aridity and Pet Database (CGIAR 2006b)
Mean Annual Actual Evapotranspiration	AET	Global High-Resolution Soil-Water Balance (CGIAR, 2006)
Relative Humidity data for 3 pm (mean)	Humidity3pm_mean	CliMond
Relative Humidity data for 3 pm (min)	Humidity3pm_min	CliMond
Relative Humidity data for 3 pm (max)	Humidity3pm_max	CliMond
Relative Humidity data for 9 am (mean)	Humidity9am_mean	CliMond
Relative Humidity data for 9 am (max)	Humidity9am_max	CliMond

Environmental variables	Code	Source
Relative Humidity data for 9 am (min)	Humidity9am_min	CliMond
Soil variables		
Soil water stress (annual mean)	SWS_mean	Global High-Resolution Soil-Water Balance
Soil water stress (min)	SWS_min	Global High-Resolution Soil-Water Balance
Soil water stress (max)	SWS_max	Global High-Resolution Soil-Water Balance
Bulk density	BulkDensity	SOIL GRIDS (HENGL et al., 2014)
Coarse fragments	Coarse	SOIL GRIDS (HENGL et al., 2014)
Clay content	Clay	SOIL GRIDS (HENGL et al., 2014)
Sand content	Sand	SOIL GRIDS (HENGL et al., 2014)
Silt content	Silt	SOIL GRIDS (HENGL et al., 2014)
Probability of occurrence of R horizon	BDRLOG	SOIL GRIDS (HENGL et al., 2014)
Depth to bedrock (R horizon) up to 200 cm	BDRICM	SOIL GRIDS (HENGL et al., 2014)
Soil organic carbon stock	CARBON	SOIL GRIDS (HENGL et al., 2014)
pH index (H2O solution)	pH_H20	SOIL GRIDS (HENGL et al., 2014)
Cation-exchange capacity	CEC	SOIL GRIDS (HENGL et al., 2014)
Topographic variables		
Elevation	elevation	https://lpdaac.usgs.gov/products/srtmgl1v003/ (SRTM)
Global relief model	Relief	United Nations Environment Programme (UNEP, 2017)
Rockness index	Roughness	ENVIREM (TITLE & BEMMELS, 2017)
Topographic wetness index	TopoWet	ENVIREM (BEMMELS et al., 2018)

APPENDIX S3 Mean and standard deviation for 59 environmental variables used in this study presented for each of the nine groups of the Neotropical Non-Flooded Evergreen Forests. NAFMC: North-Andean and Caribbean Montane Forests; SANFL: Sub-Andean and Northern Lowland Forests.

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Elevation (m)	264.34	299.10	2207.08	718.63	507.54	473.48	567.45	402.84	567.45	402.84	498.79	361.10	767.08	708.59	1154.24	512.87	661.56	422.04
bio01 (°C)	24.73	1.61	15.33	3.59	22.13	2.93	23.39	2.50	23.39	2.50	22.53	3.99	22.08	3.66	20.87	3.02	23.20	2.27
bio02 (°C)	5.26	0.81	6.13	1.09	5.66	1.41	3.51	2.33	3.51	2.33	4.15	2.14	5.39	1.63	5.47	1.24	5.41	1.23
bio03 (BIO2/BIO7) (×100)	62.17	5.31	70.39	4.85	50.38	5.73	44.84	13.15	44.84	13.15	60.64	17.48	55.71	6.26	65.31	4.88	69.13	5.79

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
bio04 (standard deviation ×100)	619.11	263.21	387.16	197.59	1728.08	440.45	1113.23	281.16	1113.23	281.16	477.73	281.61	1154.09	682.56	506.36	112.38	448.87	189.83
bio05 (°C)	29.30	2.02	19.67	3.58	27.49	2.20	26.76	2.04	26.76	2.04	25.54	4.34	27.16	3.72	25.09	2.99	27.18	2.36
bio06 (°C)	20.72	2.06	10.87	3.99	16.24	4.40	19.74	3.79	19.74	3.79	19.29	4.05	17.24	4.50	16.78	3.39	19.26	2.70
bio07 (BIO5-BIO6)	8.59	1.86	8.80	1.89	11.24	2.59	7.02	3.21	7.02	3.21	6.38	2.64	9.92	3.55	8.31	1.67	7.92	2.05
bio08 (°C)	24.45	1.61	15.41	3.53	23.32	2.24	24.04	2.56	24.04	2.56	22.99	4.01	22.51	3.67	20.81	2.99	23.15	2.30

Floristic group	**Amazon**		**Andean Cloud Forest**		**Atlantic Forest**		**Bolivian Andes**		**Caribbean**		**Choco**		**Mesoamerica**		**NAFMC**		**SANLF**	
	MEAN	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**
bio09 (°C)																		
	24.77	1.98	15.04	3.67	20.33	4.06	22.00	2.78	22.00	2.78	22.07	3.87	21.91	4.09	20.56	3.03	22.97	2.29
bio10 (°C)																		
	25.61	1.78	15.78	3.62	24.34	2.53	24.75	2.43	24.75	2.43	23.18	4.10	23.55	3.72	21.62	3.13	23.76	2.31
bio11 (°C)																		
	23.79	1.69	14.66	3.59	19.56	3.49	21.77	2.64	21.77	2.64	21.88	3.86	20.30	3.84	20.11	2.91	22.46	2.30
bio12 (mm)																		
	2406.01	651.60	1941.79	794.29	1575.24	296.48	1724.92	450.72	1724.92	450.72	1908.33	755.39	2489.28	798.31	1313.35	360.93	2647.83	1275.13
bio13 (mm)																		
	348.83	80.81	256.21	90.54	236.22	53.17	236.33	58.53	236.33	58.53	299.98	99.20	389.99	109.77	189.29	52.51	340.29	137.04
bio14 (mm)																		
	76.35	60.65	77.71	49.60	51.53	24.85	64.53	25.40	64.53	25.40	55.47	47.11	57.66	35.72	26.88	15.56	95.28	87.47

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**
bio15 (Coefficient of Variation)	48.99	18.27	38.39	16.61	48.56	16.18	41.11	10.35	41.11	10.35	60.95	27.50	57.72	14.39	51.42	10.36	38.84	14.05
bio16 (mm)	1007.40	233.34	734.52	263.43	686.01	154.19	664.51	165.30	664.51	165.30	872.25	299.43	1107.96	314.22	546.49	147.43	977.20	398.59
bio17 (mm)	243.34	186.25	252.99	154.28	163.54	75.99	202.36	76.13	202.36	76.13	177.60	148.19	185.71	113.50	89.07	51.64	311.21	266.78
bio18 (mm)	402.18	230.37	542.66	238.80	532.06	177.34	520.46	184.27	520.46	184.27	791.24	327.09	467.44	179.94	330.49	130.21	655.50	388.45
bio19 (mm)	699.89	419.66	432.94	329.49	251.53	165.22	223.31	85.72	223.31	85.72	238.15	201.16	525.28	381.75	215.02	178.61	634.32	480.10

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**
Solar.Rad_Mean (kJ m-2 day-1)	15160.43	1413.07	15331.53	1722.63	15663.73	1618.69	18800.63	609.82	18800.63	609.82	14129.14	3409.61	18631.04	1068.94	17680.24	809.98	16473.63	1797.70
Solar.Rad_Max (kJ m-2 day-1)	17908.52	1973.40	16845.63	1719.77	19259.19	1885.18	21738.81	867.89	21738.81	867.89	15940.10	3853.11	21425.76	1279.01	19729.04	1153.54	18328.56	1919.88
Solar.Rad_Min (kJ m-2 day-1)	12883.49	1185.70	13939.02	1844.70	11672.01	1235.20	14412.46	917.58	14412.46	917.58	12241.89	2640.43	15368.51	1520.37	15640.57	548.25	14817.77	1825.94
Water.Vapor.Press_Mean (kPa)	2.66	0.23	1.50	0.34	2.07	0.38	2.18	0.34	2.18	0.34	2.36	0.42	2.21	0.46	1.94	0.29	2.37	0.31

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Water.Vapor.Press_Max (kPa)	2.80	0.20	1.58	0.35	2.38	0.30	2.40	0.36	2.40	0.36	2.50	0.44	2.43	0.48	2.11	0.31	2.48	0.31
Water.Vapor.Press_Min (kPa)	2.47	0.30	1.41	0.33	1.72	0.45	1.91	0.32	1.91	0.32	2.23	0.41	1.95	0.47	1.72	0.26	2.23	0.32
Wind.Speed_Mean (m s-1)	1.33	0.43	1.74	0.81	2.07	0.36	3.13	0.84	3.13	0.84	2.18	1.09	2.35	0.55	2.47	0.58	1.48	0.76
Wind.Speed_Max (m s-1)	1.60	0.57	2.07	1.02	2.49	0.42	3.62	0.99	3.62	0.99	2.46	1.29	3.02	0.76	2.86	0.71	1.77	0.91

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**
Wind.Speed_Min (m s-1)	1.10	0.34	1.49	0.66	1.69	0.33	2.57	0.63	2.57	0.63	1.89	0.84	1.79	0.40	2.10	0.46	1.25	0.61
Relief (m)	269.42	300.32	2210.22	698.91	519.72	468.41	571.58	399.61	571.58	399.61	515.82	376.37	780.74	695.92	1163.20	503.37	691.18	427.59
Roughness (%)	22.50	31.68	151.48	44.77	54.89	41.34	87.42	37.33	87.42	37.33	73.92	42.48	81.49	51.59	145.80	49.44	88.37	52.24
TWI (%)	11.61	1.36	7.89	0.56	10.07	1.42	8.79	1.01	8.79	1.01	9.11	1.91	9.24	1.56	7.93	0.68	9.22	1.38
Annual.PET (mm yr^{-1})	1690.96	99.54	1344.59	197.52	1376.55	88.84	1476.25	115.43	1476.25	115.43	1435.44	240.51	1510.28	149.66	1478.91	99.50	1610.83	113.16

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
PET_ColdQuart (mm month^{-1})	127.16	8.92	102.62	14.89	83.64	7.40	100.90	8.71	100.90	8.71	112.31	20.11	103.38	11.44	112.92	8.22	122.55	8.86
PET_DriQuart (mm month^{-1})	141.20	10.79	109.37	15.38	95.29	21.65	109.26	13.89	109.26	13.89	118.70	19.40	130.60	17.95	122.95	10.03	132.69	9.90
PET_WarmQuart (mm month^{-1})	151.78	11.24	116.79	19.41	136.72	10.01	137.09	12.51	137.09	12.51	125.68	21.00	144.12	18.13	128.01	9.73	141.68	11.13

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
PET_WetQuart (mm month^{-1})	135.37	12.50	108.09	17.64	129.06	23.88	126.44	16.85	126.44	16.85	123.80	20.06	126.32	15.57	120.40	8.70	130.14	11.85
PET_Seas (mm month^{-1})	1204.79	372.60	775.57	285.43	2469.07	370.14	1900.08	406.14	1900.08	406.14	873.06	340.70	1851.43	660.90	931.76	157.85	949.31	260.37
Aridity (Mean Annual Precipitation * Mean Annual Potential Evapotranspiration-1)	14064.98	3577.05	13418.73	5358.25	11339.02	3176.50	13237.27	4090.46	13237.27	4090.46	14304.46	4815.06	16383.39	5554.81	9099.23	2903.76	17181.73	7855.94

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**
AET (mm yr^{-1})	1429.69	172.36	1111.78	248.64	1094.36	113.81	1267.98	121.74	1267.98	121.74	1163.74	297.25	1282.49	159.19	1023.54	182.17	1435.68	210.58
SWS_mean (%)	85.22	10.91	83.65	15.99	79.90	10.48	86.61	9.71	86.61	9.71	79.09	19.85	86.24	8.38	70.03	12.39	89.16	11.54
SWS_min (%)	62.05	23.34	69.85	21.87	62.03	16.05	69.84	14.28	69.84	14.28	57.07	24.65	58.95	16.72	44.78	12.53	72.71	19.42
SWS_max (%)	99.74	1.89	94.36	10.01	94.77	9.18	96.82	6.37	96.82	6.37	94.64	18.21	99.60	1.98	88.15	12.67	97.75	7.06

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Humidity3pm_mean (%)	64.93	4.77	62.38	6.03	64.76	3.57	63.21	3.38	63.21	3.38	68.35	11.66	62.53	5.28	62.02	1.89	64.07	4.76
Humidity3pm_min (%)	58.10	6.84	58.06	7.18	60.22	5.13	59.02	2.86	59.02	2.86	65.04	11.71	55.71	6.04	56.09	3.55	59.61	5.83
Humidity3pm_max (%)	70.51	4.01	66.13	4.72	68.51	3.73	66.34	3.64	66.34	3.64	70.74	11.91	67.58	4.64	66.06	1.51	67.75	4.06
Humidity9am_mean (%)	87.08	5.31	86.14	5.41	85.49	2.01	84.29	2.73	84.29	2.73	88.46	14.99	83.91	4.79	84.08	2.17	85.81	4.44

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Humidity9am_max (%)	91.02	4.48	88.93	4.06	88.80	1.98	87.33	2.78	87.33	2.78	90.19	15.08	88.13	4.39	87.69	2.07	88.84	3.64
Humidity9am_min (%)	81.70	7.09	82.78	6.61	81.95	2.99	80.51	3.19	80.51	3.19	85.71	15.15	78.36	5.70	78.74	3.49	81.91	5.83
BulkDensity (cg/cm^3)	1304.45	64.38	1016.39	105.42	1282.53	75.21	1256.78	58.63	1256.78	58.63	1139.64	206.16	1200.37	93.33	1208.30	76.55	1213.29	95.94
Clay (g/kg)	29.39	5.31	26.71	5.41	32.02	3.59	37.04	4.26	37.04	4.26	32.64	6.66	33.36	3.47	30.92	3.50	32.98	3.31
Coarse (cm3/dm3)	3.36	3.44	10.71	4.14	3.21	1.67	8.05	2.67	8.05	2.67	9.94	3.82	10.54	3.60	10.40	2.38	8.41	4.02

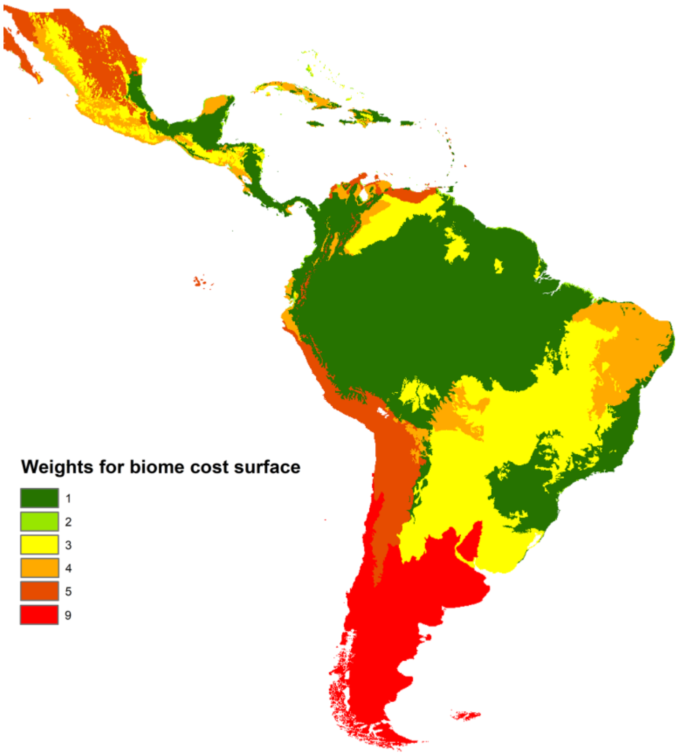
Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Sand in (g/kg)	46.40	7.09	41.10	3.25	49.49	5.15	33.89	5.50	33.89	5.50	37.15	7.59	39.48	2.55	40.02	2.97	39.94	3.14
Silt in (g/kg)	24.21	5.42	32.20	3.18	18.49	2.58	29.08	2.63	29.08	2.63	27.85	5.17	27.16	3.36	29.06	2.02	27.09	2.46
BDRLOG (%)	10.18	7.51	34.89	10.11	18.68	7.90	24.74	6.42	24.74	6.42	20.77	6.85	30.79	10.93	30.24	6.31	23.01	8.40
BDRICM (cm)	197.81	6.12	166.44	21.48	191.79	10.77	189.39	12.61	189.39	12.61	187.23	30.66	176.89	20.70	179.29	12.94	186.23	13.43
CARBON (t*ha^{-1})	34.78	17.23	75.16	17.24	35.17	9.16	44.58	12.03	44.58	12.03	56.86	17.91	47.99	19.51	47.24	12.48	48.78	15.82
pH_H20 (pH * 10)	46.82	3.51	53.92	2.25	52.63	2.10	57.04	3.88	57.04	3.88	53.98	8.96	56.46	3.96	55.83	3.20	53.38	3.15

Floristic group	Amazon		Andean Cloud Forest		Atlantic Forest		Bolivian Andes		Caribbean		Choco		Mesoamerica		NAFMC		SANLF	
	MEAN	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**	**MEAN**	**SD**
CEC (mmol(c)/kg)	12.12	4.21	32.66	8.25	13.27	2.70	29.24	4.77	29.24	4.77	26.93	7.34	28.80	7.07	21.71	4.26	22.06	5.87

APPENDIX S4 Weights for the biome and elevation cost surface rasters.

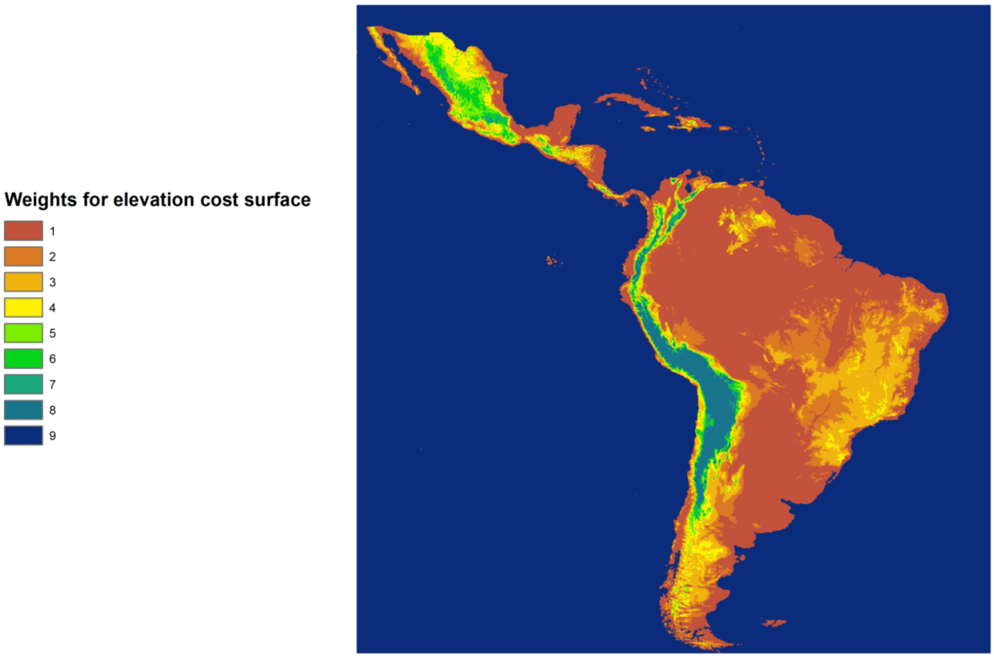
a) Weights for the cost surface raster for biomes *sensu* Olson et al. (2001).

Biomes *sensu* Olson et al. (2001)	Weights
Tropical & Subtropical Moist Broadleaf Forests	1
Mangroves	2
Tropical & Subtropical Dry Broadleaf Forests	4
Deserts & Xeric Shrublands	5
Tropical & Subtropical Grasslands, Savannas & Shrublands	3
Tropical & Subtropical Coniferous Forests	3
Mediterranean Forests, Woodlands & Scrub	9
Montane Grasslands & Shrublands	5
Flooded Grasslands & Savannas	3
Boreal Forests/Taiga	9
Temperate Grasslands, Savannas & Shrublands	9
Temperate Broadleaf & Mixed Forests	9



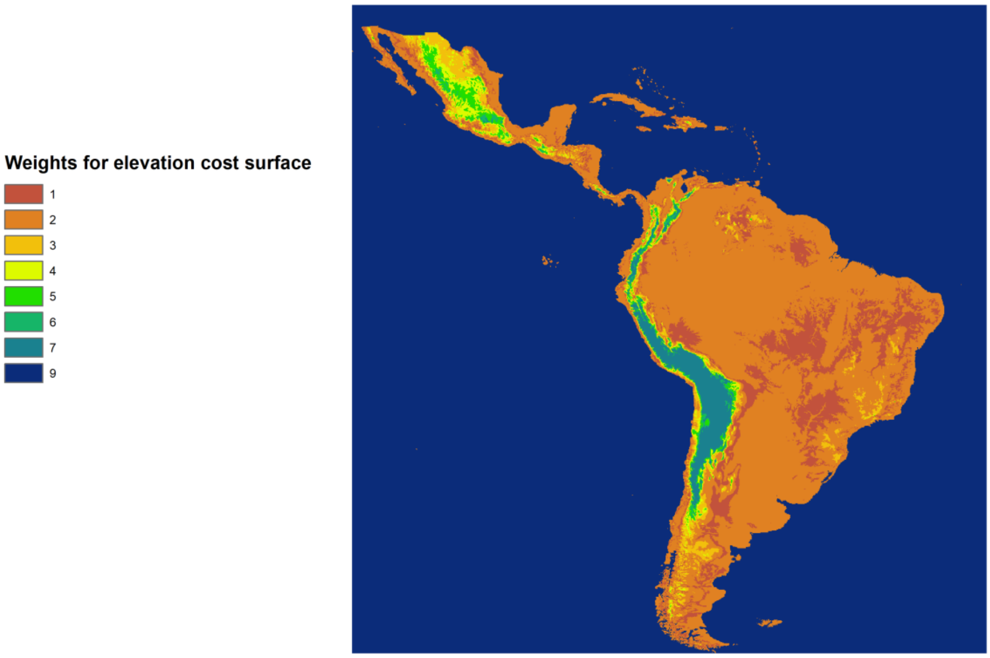
b) Weights for the elevation cost surface - Quota 1 – 0-300 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	**1**
Lower hills 301-500 m	2
Upper hills 501-1000 m	3
Lower highlands 1001-1500 m	4
Upper highlands 1501-2000 m	5
Lower montane 2001-2500 m	6
Upper montane 2501-3000 m	7
Upper Andean >3000 m	8
Ocean	9



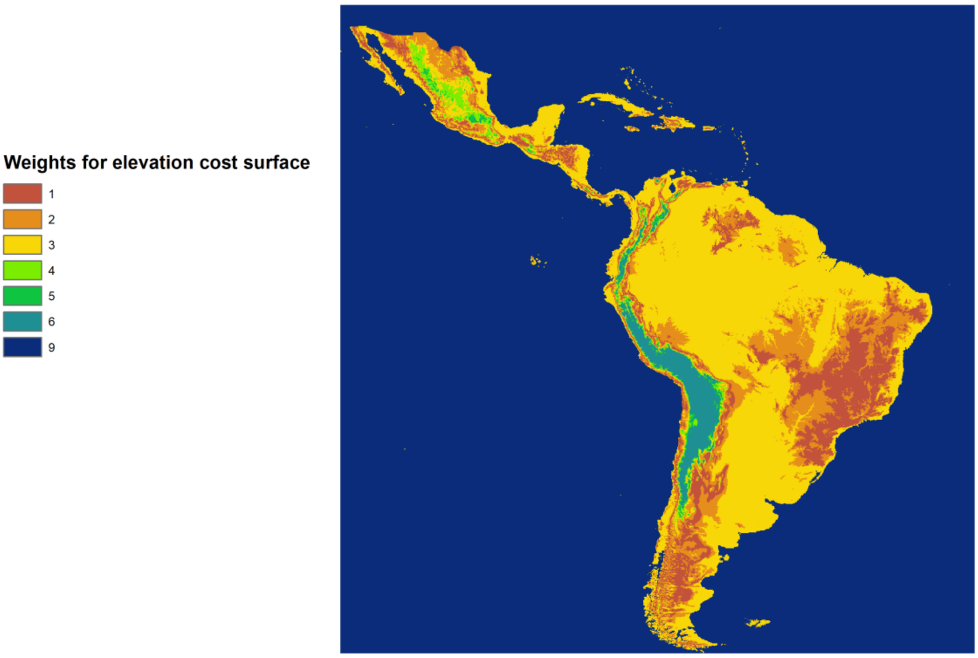
c) Weights for the elevation cost surface - Quota 2 – 301-500 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	2
Lower hills 301-500 m	**1**
Upper hills 501-1000 m	2
Lower highlands 1001-1500 m	3
Upper highlands 1501-2000 m	4
Lower montane 2001-2500 m	5
Upper montane 2501-3000 m	6
Upper Andean >3000 m	7
Ocean	9



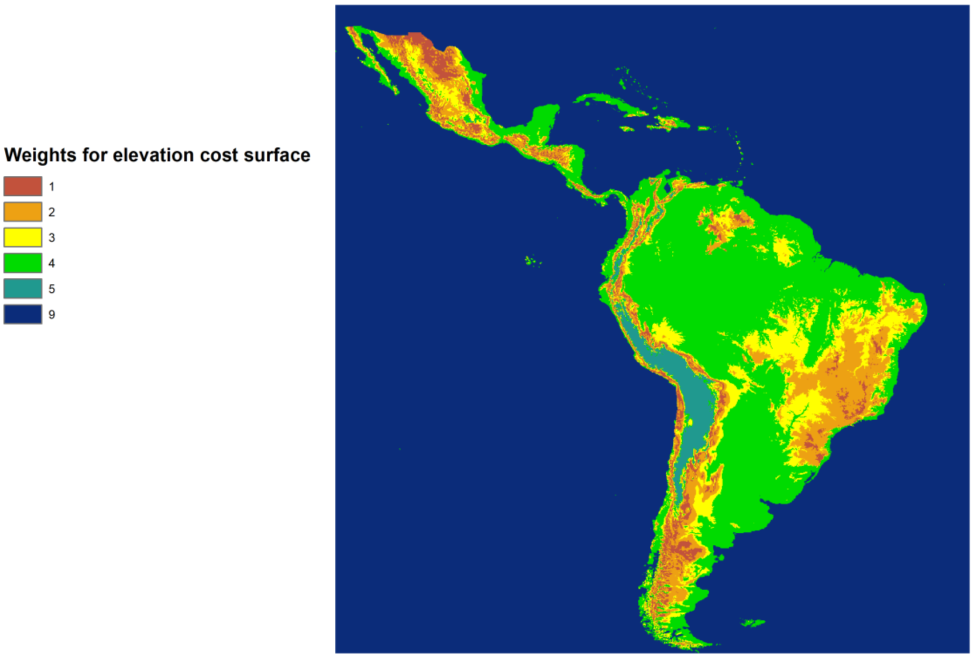
d) Weights for the elevation cost surface - Quota 3 – 501-1000 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	3
Lower hills 301-500 m	2
Upper hills 501-1000 m	**1**
Lower highlands 1001-1500 m	2
Upper highlands 1501-2000 m	3
Lower montane 2001-2500 m	4
Upper montane 2501-3000 m	5
Upper Andean >3000 m	6
Ocean	9



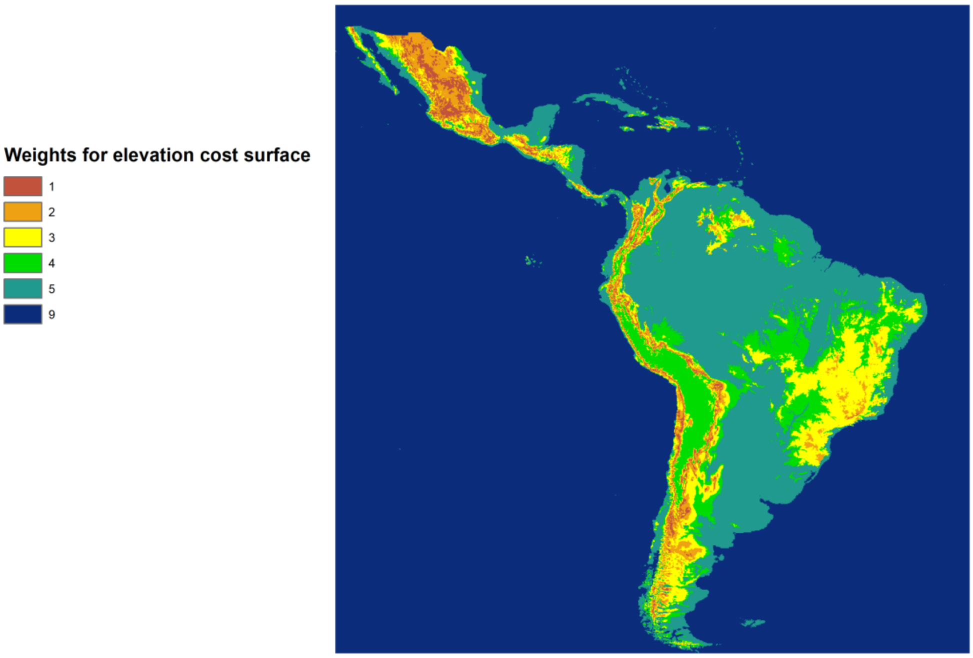
e) Weights for the elevation cost surface - Quota 4 – 1001-1500 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	4
Lower hills 301-500 m	3
Upper hills 501-1000 m	2
Lower highlands 1001-1500 m	**1**
Upper highlands 1501-2000 m	2
Lower montane 2001-2500 m	3
Upper montane 2501-3000 m	4
Upper Andean >3000 m	5
Ocean	9



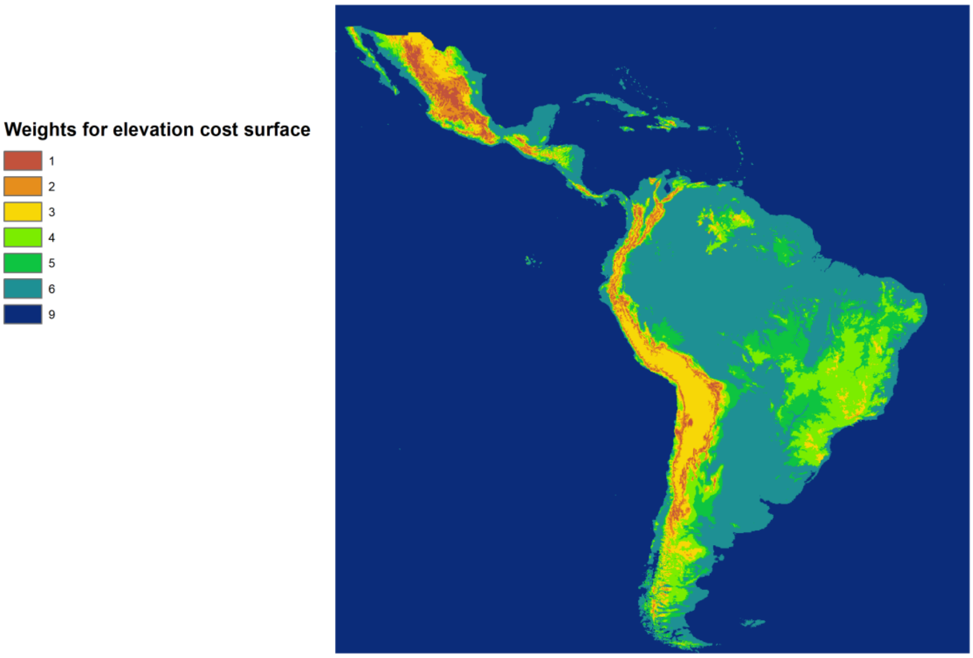
f) Weights for the elevation cost surface - Quota 5 – 1501-2000 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	5
Lower hills 301-500 m	4
Upper hills 501-1000 m	3
Lower highlands 1001-1500 m	2
Upper highlands 1501-2000 m	**1**
Lower montane 2001-2500 m	2
Upper montane 2501-3000 m	3
Upper Andean >3000 m	4
Ocean	9



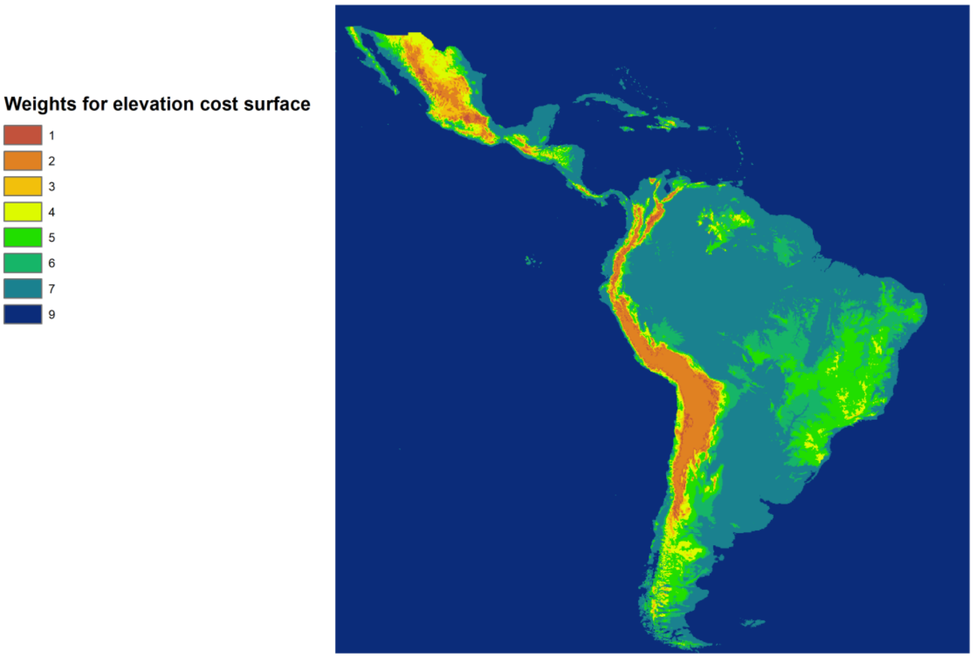
g) Weights for the elevation cost surface - Quota 6 – 2001-2500 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	6
Lower hills 301-500 m	5
Upper hills 501-1000 m	4
Lower highlands 1001-1500 m	3
Upper highlands 1501-2000 m	2
Lower montane 2001-2500 m	**1**
Upper montane 2501-3000 m	2
Upper Andean >3000 m	3
Ocean	9



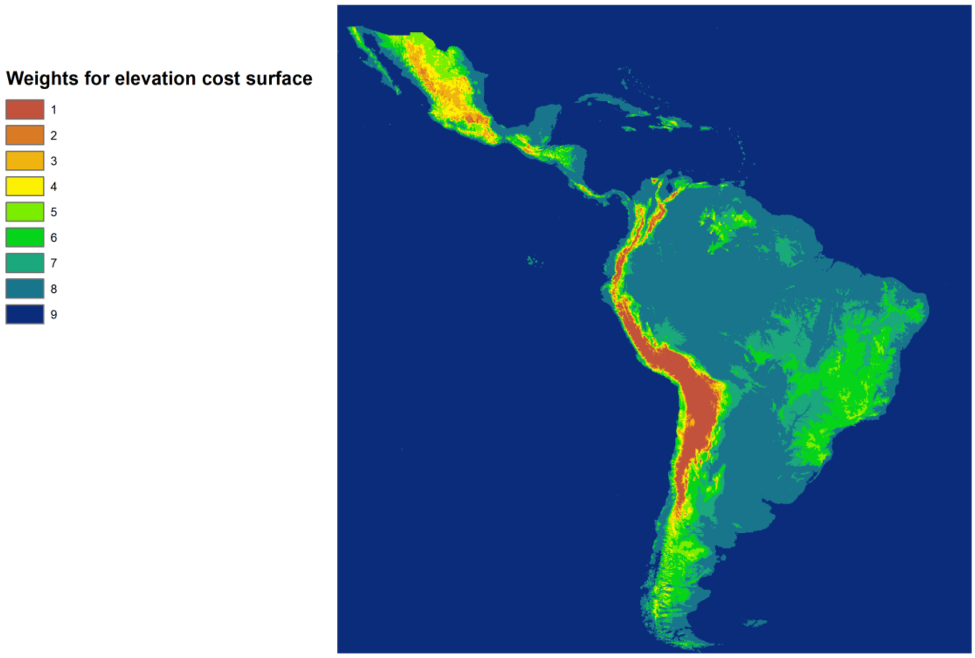
h) Weights for the elevation cost surface - Quota 7 – 2501-3000 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	7
Lower hills 301-500 m	6
Upper hills 501-1000 m	5
Lower highlands 1001-1500 m	4
Upper highlands 1501-2000 m	3
Lower montane 2001-2500 m	2
Upper montane 2501-3000 m	**1**
Upper Andean >3000 m	2
Ocean	9



i) Weights for the elevation cost surface - Quota 8 – >3000 m

Altitudinal quotas *sensu* Oliveira-Filho (2015)	Weights
Lowland 0-300 m	8
Lower hills 301-500 m	7
Upper hills 501-1000 m	6
Lower highlands 1001-1500 m	5
Upper highlands 1501-2000 m	4
Lower montane 2001-2500 m	3
Upper montane 2501-3000 m	2
Upper Andean >3000 m	**1**
Ocean	9



APPENDIX S5 Reduction of the dimensionality of the dispersal barriers matrix through Principal Coordinate Analysis and selection of significant axes according to the Broken Stick null model.

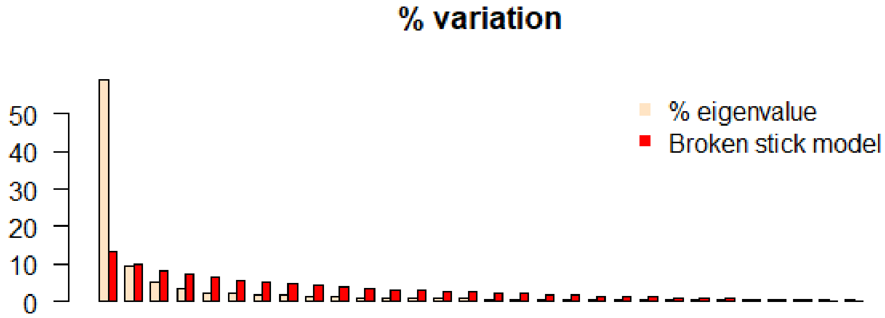


Figure 01: Significant axes of Principal Coordinate Analysis based on the Broken Stick null model.

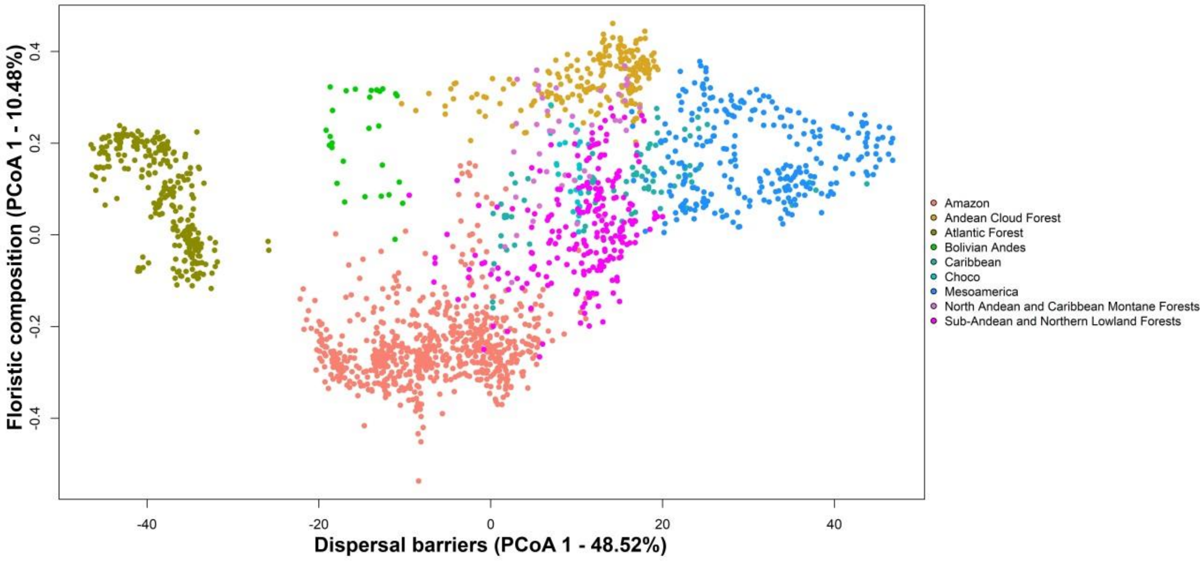


Figure 02: Correlations between dispersal barriers and floristic composition of Neotropical Non-Flooded Evergreen Forests. Both variables were reduced by means of Principal Coordinate Analysis.

APPENDIX S6 Explanation of environmental variables to Flexible Discriminant Analysis (FDA). In bold, the environmental variable with the highest fit with FDA model.

Environmental variables	**R^2**	***p***
Topographic wetness index	0.6565	0.001
Mean Diurnal Temperature Range	0.0942	0.001
Isothermality	0.6414	0.001
Precipitation of Warmest Quarter	0.0931	0.001
Solar radiation (max)	0.5503	0.001
Solar radiation (min)	0.4944	0.001
Wind speed (min)	0.4130	0.001
Potential evapotranspiration of the driest quarter	0.6542	0.001
Potential evapotranspiration of the wettest quarter	0.2153	0.001
Mean Annual Actual Evapotranspiration	0.3940	0.001
Relative Humidity data for 9 am (max)	0.1082	0.001
Clay content	0.1980	0.001
Coarse fragments	0.5829	0.001
Silt content	0.5376	0.001
Depth to bedrock (up to 200 cm)	0.4087	0.001
Soil organic carbon stock	0.4575	0.001
pH index (H2O solution)	**0.7296**	0.001

APPENDIX S7 Correlations of environmental variables with the axes of Principal Component Analysis. In bold, the two environmental variables with the highest correlation with the respective axis.

Environmental variables	**PCA1**	**PCA2**	***p***
Topographic wetness index	**-0.9823**	-0.0736	0.001
Mean Diurnal Temperature Range	0.1675	-0.1613	0.001
Isothermality	0.0261	**0.9292**	0.001
Precipitation of Warmest Quarter	0.2174	**0.8320**	0.001
Solar radiation (max)	0.2072	-0.5675	0.001
Solar radiation (min)	0.3736	0.0277	0.001
Wind speed (min)	0.7131	-0.6977	0.001
Potential evapotranspiration of the driest quarter	-0.5012	0.1640	0.001
Potential evapotranspiration of the wettest quarter	-0.6529	-0.5165	0.001
Mean Annual Actual Evapotranspiration	-0.6698	0.5754	0.001
Relative Humidity data for 9 am (max)	-0.5351	0.7613	0.001
Clay content	0.0721	**-0.9266**	0.001
Coarse fragments	**0.9070**	0.2485	0.001
Silt content	0.5761	**0.8016**	0.001
Depth to bedrock (up to 200 cm)	**-0.8527**	-0.2222	0.001
Soil organic carbon stock	0.5733	**0.8078**	0.001
pH index (H2O solution)	**0.8180**	-0.5557	0.001

CAPÍTULO III

Variation of phylogenetic diversity in Neotropical Non-Flooded Evergreen Forests

Este capítulo será submetido para a revista Journal of Biogeography.

ABSTRACT

Questions: We investigated how the variation of diversity and phylogenetic structure occurs along Neotropical Non-Flooded Evergreen Forests (NEF). We addressed the following questions: (i) what are the main NEF evolutionary groups? (ii) is the variation in phylogenetic diversity associated with NEF altitudinal gradient?

Location: Neotropical region.

Material and Methods: Based on a phylogeny of 1,085 tree genera distributed over 1,843 NEF sites, we examined the phylogenetic differentiation of these forests by means of cluster analysis (UPGMA) and ordination (evopca). We measured variation in phylogenetic diversity using the ses.PD, ses.MPD and ses.MNTD metrics and tested their response to the altitudinal gradient using linear models.

Results: Phylogenetic dissimilarity allowed differentiating NEF into 12 evolutionary groups. Considering the deepest phylogenetic relationships (ses.MPD), the NEF is structured in an overdispersed way, while the phylogenetic relationships linked to the tip of the phylogenetic tree (ses.MNTD) indicated clustering. We found greater overdispersion and phylogenetic diversity as altitude values increased.

Conclusion: The distinction of evolutionary groups throughout NEF demonstrates that multiple evolutionary and ecological processes acted in structuring these forests. We highlight the phylogenetic consistency of floristic groups previously registered for NEF, as well as the singularity of the Amazon and Atlantic Forest tree assemblages. In addition, the variation in phylogenetic diversity along NEF consistently responds to the altitudinal gradient. Finally, we reinforce that conservation strategies should consider the evolutionary history of NEF, and therefore include protected areas in all its 12 evolutionary groups; however, as mountain and nebular environments are the most susceptible to global climate changes, we suggest specific attention to these regions, aiming at the preservation of evolutionary lineages restricted to these environments.

KEYWORDS

Tree assemblages; Phylogenetic dissimilarity; Evolutionary groups; Altitudinal gradient; NeoTropTree

1 INTRODUCTION

The diversification of the Neotropical biota resulted from processes of vicariance, dispersion and ecological specialization that operate at different times and intensities (Antonelli et al., 2018a). Therefore, ecological and evolutionary processes operate together in structuring species assemblages (Wiens & Donogue, 2004; Graham & Fine, 2008). It is possible to consider both processes is possible through beta phylogenetic diversity measures, which provide an ecological-evolutionary approach to assess how the community structure changes due to spatial and environmental gradients (Chave, Chust, & Thébaud, 2007; Qian, Zhang, Sandel, & Jin, 2020). In addition, evolutionary diversity has been useful in defining biogeographic units that can capture historical processes, such as, for example, diversification, niche conservatism, dispersion and extinction, thus allowing the identification of evolutionarily unique regions (Holt et al., 2013; Daru, Holt, Lessard, Yessoufou, & Davies, 2017).

Some hypotheses have been proposed to explain the variation in phylogenetic diversity along altitudinal gradients (e.g., Latham & Ricklefs, 1993; Wiens & Graham, 2005; Jablonski, Roy, & Valentine, 2006; Qian & Ricklefs, 2016; Segovia et al., 2020). The Neotropical Non-Flooded Evergreen Forests (NEF) offers a useful model here. The NEF occurs from the south of Mexico to the south of the Brazilian Atlantic Forest, from plains of warm and humid climate to regions above 4,000 m in altitude in the Andes where pockets of forests protected from the wind occur (Cupertino-Eisenlohr, Oliveira-Filho, & Simon, 2020; Kappelle, 2004), thereby presenting wide altitudinal variation. In addition, NEF comprises one of the richest and most threatened ecosystems in the world (Wilson, 1988; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Corlett & Primack, 2011; Zachos & Habel, 2011).

In this context, the distinction of biogeographic units through phylogenetic similarity can be useful to promote effective actions for the conservation of NEF, as it allows regions with similar ecological-evolutionary histories to be target of objective and specific protective measures (Holt et al., 2013). In addition, testing whether the NEF phytogeographic groups obtained by Cupertino-Eisenlohr et al. (2020) based on the floristic composition are corroborated by data of phylogenetic diversity will provide additional evidence to understand the historical processes related to phylogenetic differentiation across the Neotropics.

In this work we investigated how the variation of diversity and phylogenetic structure occurs throughout NEF. For that, we used a phylogeny composed of 1,085 tree genera distributed over 1,843 NEF communities and tested the following hypotheses: (i) the geographical disjunction and the different diversification processes that occurred throughout the Neotropical region (Rull, 2020) may have contributed to the phylogenetic dissimilarity between the NEF blocks. Thus, we hypothesize that phylogenetic dissimilarity between NEF blocks will make it possible to differentiate this forest into evolutionary groups; (ii), Altitudinal gradients in the tropical flora allow the occurrence of phylogenetically diverse tree assemblages, where taxa typical of temperate lineages establish in Neotropical mountains (Qian & Ricklefs, 2016; Ramirez et al., 2019). Therefore, we expected that overdispersion and phylogenetic diversity would increase with elevation along NEF sites.

2 MATERIAL AND METHODS

2.1 Study area

Our study area comprised the Neotropical Non-Flooded Evergreen Forests (NEF), whose delimitation was based on the leaf renewal and flood regime (Oliveira-Filho, 2009; 2015). In the Neotropical region, the perennial leaf renewal regime occurs in the equatorial and tropical thermal domains, under the pluvial, seasonally dry and cloud climatic regimes (Oliveira-Filho, 2017). Areas included here correspond to rainforest, seasonal, montane and cloud forests – all of them with evergreen leaf renewal and non-flooded regime – that occur between latitudes 23.4 ° S and 23.4 ° W (Tropics of Cancer and Capricorn, respectively).

2.2 Database

We obtained the floristic data from the NeoTropTree (NTT) database (Oliveira-Filho, 2017). NTT comprises floristic lists of tree species (freestanding plants, at least 3 m high) compiled between 1992-2017 from herbarium data, online platforms (eg, speciesLink), tree surveys and inventories, and taxonomic monographs for the entire Neotropical region (Oliveira-Filho, 2017). NTT's floristic lists are georeferenced and organized in sites 10 km in diameter, with each NTT site being composed of a single phytophysiognomy (*sensu* Oliveira-Filho, 2015). When two or more phytophysiognomies overlap at the same site, each represents a distinct habitat. For more details about NTT, one can access http://neotroptree.info; for more details on the additional taxonomic checks carried out on the floristic data used in this manuscript, see Cupertino-Eisenlohr et al. (2020).

Our database comprised 502,963 occurrence records of 14,427 species, 1,259 genera and 163 families of angiosperms, distributed over 1,843 NEF sites. Although the NTT contains data from tree ferns and gymnosperms, we did not include these records in our study to avoid bias in the calculation of phylogenetic metrics (Kembel & Hubbell, 2006, Honorio-Coronado et al., 2015), considering the large phylogenetic distance between these groups and angiosperms, which comprise the vast majority of plants in NEF. Tree ferns and gymnosperms comprise 6,830 (1.3%) ocurrences in our dataset.

For phylogenetic analyzes, we reduced the occurrence data at the genus level, considering that DNA sequences for most of the species in our database are not available. We used a phylogenetic tree temporally calibrated at the genus level, built based on a maximum likelihood analysis of the *rbcL* and *matK* plastid regions (Segovia et al., 2020). We chose the molecular phylogeny of Segovia et al. (2020) because it is the most comprehensive and well resolved for Neotropical trees, with 1,358 genera sampled, including 1,085 (86.2%) of the angiosperm genera in our dataset (Appendix 1). In addition, our community data were converted to the occurrence of genera and, in order to standardize the community matrix with the phylogenetic matrix, we excluded from the community dataset 174 (13.8%) genera that were absent in the phylogeny of Segovia et al. (2020). In general, these absent genera were rare or with restricted distribution and comprised 7,434 (1.5%) occurrence of angiosperms in our dataset.

From the phylogenetic tree and the community matrix, we calculated the phylogenetic dissimilarity matrix based on Simpson's distance index (Balselga, 2010). This measure of dissimilarity is also called true turnover (Balselga, 2010). Here we used the *phylo.beta.pair* function of ‘betapart’ package

(Baselga, Orme, Villeger, Bortoli, & Leprieur, 2018). From the Simpson's phylogenetic dissimilarity matrix, we tested the possible differentiation of NEF into evolutionary groups through cluster analysis. We obtained clusters based on all methods available in the *hclust* function of the ‘stats’ package (R Core Team, 2020). The method selected was the Unweighted Pair Group Method with Arithmetic mean (UPGMA), as this presented the highest coefficient of cophenetic correlation (0.71). To define the number of significant evolutionary groups we used the "Elbow" method, which is based on the maximum point of curvature of a graph, where x is the number of clusters and y is the variation explained (Salvador & Chan, 2004). In this step we used the *elbow.batch* function of ‘GMD’ package (Zhao, Valen, Parker, & Sandelin, 2011). In the end, we excluded 28 outliers, of which four represented evolutionary groups with only one site and the others were isolated from the central nucleus of their geographical evolutionary group at UPGMA, thus resulting in 12 evolutionary groups.

In order to detect phylogenetic patterns along evolutionary gradients, we carried out an evolutionary principal components analysis based on the phylogenetic composition of genera from NEF communities (Pavoine, 2016; 2019). For this, we used the *evopca* function of the ‘adiv’ package (Pavoine, 2020).

Considering that the sites along NEF present great variation in genus richness (Cupertino-Eisenlohr et al., 2020), we used only metrics of phylogenetic diversity and structure that discount this richness effect (Swenson, 2014). This standardization is particularly important when considering datasets as heterogeneous as those available at NTT. Thus, we verified the variation of phylogenetic diversity throughout NEF using the standardized effect size of Phylogenetic Diversity (ses.PD). We verified the variation of phylogenetic structure based on (i) the standardized effect size of the Mean Pairwise Distance (ses.MPD), which reflects the deepest phylogenetic relationships, and (ii) the standardized effect size of the Mean Nearest Taxon Distance (ses.MNTD), which reflects the relationships closest to the ends of the phylogeny (Webb, 2000; Webb, Ackerly, McPeek, & Donoghue, 2002). The ses.MPD and ses.MNTD metrics are equivalent to the complement of the Net Relationship Index (1-NRI) and the Nearest Taxa Index (1-NTI), respectively

(Webb et al., 2002; Kembel et al., 2010). Positive values of these metrics indicate phylogenetic overdispersion, while negative values indicate phylogenetic clustering, and values that do not deviate significantly from zero indicate random assemblages of species (Webb et al., 2002; Swenson, 2014). We used unilateral t-tests for a sample to assess whether the mean values of ses.PD, ses.MPD and ses.MNTD were different from zero. For the calculation of all the metrics above we used the 'picante' package and the functions homonymous to the metrics (ses.pd, ses.mpd and ses.mntd) (Kembel et al., 2010). The null model used was taxa.labels, with 10,000 randomizations (Swenson, 2014).

From the values of phylogenetic metrics (ses.PD, ses.MPD and ses.MNTD) we processed ANOVAs with permutations to test whether they differ between the 12 evolutionary groups of NEF obtained in the UPGMA using the *IndependenceTest* function of the ‘coin’ package (Hothorn, Hornik, Van De Wiel, & Zeileis, 2008). To avoid inflation of type I error, we discounted the effects of spatial autocorrelation by including spatial filters as covariates (Peres-Neto & Legendre, 2010). We used Moran eigenvector maps (MEMs) as spatial filters and applied the *listw.candidates* and *listw.select* functions of 'adespatial' package (Dray et al., 2020). We optimized the selection of the best spatial weighted matrix (SWM) by minimizing the spatial autocorrelation in the ANOVA residuals (Bauman et al., 2018) and performed an a posteriori test with permutations based on the *pairwisePermutationMatrix* function of the 'rcompanion' package (Mangiafico, 2019). We used adjusted p-value to avoid inflation of the type I error rate due to multiple comparisons with the same dataset (Mangiafico, 2019).

Finally, to verify the variation of the ses.PD, ses.MPD and ses.MNTD metrics along the altitudinal gradient of NEF, we run linear Gaussian models (LM) using the lm function of the 'stats' package. For ses.MPD, we performed the Box-Cox transformation allowing for negative values, using the *bcnPower* function of the ‘car’ package (Fox & Weisberg, 2019), which was useful for approximating the residuals distribution to the normal curve. Instead of using the original metrics, we chose to work with the residuals after discounting the effect of spatial autocorrelation, in order to avoid inflation of type I error (Peres-Neto & Legendre, 2010). To obtain such residuals, we built MEMs from the

SWM (Bauman, Drouet, Dray, & Vleminckx, 2018) that best fitted to the respective metric. We conducted a forward selection of MEMs using the *listw.select* function of the ‘adespatial’ package (Dray et al., 2020). Then, we modeled the residuals of these LMs (metric ~ MEMs) as a function of altitude to verify how ses.PD, ses.MPD and ses.MNTD varied along the NEF altitudinal gradient. We validated the LMs using residuals distribution graphs, thereby confirming compliance with the assumptions of normality, homoscedasticity and linearity.

3 RESULTS

The phylogenetic dissimilarity analysis (UPGMA) among the 1,815 investigated sites allowed the distinction of 12 evolutionary groups along the NEF (Figure 1): Amazon, Andean Cloud Forest, Atlantic Forest, Bolivian Andes, Caribbean, Central Mesoamerican Submontane Limestone Forest (CMSLF), Guyana Shield, Northern Mesoamerican Cloud Forest (NMCF), Northern Mesoamerican Submontane and Lower Highlands Forest (NMSLHF), Northern Mesoamerican Submontane Limestone Forest (NMSLF), Southern Mesoamerican Cloud Forest (SMCF), and Sub-Andean and Mesoamerica Lowland and Montane Forest (SAMLMF). The evolutionary groups with the greatest number of sites and genera were Amazon and SAMLMF, respectively (Table 1).

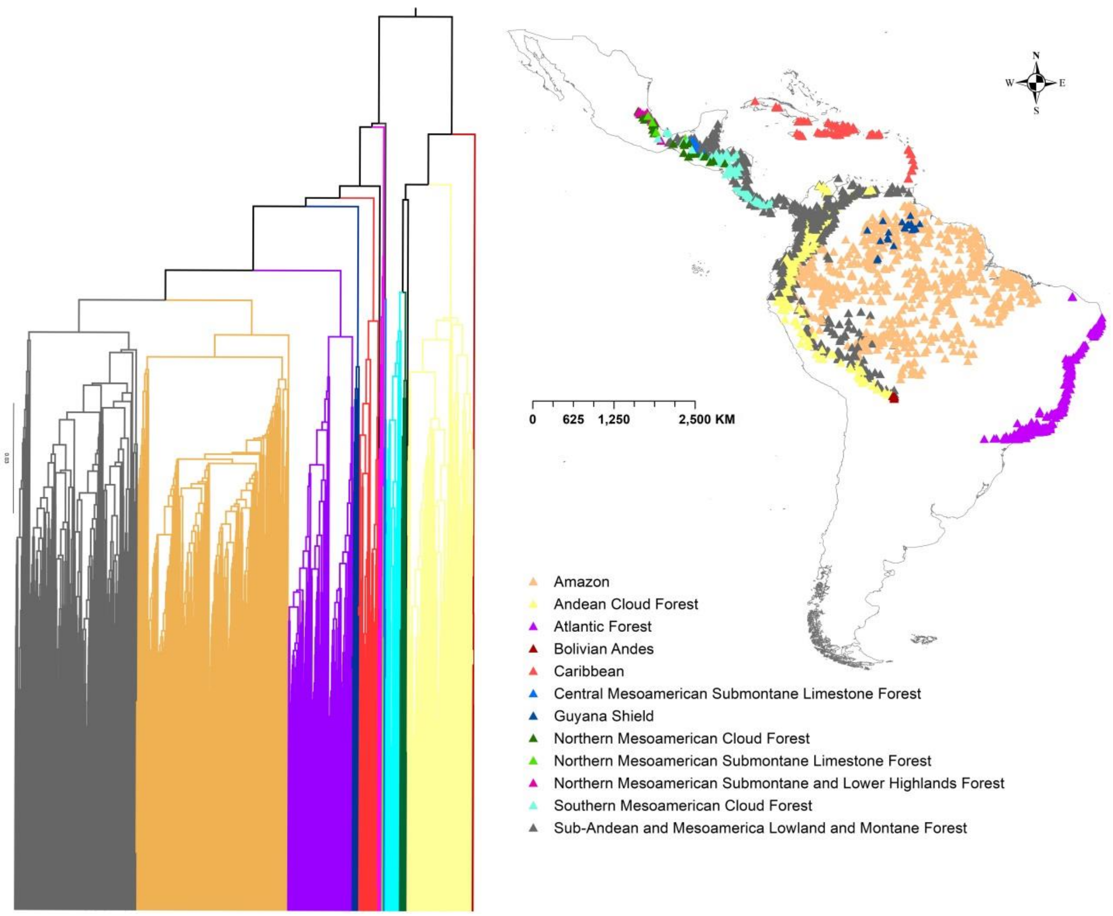


Figure 1: Evolutionary groups obtained in the UPGMA cluster analysis based on the phylogenetic dissimilarity of 1,815 Neotropical Non-Flooded Evergreen Forests tree assemblages.

Table 1: Number of sites and genera that comprises the 12 evolutionary groups obtained in the cluster analysis based on the phylogenetic dissimilarity of tree assemblages from Neotropical Non-Flooded Evergreen Forests. Mean and standard deviation (SD) of the number of genera per site are shown for each evolutionary group and for the entire NEF.

Evolutionary groups	**n° of sites**	**n° of genera**	**Mean**	**SD**
Amazon	601	737	177.0	37.4
Andean Cloud Forest	259	546	95.2	31.1
Atlantic Forest	258	532	179.7	41
Bolivian Andes	4	108	80.5	5.5
Caribbean	77	240	79.5	24.4
Central Mesoamerican Submontane Limestone Forest (CMSLF)	5	208	107.6	14.6
Guyana Shield	25	271	90.3	16.1
Northern Mesoamerican Cloud Forest (NMCF)	26	228	71.23	22.7
Northern Mesoamerican Submontane and Lower Highlands Forest (NMSLHF)	15	258	94.1	15.7
Northern Mesoamerican Submontane Limestone Forest (NMSLF)	4	181	99.2	10.6
Southern Mesoamerican Cloud Forest (SMCF)	58	322	89.8	29.0
Sub-Andean and Mesoamerica Lowland and Montane Forest (SAMLMF)	483	809	155.9	48.2
Total Neotropical Non-Flooded Evergreen Forests	1.815	1.085	145.6	52.6

The first ordination axis of the evolutionary principal components analysis explained 19.5% of the total variance of the assemblages (Figure 2). In this axis we verified the separation of Amazon from other groups and a gradient starting from Amazon to Andean Cloud Forest. The second axis explained 5.4% of the variation in the data and pointed to the separation of Atlantic Forest from other groups. Both axes indicated differentiation of Amazon from Atlantic Forest (Figure 2).

The mesoamerican cloud forests (NMCF and SMCF) and Bolivian Andes presented the highest mean values of phylogenetic diversity; in turn, Amazon, CMSLF and Atlantic Forest were the evolutionary groups with the lowest phylogenetic diversity (Table 2; Appendix 2). The pattern of phylogenetic structure prevalent in NEF varied according to the metric evaluated. According to ses.MPD, the overdispersed pattern was evidenced, whereas considering ses.MNTD the sites were, on average, more grouped than expected by chance (Table 2). In the Andean Cloud Forest and in the Mesoamerican Nebular Forest (NMCF and SMCF), the predominant pattern was overdispersion for ses.MPD and ses.MNTD; in the Atlantic Forest, CMSLF and NMSLF, the assemblages were clustered for both ses.MPD and ses.MNTD. In the other evolutionary groups, ses.MPD indicated overdispersion and ses.MNTD, clustering, except for Bolivian Andes, in which ses.MPD indicated clustering and ses.MNTD, overdispersion (Table 2).

In general, ses.PD, ses.MPD and ses.MNTD differed significantly across all NEF groups (Figure 3). Phylogenetic diversity throughout NEF was positively associated with altitude (R^2 = 5.88%; $p < 0.0001$) (Figure 4a). The phylogenetic structure along the NEF also positively associated with altitude (ses.MPD: R^2 = 0.54%; $p = 0.0010$ and ses.MNTD: R^2 = 3.72%; $p < 0.0001$) (Figure 4b and 4c).

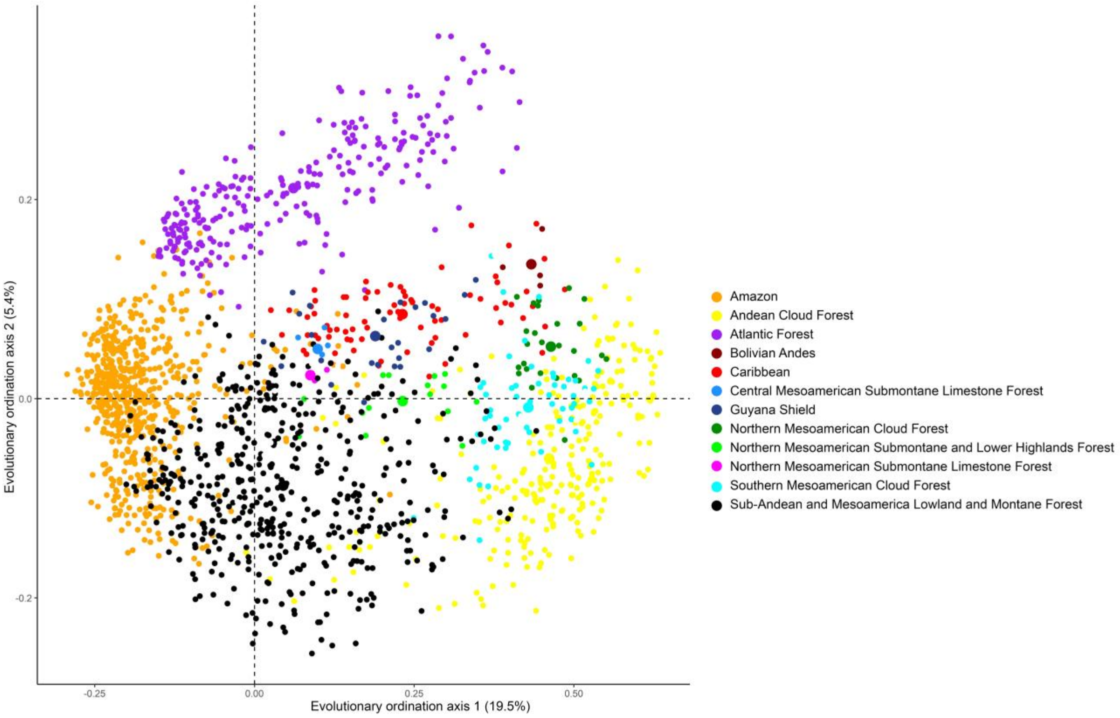


Figure 2: Axes 1 and 2 of the evolutionary principal components analysis of 1,815 tree assemblages of Neotropical Non-Flooded Evergreen Forests, demonstrating the phylogenetic affinity of the 12 evolutionary groups obtained in the cluster analysis.

Table 2: Unilateral t-tests to assess whether the mean values of ses.PD, ses.MPD and ses.MNTD for the Neotropical Non-Flooded Evergreen Forests and their 12 evolutionary groups were different from chance.

		ses.PD			**ses.MPD**			**ses.MNTD**		
Evolutionary groups	n.º of sites	Mean	SD	p-value	Mean	SD	p-value	Mean	SD	p-value
Neotropical Non-Flooded Evergreen Forests	1,815	-1.1331	1.2779	<0.0001	0.3757	1.1063	<0.0001	-0.9101	1.2011	<0.0001
Amazon	601	-1.8609	0.9296	<0.0001	0.4709	1.0339	<0.0001	-1.6637	0.8811	<0.0001
Andean Cloud Forest	259	-0.1404	1.0352	0.0150	0.8138	0.8727	<0.0001	0.1617	0.9533	0.0034
Atlantic Forest	258	-1.4615	0.9436	<0,0001	-0.3553	1.2109	0.0000	-1.1228	0.9501	<0.0001
Bolivian Andes	4	0.6922	0.2651	0.0068	-0.4739	0.3275	0.0314	1.1777	0.2373	0.0011
Caribbean	77	-0.4135	1.0175	0.0003	0.2363	0.7997	0.0057	-0.2676	1.0504	0.0142
Central Mesoamerican Submontane Limestone Forest (CMSLF)	5	-1.6978	0.4917	0.0008	-3.1105	0.7063	0.0003	-1.2424	0.3668	0.0008
Guyana Shield	25	-0.3744	0.6447	0.0039	0.8207	0.6733	<0.0001	-0.4792	0.6896	0.0010
Northern Mesoamerican Cloud Forest (NMCF)	26	1.8650	0.8988	<0.0001	0.7698	0.8055	<0.0001	1.5498	0.9402	<0.0001

		ses.PD			ses.MPD			ses.MNTD		
Evolutionary groups	n.º of sites	Mean	SD	p-value	Mean	SD	p-value	Mean	SD	p-value
Northern Mesoamerican Submontane and Lower Highlands Forest (NMSLHF)	15	0.4457	0.9445	0.0445	0.8409	0.6157	0.0001	0.3603	0.8505	0.0615
Northern Mesoamerican Submontane Limestone Forest (NMSLF)	4	-1.2211	0.6682	0.0177	-2.4316	1.1770	0.0129	-0.7650	0.5313	0.0318
Southern Mesoamerican Cloud Forest (SMCF)	58	1.3132	0.8616	<0.0001	1.4235	0.7395	<0.0001	1.0014	0.8675	<0.0001
Sub-Andean and Mesoamerica Lowland and Montane Forest (SAMLMF)	483	-1.2726	0.9985	<0.0001	0.3246	1.0515	<0.0001	-0.9861	0.9315	<0.0001

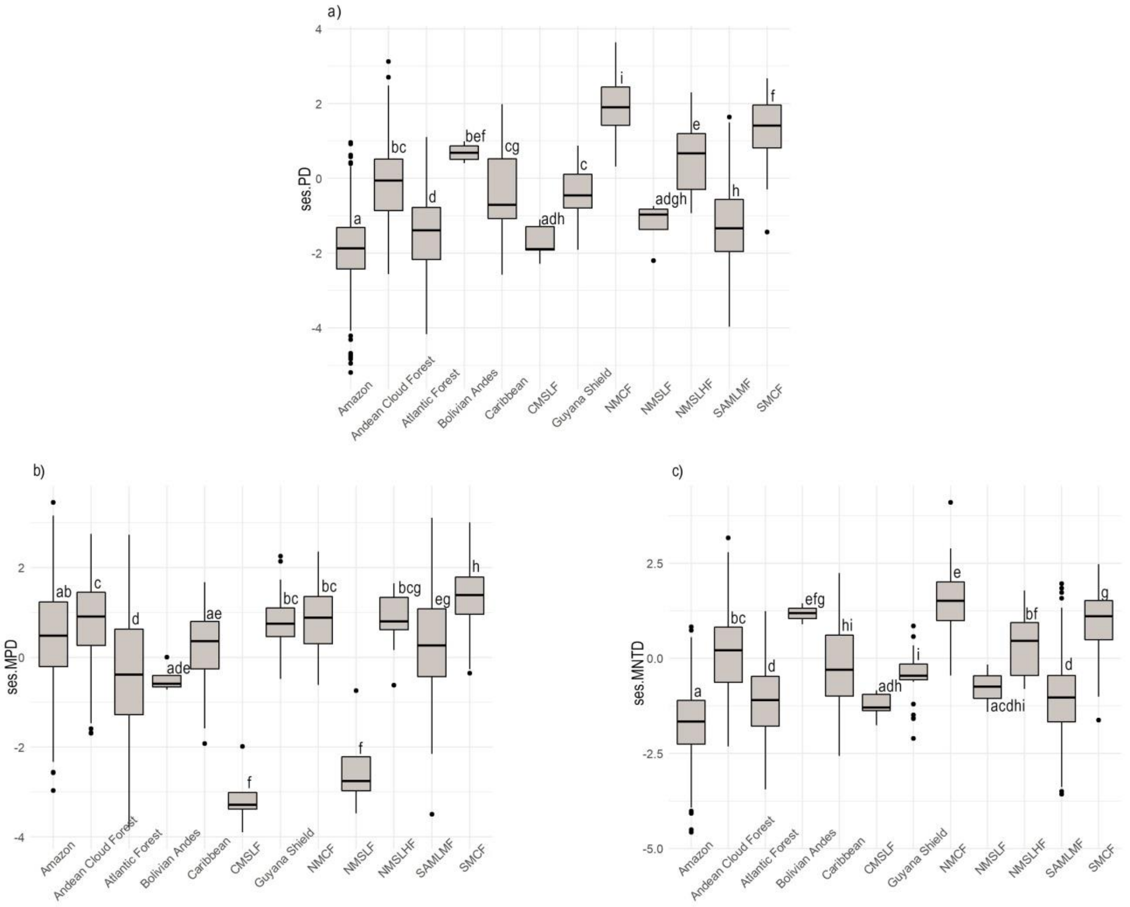


Figure 3: Mean pairwise comparisons between the 12 evolutionary groups of Neotropical Non-Flooded Evergreen Forests for ses.PD (a), ses.MPD (b) and ses.MNTD (c) phylogenetic metrics. Different letters correspond to evolutionary groups that differed from each other ($p \leq 0.05$) by the *a posteriori test* with permutations. CMSLF: Central Mesoamerican Submontane Limestone Forest; NMCF: Northern Mesoamerican Cloud Forest; NMSLF: Northern Mesoamerican Submontane Limestone Forest; NMSLHF: Northern Mesoamerican Submontane and Lower Highlands Forest; SAMLMF: Sub-Andean and Mesoamerica Lowland and Montane Forest; SMCF: Southern Mesoamerican Cloud Forest.

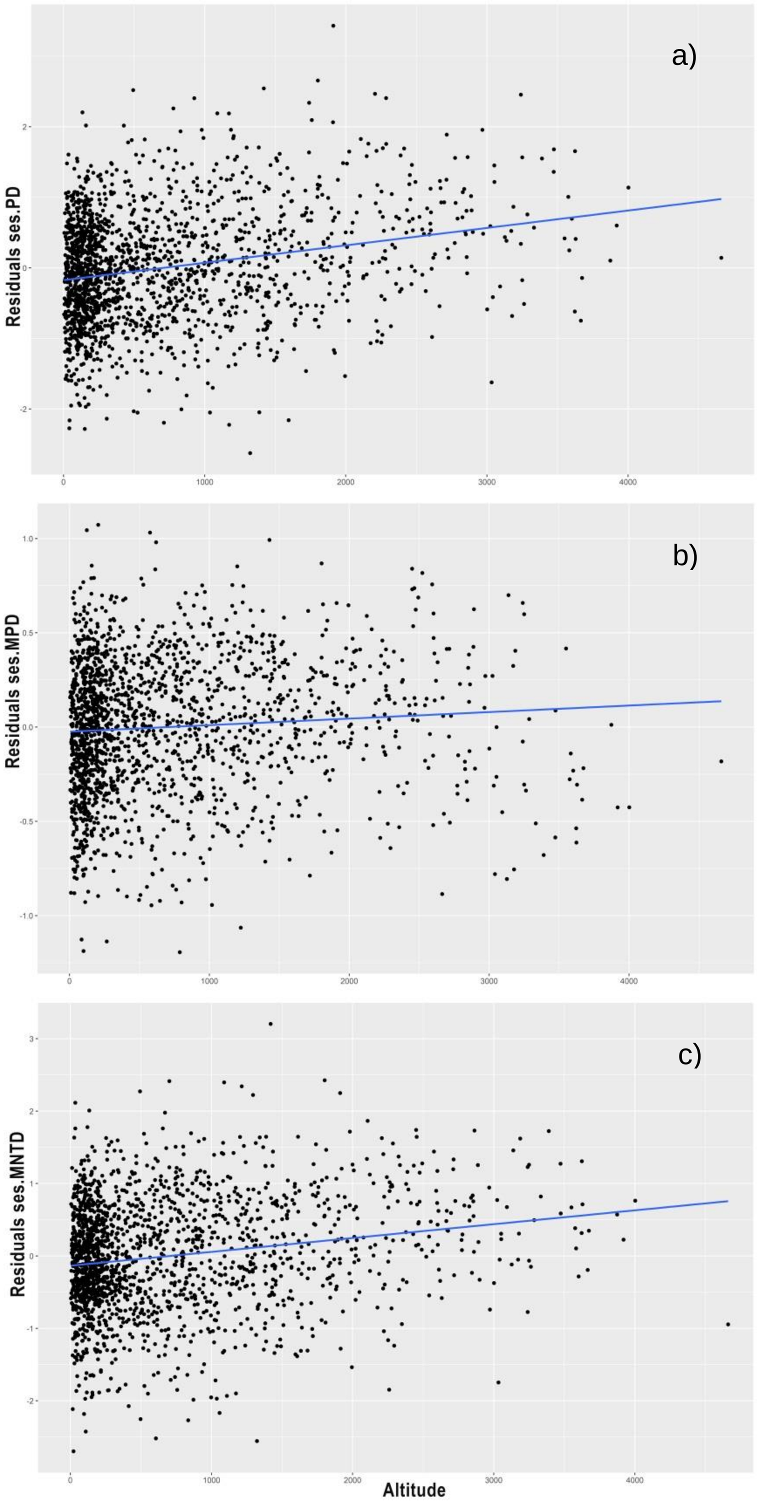


Figure 4: Fitted graph of the residuals of the Gaussian linear model of ses.PD (a), ses.MPD (b) and ses.MNTD (c) metrics for 1,815 sites of the Neotropical Non-Flooded Evergreen Forests as a function of altitude. We obtained the residuals after discounting the effect of spatial autocorrelation on the metrics above.

4 DISCUSSION

Phylogenetic dissimilarity allowed differentiation of NEF into 12 evolutionary groups, confirming our first hypothesis. Part of these evolutionary groups (Amazon, Atlantic Forest, Andean Cloud Forest, Caribbean and Bolivian Andes) corresponds to the floristic groups identified by Cupertino-Eisenlohr et al. (2020), which were based on the similarity of species composition using the same database as the present work. However, some novelties were found, among which we highlight the extensive group that connects the Amazonian flora to the Mesoamerican (SAMLMF), in addition to the differentiation of six groups in Mesoamerica, and also the Guyana Shield, which were not recovred in the analysis of Cupertino-Eisenlohr et al. (2020). Our second hypothesis was also confirmed: for all the metrics evaluated (ses.PD, ses.MPD and ses.MNTD), we found greater phylogenetic overdispersion in sites with higher altitude, although such associations were not very strong.

The large evolutionary group Sub-Andean and Mesoamerica Lowland and Montane Forest encompasses part of the Amazonian, Andean and Mesoamerican flora of lowland and montane. Thus, SAMLMF can be considered an evolutionary ecotone in NEF and its differentiation reflects the sharing of lineages and reinforces the role of floristic exchange between the Neotropical tree assemblages (Dick & Pennington, 2019). In this sense, Mesoamerica has been recognized as the region that received the most lineages within the Neotropics (Antonelli et al., 2018b). Thus, its subdivision into six evolutionary groups corroborates the view that that the Mesoamerican flora is composed mainly of South American lineages, but also by elements from various other sources through different routes and times over the Neotropical evolutionary history (Burnham & Graham, 1999 and references therein). On the other hand, the distinction of the Guyana Shield as an independent evolutionary group within the Amazon seems to be associated with the fact that it consists mainly of montane forest sites (> 1,000 m altitude). The presence of elements typical of these highland environments such as *Drimys*, *Hedyosmum*, *Symplocos* and *Weinmannia* (Pinaya et al., 2019), which are absent from lowland Amazonia, can be responsible for such differentiation.

The northern Mesoamerican cloud forest (NMCF) presented the highest values of phylogenetic diversity for the NEF and assemblages structured in an overdispersed manner. In particular, the biogeographic history of NMCF is complex in relation to the other regions of the NEF, as this forest is composed of a mixture of North American deciduous temperate tree lineages (*Arbustus, Carpinus, Cornus*, *Fagus*, *Quercus*, *Liquidambar* and *Ulmus*) and tropical lineages that are typical of lower altitudes (*Cinnamomum, Clethra, Hedyosmum, Meliosma, Oreopanax, Piper, Trema, Trichilia* and *Turpinia*) (Miranda & Sharp, 1950; Williams-Linera, 1997).

We highlight the tree phylogenetic singularity of Amazon and Atlantic Forest, which separated from other groups of the NEF in the evolutionary ordination analysis. This evidence validates again the flora idiosyncrasy of the Amazon and Atlantic NEF (Cupertino-Eisenlohr et al., 2020; Miranda et al., 2018). Factors responsible for the uniqueness of the Amazon flora are associated with the geo-hidrological and climatic history of the region, which culminated in an opportunity for high rates of *in situ* speciation and habitat specialization (Pennington & Dick, 2010). In the case of Atlantic Forest, the floristic singularity seems to be associated mainly with the complex evolutionary history that is distinguished along the northern and southern portion and with the topographic heterogeneity (Peres et al., 2020 and references therein), as well as its geographical isolation from other NEF blocks. Here, we also recorded a phylogenetic gradient from Amazon to Andean Cloud Forest, which corroborates the recognized species turnover from the Amazonian plains towards the Andes (Gentry, 1988; Corlett & Primack, 2011). We thus reinforce the non-random pattern of replacing lineages – and even complete clades - along altitudinal gradients, such as Fabaceae predominating in the plains, Lauraceae in intermediate altitudes, and Asteraceae and Rubiaceae in tropical mountainous environments (Gentry, 1988; Griffiths et al., 2020 and references therein).

Amazon, although presenting the greatest richness of genera among the NEF groups, had the lowest average value of phylogenetic diversity, which may be associated with the fact that this region is composed predominantly of lineages of regional origin and has less influence of lineages from other regions (Dexter et al., 2017; Antonelli et al., 2018b). In addition, the processes associated with the phylogenetic diversity of trees in the Amazon vary regionally (Honorio-Coronado et al., 2015). Higher values of phylogenetic diversity have been recorded in the Brazilian Plateau and Guianas, and are due to the geological history of the region and the accumulation of lineages over millions of years, while in western Amazonia the highest values of phylogenetic diversity could be explained by the environment, which is more favorable and easier to colonize (Honorio-Coronado et al. 2015). In the case of Amazon NEF, we recorded the highest values of phylogenetic diversity (ses.PD) for the Brazilian Plateau and the Guianas (Appendix S2a). However, the structure pattern varied according to the metric considered. The phylogenetic relationships associated with the oldest lineages indicated phylogenetic overdispersion and the most recent indicated clustering. These results may reflect the complex events of diversification of the Amazon flora that left a spatially structured signature in the patterns of evolutionary diversity. In this sense, Amazon flora diversification events range from the migration of lineages from other continents during the Neogen and previous periods, pre-Pleistocene speciation associated with geological processes and marine transgressions to recent radiations promoted by ecological changes related to habitat specialization (Bush, 1994; Richardson, Pennington, Pennington, & Hollingsworth, 2001; Fine, Daly, & Cameron, 2005; Pennington & Dick, 2010).

In the Atlantic Forest, our results indicated that tree genera assemblages are structured in a clustered way considering both the deepest and most recent phylogenetic divergences. The processes underlying the diversification of the Atlantic biota vary along its length (Carnaval et al., 2014; Peres et al., 2020) and are associated with several factors of climatic and geo-morphological order, such as, for example, variation in climatic stability along the northern and southern regions and topographic complexity (Carnaval et al., 2014; Peres et al., 2020). In this sense, environmental filtering seems to have an influence in structuring current Atlantic Forest tree assemblages (Oliveira-Filho & Fontes, 2000), as reflected in altitudinal gradients of phylobetadiversity (Mariano et al., 2020). In addition, the high endemism of the Atlantic Forest flora (Werneck, Sobral, Rocha, Landau, & Stehmann, 2011), as well as its isolation from other NEF blocks, may help to explain the fact that their communities tend to the greater coexistence of tree taxa.

We found greater phylogenetic overdispersion with increased altitude. An analysis restricted to the tree flora of Neotropical lowlands found that the highest values of phylogenetic tree diversity were recorded in regions of intermediate precipitation, which represent an ecotone and allow the coexistence of species adapted to both humid and seasonally dry environments (Neves et al., 2020). On the other hand, when considering the Neotropical altitudinal gradient, the coexistence of lineages of temperate and tropical climate adapted to low temperatures contributes to the fact that the highest values of phylogenetic diversity are found in mountain and nebular environments. In this sense, the mixture of lineages typical of tropical plains (Gentry, 1982a; Gentry, 1982b; Miranda & Sharp, 1950; Williams-Linera, 1997) adapted to low temperatures and temperate lineages that migrated to the tropical mountains (*Alnus*, *Drimys, Fagus*, *Juglans*, *Quercus*, *Salix*, *Ulmus*, *Viburnum* and *Weinmannia*) seems to explain the greater phylogenetic diversity in the areas with the highest elevation within NEF. In addition, the presence of restricted or predominant temperate lineages in the Mesoamerican cloud forest and absent in the Andean cloud forest, such as *Arbutus*, *Carpinus*, *Fagus*, *Liquidambar* and *Ulmus*, may help to explain the higher values of phylogenetic diversity found in Mesoamerica. Thus, extratropical niche conservatism seems to have an important contribution to the increase of lineages in higher altitude environments in the tropics. The rise of the Andes and the appearance of new environments with low temperatures opened the opportunity for extratropical lineages from both north and south migrated to equatorial latitudes (Segovia et al., 2020).

We conclude that the distinction of phylogenetic groups throughout NEF highlights multiple evolutionary and ecological processes, such as niche conservatism, migration and environmental filtering, which acted in the structuring of this forest. In addition, we show that the variation in phylogenetic diversity along NEF is associated with the altitudinal gradient. Finally, conservation strategies to preserve the evolutionary history of NEF must comprise protected areas in the different evolutionary groups recorded in this work. Considering that montane and cloud environments are more vulnerable to global climate change (Rahbek et al., 2019; Griffiths et al., 2020) special attention should be given to these regions, aiming to protect evolutionary lineages restricted to these environments.

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SUPPLEMENTARY MATERIAL

APPENDIX S1 Phylogeny of 1,085 genera of the Neotropical Non-Flooded Evergreen Forests based on Segovia et al. (2020).

((((((Magnolia:108.000001,((((((Cremastosperma:14.522321,Pseudoxandra:14.522321):5.361351,(((Tridimeris:7.306043,Stenanona:7.306043):5.326133,(Desmopsis:12.160539,Sapranthus:12.160539):0.471636):6.972296,((Diclinanona:8.401761,Mosannona:8.401761):6.805967,(Ruizodendron:12.340529,(((Oxandra:8.975123,Pseudomalmea:8.975123):0.796536,(Pseudephedranthus:5.485055,Klarobelia:5.485055):4.286604):1.70767,Ephedranthus:11.479329):0.8612):2.867199):4.396744):0.2792):1.085215,(Unonopsis:7,((Cardiopetalum:3.059102,Onychopetalum:3.059102):2.476831,Bocageopsis:5.535934):1.464066):13.968887):0.470153,Malmea:21.43904):38.848863,(((Trigynaea:22.380549,(Hornschuchia:20.009663,(Porcelia:14.648911,Cymbopetalum:14.648911):5.360752):2.370886):34.554222,((Annona:53.465085,((Duguetia:34,Fusaea:34):18.939211,Xylopia:52.939211):0.525874):0.700384,Guatteria:54.165469):2.769301):2.219797,Tetrameranthus:59.154566):1.133336):20.712097,Anaxagorea:81):27):5.15,(Compsoneura:18.187759,(Virola:17.578036,(Iryanthera:17,Osteophloeum:17):0.578036):0.609722):94.962242):18.360091,(Siparuna:112.739206,((Hernandia:83.309466,(Sparattanthelium:65,Gyrocarpus:65):18.309466):20.380534,(((Cryptocarya:36.142417,Beilschmiedia:36.142417):32.784177,(((((Cinnamomum:51.494175,(Persea:51.159365,Litsea:51.159365):0.33481):0.356165,Aiouea:51.85034):0.130014,(((Endlicheria:8.221092,Rhodostemonodaphne:8.221092):1.084923,(Pleurothyrium:6.111102,Nectandra:6.111102):3.194913):2.75745,(((Dicypellium:2.414828,((Paraia:1.697471,(Aniba:1.406845,Licaria:1.406845):0.290626):0.270912,Urbanodendron:1.968383):0.446445):0.680945,Ocotea:3.095773):8.39836,Povedadaphne:11.494132):0.569332):39.916889):8.021421,((((Mezilaurus:4.777818,Williamodendron:4.777818):0.541565,Sextonia:5.319383):35.016594,Chlorocardium:40.335977):14.547479,Anaueria:54.883456):5.118318):3.866375,Caryodaphnopsis:63.86815):5.058445):34.073404,(((Macropeplus:10.001451,Mollinedia:10.001451):2.998549,Hennecartia:13):3.126826,Macrotorus:16.126825):86.873175):0.69):9.049206):18.770885):1.972331,(Piper:132.350922,((Cinnamodendron:9.910281,Pleodendron:9.910281):115.089719,Drimys:125):7.350922):1.131501):1.027578,Hedyosmum:134.51):1.87,((((((Mauritiella:2.299349,Mauritia:2.299349):13.021584,Lepidocaryum:15.320932):48.709067,(((Ceroxylon:11.048583,(Aphandra:2.708764,Phytelephas:2.708764):8.339819):2.768011,((Socratea:7.156743,((Wettinia:5.076107,Iriartea:5.076107):0.672021,(Iriartella:5.209317,Dictyocaryum:5.209317):0.538811):1.408615):5.537652,((Synechanthus:7.759716,Roystonea:7.759716):4.00299,(((Pholidostachys:3.728356,(Welfia:3.109247,Manicaria:3.109247):0.619109):6.922243,((Geonoma:9.197864,((((Gaussia:4.809884,(Allagoptera:3.79951,Reinhardtia:3.79951):1.010374):0.749559,Asterogyne:5.559443):0.833463,Calyptronoma:6.392906):2.278849,Calyptrogyne:8.671755):0.526109):1.298841,((Bactris:8.942478,((Acrocomia:8.114604,Aiphanes:8.114604):0.324031,(Elaeis:7.127498,Astrocaryum:7.127499):1.311135):0.503843):1.038383,(((Butia:2.007866,Lytocaryum:2.007866):0.323795,Syagrus:2.33166):2.069853,((Parajubaea:2.786067,Cocos:2.786066):1.251159,Attalea:4.037225):0.364288):5.579348):0.515844):0.153894):0.953415,(Chamaedorea:10.678953,(Oenocarpus:8.039242,(Euterpe:6.649509,(Hyospathe:5.826162,Prestoea:5.826162):0.823347):1.389733):2.63971):0.925062):0.158692):0.931689):1.122199):20.798631,(((Itaya:10.58035,(Sabinaria:9.615249,(Thrinax:8.993193,(Cryosophila:7.586261,Chelyocarpus:7.586262):1.406932):0.622056):0.965101):8.639507,(Acoelorrhaphe:11.313464,(Brahea:10.115172,Colpothrinax:10.115172):1.198292):7.906393):0.505172,Sabal:19.725029):14.890195):29.414775):46.547625,(Guadua:104.04,Phenakospermum:104.04):6.537625):7.027894,((Furcraea:5.783933,Yucca:5.783933):70.110722,(Cordyline:72.569126,(Beaucarnea:34.885584,Dracaena:34.885584):37.683542):3.325528):41.710865):18.530038,((((Hyperbaena:33.532344,Abuta:33.532342):74.19405,Berberis:107.726394):13.239494,Bocconia:120.965888):9.354112,(((Ophiocaryon:60.455947,Meliosma:60.455947):67.71765,(((Euplassa:34.015657,Panopsis:34.015656):32.696585,(Roupala:66.431348,(Oreocallis:65.025325,Lomatia:65.025325):1.406023):0.280893):37.753239,Platanus:104.465481):23.708117):0.207392,((Styloceras:105.9,Buxus:105.9):19.93,((((((Maburea:95.055731,Heisteria:95.055731):12.382104,((Minquartia:104.649914,((((Jodina:21.52422,Acanthosyris:21.52422):1.300865,Cervantesia:22.825085):62.878686,Agonandra:85.70377):5.252758,(Schoepfia:79.83,Gaiadendron:79.830001):11.126528):13.693385):0.175571,(((Ptychopetalum:68.80262,Dulacia:68.802621):31.866984,(Ximenia:20.470228,Curupira:20.470228):80.199376):2.994145,(Cathedra:83.481423,(Hondurodendron:80.815689,(Chaunochiton:75.805477,Aptandra:75.805477):5.010212):2.665734):20.182327):1.161735):2.612351):1.175501,Tetrastylidium:108.613336):13.729128,((((Achatocarpus:76.306208,(Iresine:26.678071,Alternanthera:26.678071):49.628137):7.817467,((Reichenbachia:56.025346,((Bougainvillea:36.762316,(Pisonia:27.082946,(Neea:3.478665,Guapira:3.478665):23.604281):9.67937):18.256249,(Seguieria: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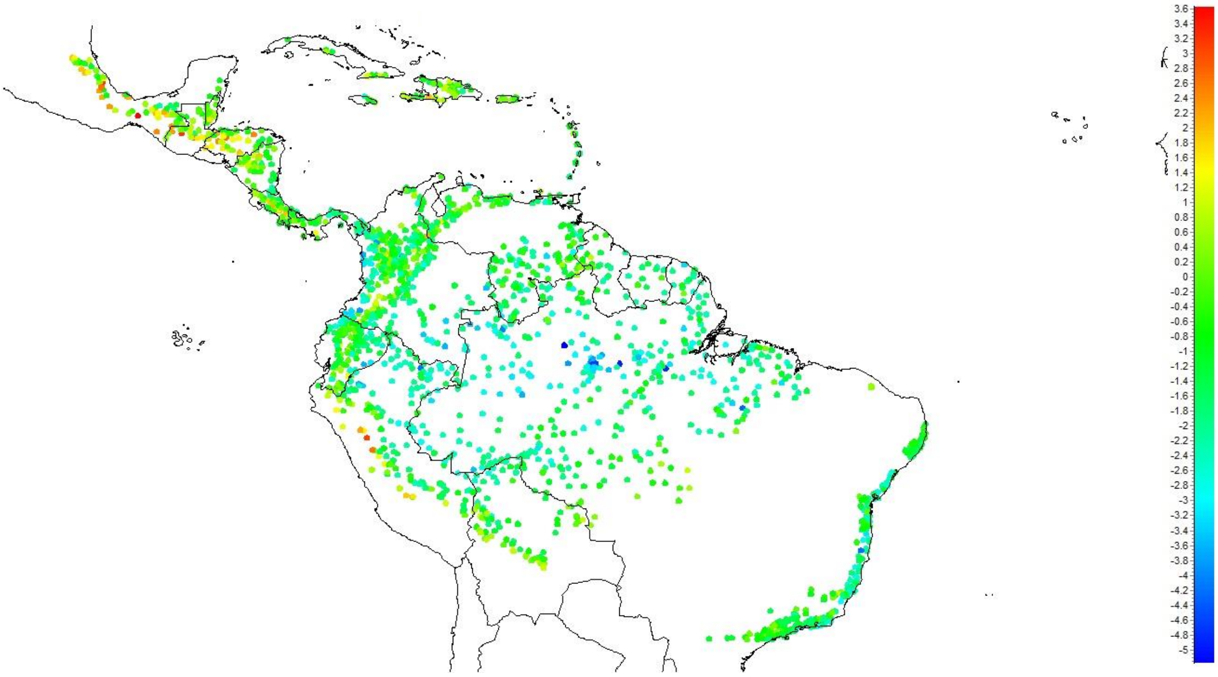
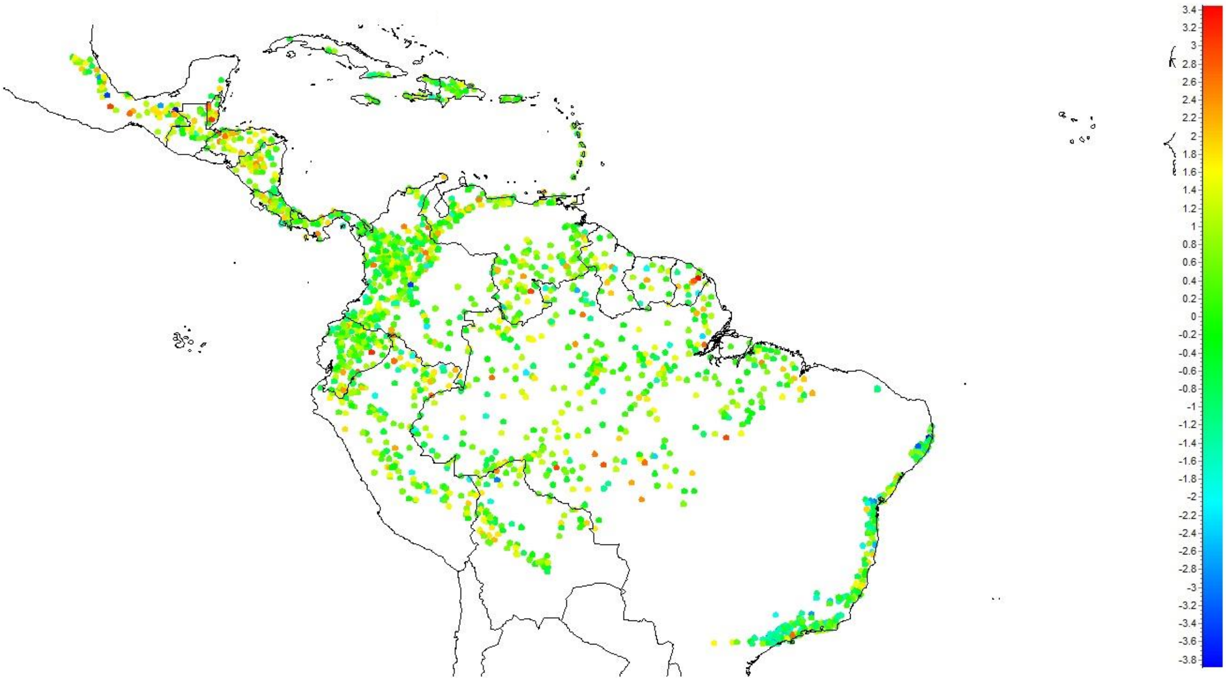
APPENDIX S2 Gradient of variation of the ses.PD (a), ses.MPD (b) and ses.MNTD (c) values for the Neotropical Non-Flooded Evergreen Forests.

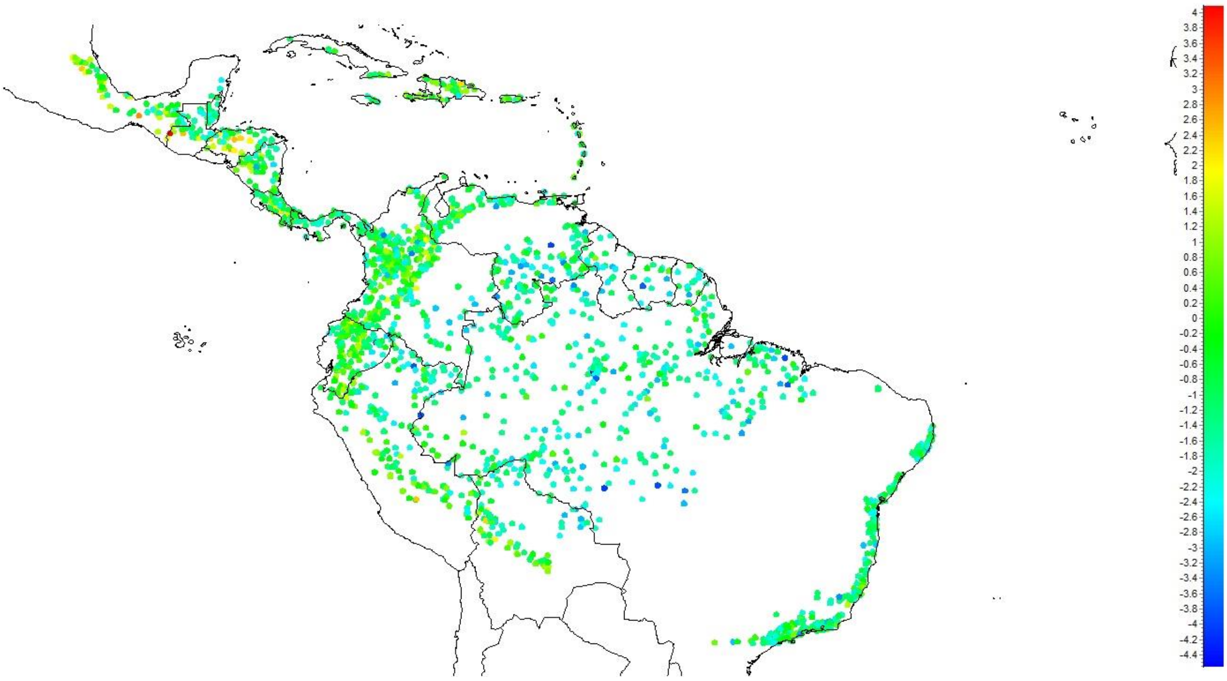
(a) ses.PD



(b) ses.MPD



(c) ses.MNTD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3.6
3.4
3.2
3
2.8
2.6
2.4
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2
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1.6
1.4
1.2
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0.4
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0
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-1.2
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-1.6
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-2
-2.2
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-4
-4.2
-4.4

CONSIDERAÇÕES FINAIS

Avançamos no entendimento dos principais padrões de composição florística e de variação da diversidade filogenética arbórea ao longo da FNP. A distinção florística registrada nos nove grupos florísticos da FNP retrata a diversidade única de espécies dessa floresta e reforça a importância da preservação de suas comunidades. A composição distinta de espécies está associada às amplas variações ambientais entre os blocos da FNP, relacionadas principalmente ao pH e índice topográfico de umidade. Além disso, as barreiras à dispersão parecem não ter impedido as trocas florísticas entre a maioria dos grupos da FNP, exceto na Floresta Atlântica. Por fim, ressaltamos que a distinção de grupos filogenéticos ao longo da FNP evidencia múltiplos processos evolutivos e ecológicos que atuaram na estruturação dessa floresta, tais como conservadorismo de nicho, dispersão, migração e filtragem ambiental. Destacamos, ainda, Amazônia e Floresta Atlântica como os blocos com maior singularidade florística e filogenética. Além disso, evidenciamos que a variação da diversidade filogenética, ao longo da FNP, responde consistentemente ao gradiente altitudinal.

Nosso estudo é pioneiro ao avaliar a variação florística e filogenética arbórea, bem como seus preditores, com base em dados secundários obtidos ao longo de toda a região Neotropical. Ressaltamos que a base de dados NeoTropTree utilizada em nosso estudo, apesar da ampla cobertura geográfica, dispõe apenas de dados de ocorrência de táxons em sítios que foram amostrados utilizando diferentes metodologias, sendo que alguns sítios carecem de melhor amostragem. Contudo, considerando as limitações dessa base de dados quando a comparamos com outros conjuntos de dados baseados em levantamentos padronizados que contemplam a abundância das espécies, nossos resultados indicam a robustez do NeoTropTree, pois registramos padrões fitogeográficos amplamente consistentes com evidências anteriores.

Esforços de amostragem de dados quantitativos de abundância de espécies se fazem necessários em toda a região Neotropical, pois somente dessa forma avançaremos no entendimento de padrões de raridade e dominância, por exemplo. É importante, de posse de dados quantitativos, revisitar os padrões evidenciados com dados de presença e ausência. Somado a isso, os padrões de diversidade e estrutura filogenética, que também são influenciados pela natureza dos dados, poderão também ser reavaliados sob a perspectiva de dados quantitativos. Também é urgente avaliar o impacto das mudanças climáticas sobre a FNP, principalmente sobre seus ambientes montanos e nebulares que são os mais vulneráveis quando consideramos o aumento da temperatura global e a alteração no padrão de distribuição de nuvens ao longo do gradiente altitudinal. Nesse sentido, avaliar a distribuição potencial de espécies indicadoras e exclusivas dos grupos florísticos da FNP sob cenários futuros pode ser útil para compreendermos os efeitos das mudanças climáticas na FNP.