

Publication status: This preprint has been published elsewhere.
DOI of the published preprint: <https://doi.org/10.1111/jbi.70054>

Blowin' in the wind: ferns and lycophytes connect biogeographic refuges in the Atlantic Forest

D. Victor Souza e Silva, Lucas Vieira Lima, Mércia Patrícia Pereira Silva, Thaís Elias Almeida,
Augusto César Pessôa Santiago

<https://doi.org/10.1590/SciELOPreprints.11710>

Submitted on: 2025-04-09

Posted on: 2025-04-17 (version 1)

(YYYY-MM-DD)

Blowin' in the wind: ferns and lycophytes connect biogeographic refuges in the Atlantic Forest

D. Victor Souza e Silva¹; Lucas Vieira Lima²; Mércia Patrícia Pereira Silva¹; Thaís Elias Almeida¹; Augusto César Pessôa Santiago³

¹Programa de Pós-graduação em Biologia Vegetal, Departamento de Botânica, Centro de Biociências, Universidade Federal de Pernambuco, Av. Professor Moraes Rego, 1235, 50.670–420, Recife, PE, Brazil

²Programa de Pós-graduação em Engenharia Florestal, Herbário Dr. Roberto Miguel Klein, Universidade Regional de Blumenau, 89030-903, Blumenau, Santa Catarina, Brasil

³ Centro Acadêmico da Vitória, Universidade Federal de Pernambuco, R. Alto do Reservatório s/n, Alto José Leal, 55608-680, Vitória de Santo Antão, PE, Brasil.

DVSS: <https://orcid.org/0009-0003-1885-6616>

LVL: <https://orcid.org/0000-0003-1517-7100>

MPPS: <https://orcid.org/0000-0002-1391-9038>

TEA: <https://orcid.org/0000-0002-1611-1333>

ACPS: <https://orcid.org/0000-0002-2330-9276>

ABSTRACT

Aim

Test the floristic structure of fern and lycophyte in the Northeastern Atlantic Forest based on sub-regions of endemism.

Location

Northeastern Atlantic Forest

Taxon

Ferns and lycophytes.

Methods

Floristic composition and environmental data were extracted from 57 remnants and PCA analyses were carried out to assess environmental structuring, NMDS to test floristic dissimilarity, and generalized dissimilarity modeling (GDM) to examine environmental effects on community distribution. Clusters were formed by K-means, and statistical analyses such as Permanova and Anosim were carried out to test the significance of the results.

Results

A total of 307 species were recorded, 93.2% of which were ferns and 6.8% lycophytes. The floristic composition showed 71.6% of species shared between the sub-regions. PCA showed significant environmental differences between montane inland wet forests and coastal forests, but NMDS did not indicate any separation in floristic composition. However, the clusters identified by K-means were highly significant ($R = 0,445$), in contrast to the groupings of the sub-regions ($R = 0,124$). GDM explained 78.8% of the distribution pattern and highlighted variables such as geographic distance, cloud cover, rainfall, silt content and soil pH as determinants of the communities.

Main Conclusions

Despite differences in environmental factors between montane inland wet forests and coastal forests, the floristic composition of ferns and lycophytes does not reflect this separation, suggesting that historical biogeography and long-distance dispersal facilitate high connectivity between these sub-regions.

Keywords: Biogeography; *Brejos de altitude*; Floristic similarity; Generalized dissimilarity modeling; Long-distance dispersal; Pleistocene.

INTRODUCTION

The Atlantic Forest is recognized as a tropical biodiversity hotspot (Myers et al., 2000) and is part of the Paraná biogeographic province. This forest extends along a large part of the Brazilian coastline, covering 17 states, and also includes remnants in Argentina and Paraguay (Morrone et al., 2022; Fundação SOS Mata Atlântica, 2023). The plant diversity of the Atlantic Forest is remarkable, with 18,103 species of terrestrial plants, 8,351 of which are endemic to this domain (Flora e Funga do Brasil, 2025). However, research across this biome is unevenly distributed, with most studies concentrated in southern and southeastern Brazil (Tabarelli et al., 2006). The Northeastern Atlantic Forest, despite containing a significant portion of the total biodiversity and representing the most anthropized area of the domain, remains underexplored, highlighting the need

for greater scientific efforts in the region (Tabarelli et al., 2005; 2006; Pôrto et al., 2006; Ribeiro et al., 2009).

The biota of the Atlantic Forest is not evenly distributed and is divided into five sub-regions based on the distribution of overlapping endemic species (Silva & Casteleti, 2003). Among these, the northern portion of the forest, referred to as the Northeastern Atlantic Forest (NAF), encompasses two sub-regions: montane inland wet forests (known in Portuguese as *Brejos Nordestinos* - BNs) and the endemism center Coastal Forests (named as Pernambuco Center - PEC) (Pôrto et al., 2006). The delineation of these sub-regions reflects the biome's geological and paleoclimatic history, alongside environmental differences such as the altitudinal variation in the BNs and the lowland forests of the PEC, which represent centers of endemism for a variety of species (Tabarelli & Santos, 2004; Pôrto et al., 2006; Tabarelli et al., 2006). Several studies have explored distribution patterns between these sub-regions for different biological groups, including angiosperms (Ferraz et al., 2004; Rodal et al., 2008), fungi (Lima et al., 2018), lichens (Santos et al., 2019), and amphibians (Castro et al., 2019). These studies have indicated that communities are structured between the sub-regions of the NAF, with BNs and the PEC showing distinct species assemblages. However, it remains unclear whether all taxonomic groups exhibit structured communities between the sub-regions. For plants, some studies suggest that lineages such as ferns and lycophytes may not exhibit community structuring between the subregions (Santiago, 2006; Silvestre et al., 2022). A key and shared characteristic of these two lineages is their reproduction through spores, which are produced in large quantities by each individual (Haufler et al., 2016). These propagules are small and possess surface ornamentation that facilitates their movement through the air, enabling ferns and lycophytes to disperse over long distances (Wolf et al., 2001; Haufler et al., 2016). This reproductive mechanism promotes the colonization of new environments and favors connections between populations (Wolf et al., 2001; Rose & Dassler, 2017).

The distribution patterns of ferns and lycophytes are closely related to environmental characteristics (Link-Pérez, 2018; Weigand et al., 2019; Suissa & Sundue, 2020). Globally, their diversity is

predominantly concentrated in tropical mountainous areas (Barrington, 1993; Tryon & Tryon, 2012; Suissa et al., 2021; Kessler & Kluge, 2022). This pattern is attributed to the high environmental heterogeneity of these environments, resulting from altitudinal variation combined with factors such as high precipitation, diverse topography, and a wide variety of soil types (Tryon, 1986; Moran, 1995; Suissa & Sundue, 2020). The concentration of diversity in mountainous regions is also linked to the historical biogeography of these areas (Tryon, 1986; Moran, 1995). These regions maintained stable vegetation and habitat diversity despite paleoclimatic events such as glaciations, which facilitated the diversification of lineages (Bigarella et al., 1975; Tryon, 1986; Kornás, 1993; Santiago et al., 2023).

Ferns and lycophytes represent an interesting model for investigating community structure due to the particularities of their reproductive biology (Barrington, 1993). Additionally, the Atlantic Forest represents one of the world's most significant centers of diversity for these lineages (Prado & Hirai, 2014). Within Brazil, the Atlantic Forest is the phytogeographic domain with the highest richness and endemism for ferns and lycophytes, comprising 943 species, 360 of which are endemic (Santiago et al., 2023). This study aims to verify whether ferns and lycophytes, which have fewer dispersal barriers due to their spore-based reproduction, exhibit community structuring between the endemism sub-regions of the Northeastern Atlantic Forest, following the pattern observed for other biological groups. We tested two alternative patterns: (1) sub-regions promote community structuring, resulting in distinct species compositions between the PEC and the BNs, as observed in other biological groups; or (2) there is no significant differentiation in composition between the sub-regions, indicating that such structuring may not occur.

MATERIALS AND METHODS

Study Area

The Northeastern Atlantic Forest, located north of the São Francisco River, represents the northernmost portion of the Atlantic Forest domain. It covers the states of Alagoas, Ceará, Paraíba,

Pernambuco, and Rio Grande do Norte (figure 1), forming the eastern portion of Northeastern Brazil (Tabarelli & Santos, 2004; Tabarelli et al., 2006). This region encompasses the lowlands of the Barreiras Formation and the Borborema Plateau, covering approximately 77,000 km² and reaching elevations over 1,200 meters above sea level (Tabarelli et al., 2006). According to the Köppen climate classification, most forest remnants of the NAF fall within the AS category, characterized by a hot and semi-humid climate (Alvares et al., 2013). However, the region also includes areas with other climate classifications (Pereira, 2009; Alvares et al., 2013). Orographic rains, particularly prevalent in the montane inland wet forests, contribute to an annual precipitation of more than 1,200 mm (Andrade-Lima, 1960; 1961). Rainfall, however, varies across the NAF: inland areas receive less than 700 mm, while coastal areas can receive up to 2,500 mm (Alvares et al., 2013). Similarly, the average annual temperature varies broadly, ranging from 20°C to over 26°C across different parts of the region (Alvares et al., 2013).

The Coastal Forests (named as Pernambuco Center - PEC) correspond to forests characterized by notable environmental heterogeneity, situated in the littoral region, north of the São Francisco River. Covering an area of 39,567 km², only 4.8% of this region remains covered by vegetation (Velooso et al., 1991; Silva & Casteleti, 2003). The PEC is considered one of the most deforested sub-regions of the Atlantic Forest and has significant gaps in knowledge regarding its biodiversity (Coimbra-Filho & Câmara, 1996; Tabarelli et al., 2002; 2005; Ribeiro et al., 2009). The montane inland wet forests (known in Portuguese as Brejos Nordestinos - BNs, also referred to as *Brejos de Altitude*), consist of humid forest remnants located at elevations above 600 m, within a matrix of seasonally dry tropical forests (Rodal et al., 1998; Pôrto et al. 2004). This sub-region spans 11,960 km², with only 19.4% of its original forest cover remaining (Silva & Casteleti, 2003).

Among the forest remnants in the NAF, 57 areas were selected (Supplementary Material 1), including 26 BNs and 31 from the PEC (Figure 1). We prioritized areas with a species richness of at least 10 species to avoid including undersampled areas and to ensure robust analyses. These areas

cover all the states within the NAF and vary widely in size, from small remnants of six hectares to large forest reserves exceeding 900,000 hectares.

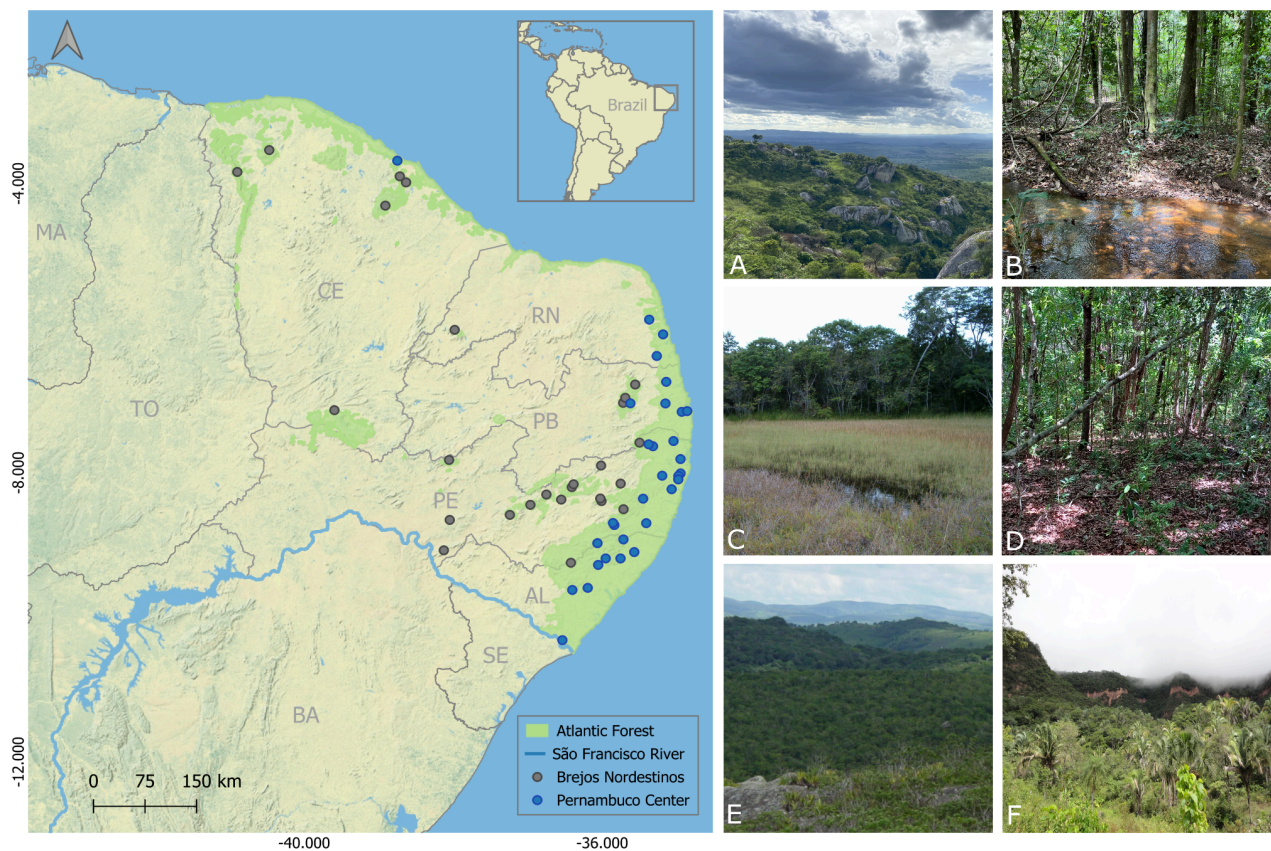


Figure 1. Study area: Northeastern Atlantic Forest with the São Francisco River delimiting the portion of the forest and dots indicating the areas analyzed, in blue the coast forests and gray the montane inland wet forests (*BNs*). A-F: NAF areas. A. Serra Negra, municipality of Bezerros, Pernambuco (PE). B. Refúgio Ecológico Charles Darwin, municipality of Igarassu, Pernambuco (PE). C. Reserva Biológica Guaribas, municipality of Mamanguape, Paraíba (PB). D. Floresta Nacional de Nísia Floresta, municipality of Nísia Floresta, Rio Grande do Norte (RN **photo: Maurício Nascimento - Photo: Maurício Nascimento**). E. Reserva Biológica de Pedra Talhada, Quebrangulo, Alagoas (AL **photo: Gilcean Jones da Silva - Photo: Gilcean Jones da Silva**). F. Floresta Nacional do Araripe-Apodi, Crato, Ceará (CE).

Collection and processing of data

The composition of the fern and lycophyte communities in the selected areas was compiled from data obtained from GBIF (<https://doi.org/10.15468/dl.2q8eys> and <https://doi.org/10.15468/dl.88gkjh>), SpeciesLink, Re flora, and the available literature. We followed the classification of PPG I (2016) and Flora e Funga do Brasil (2025) to update the names of species and genera names, with each name manually verified and validated with reliable vouchers. To complement the data, we visited major herbaria in northeastern Brazil, such as EAC, EAN, HST,

IPA, JPB, PEUFR, RN, UFP, and UFRN (herbarium acronyms following Thiers, 2024), and requested photographs of relevant samples from other herbaria.

Environmental data from the sampled areas included 19 bioclimatic variables from CHELSA 2.1 (Karger et al., 2018), average annual and seasonal cloud cover (Wilson & Jetz, 2016), enhanced vegetation index (EVI) (Tuanmu & Jetz, 2015), elevation, terrain roughness and topography from EarthEnv (Amatulli et al., 2018), potential evapotranspiration (PET) (Title & Bemmels, 2018), eight soil property layers from SoilGrids 2.0, including clay, sand and silt content, volumetric water content at -10kpa, carbon exchange, nitrogen, soil organic carbon, and water pH. (Hengl et al., 2017), wind speed (Badger et al., 2019) and aridity index (Zomer & Trabucco, 2019). All layers were used at a resolution of 30 arc-seconds (1 km²). To avoid multicollinearity, we applied the variance inflation factor (VIF) test calculated using the R package 'usdm' (Naimi & Araújo, 2016), with a threshold of 0.7 (Pradhan & Setyawan, 2021). The selected environmental factors included: temperature seasonality, precipitation of the warmest quarter and the coldest quarter (CHELSA 4, 18, and 19), average annual cloud cover, topography, terrain roughness index, cation exchange capacity at pH 7, clay content, water pH, silt, soil organic carbon, aridity index, wind speed, and elevation. All analyses were conducted using the R programming language (R Core Team, 2022) implemented in RStudio (Posit Team, 2022). The dataset, scripts, and matrixes, are available on GitHub (<https://github.com/xxxxxxx>).

Analysis of environmental factors

The selected environmental data were used to perform a Principal Components Analysis (PCA). This analysis was conducted to reduce data dimensionality and assess whether the studied areas exhibit distinct environmental structuring regarding the NAF sub-regions. Following the PCA, a permutational analysis of variance (Permanova) was conducted to assess the significance of the differences between the two sub-regions.

Analysis of floristic affinities

Using the species occurrence data, a binary presence-absence matrix of the studied areas was created. Non-metric multidimensional scaling (NMDS) was then applied to visualize the arrangement of the areas based on their floristic composition. The NMDS analysis used Jaccard's dissimilarity index, as implemented in the *vegan* package (Oksanen et al., 2022). To analyze the groupings of areas represented in the NMDS, the K-means algorithm was applied to segment the areas from the dissimilarity analysis into distinct groups. The number of clusters was determined using the silhouette method, which evaluates the cohesion and separation of the formed groups. Additionally, an analysis of similarities (ANOSIM), a non-parametric statistical test, was conducted to assess the significance of the groups formed by K-means, comparing them to the NAF sub-regions. All analyses were performed in R (R Core Team, 2022) implemented in R Studio (Posit Team, 2022).

Generalized dissimilarity modeling (GDM) was used to examine the relationship between communities and environmental variables, enabling the assessment of how environmental factors influence floristic composition (Ferrier et al., 2007). GDM was conducted using the BioDinamica toolset (Oliveira et al., 2019) within the Dinamica Ego software (Soares-Filho et al., 2013). The GDM was calibrated to the provided data and to the Euclidean distance between the areas to evaluate the main distribution patterns of the communities in the NAF. To classify the GDM output, the K-means method was applied to classify the GDM output into 2 to 4 classes, as implemented in BioDinamica.

RESULTS

A total of 307 species were recorded, including 21 lycophytes (6.8%) and 286 ferns (93.2%). Of these, 228 species (74.3%) occur in both biogeographical sub-regions. In the BNs, 291 species (95% of the total) were recorded, of which 63 species (20.5%) are exclusive to this sub-region. In the PEC, 254 species (82.7%) were recorded, with only 15 species (4.9%) being exclusive (Figure

2; Supplementary Material 2). Across the 57 sampled areas, species richness ranged from 10 to 150 species.



Figure 2. Images of some ferns and lycophytes found in the Northeastern Atlantic Forest. A-B. Species occurring only in BNs. A. *Phlegmariurus taxifolius* (Sw.) Á.Löve & D.Löve. B. *Pleopeltis pleopeltidis* (Fée) de la Sota. C-H. Species found in both sub-regions. C. *Serpocaulon triseriale* (Sw.) A.R.Sm. D. *Christella dentata* (Forssk.) Brownsey & Jermy. E. *Nephrolepis biserrata* (Sw.) Schott. F. *Cyathea microdonta* (Desv.) Domin. G. *Selaginella producta* Baker. H. *Gleichenella pectinata* (Willd.) Ching.

The PCA showed a clear environmental distinction between the two Northeastern Atlantic Forest sub-regions (Figure 3). The first two principal components accounted for 51.7% of the total variation in the data, with PC1 explaining 31% and PC2 20.7%, capturing the main differences between the areas. Most study sites were grouped according to their respective sub-regions, showing the environmental structuring of the areas (Figure 3). However, some areas occupied intermediate positions, suggesting an overlap in the environmental characteristics of certain remnants. The Permanova confirmed that the groupings differed significantly ($p < 0.0001$), indicating that the sub-regions are strongly differentiated by the analyzed environmental variables.

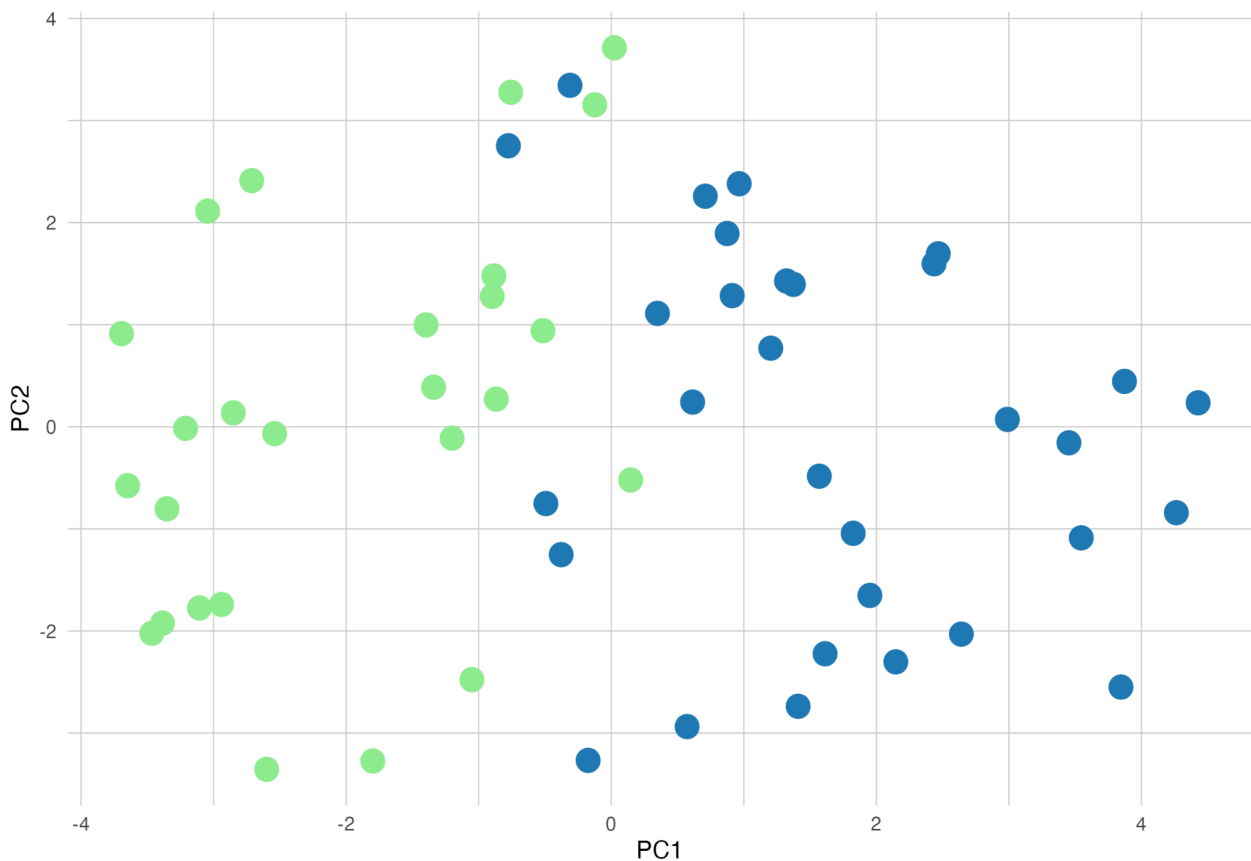


Figure 3. PCA results show the environmental distinction of the NAF subregions. Green represents montane inland wet forests (BNs) areas and blue represents coastal forests (PEC) areas.

The GDM results further highlighted the critical role of the environmental variables in explaining the dissimilarity of the areas. The model, incorporating all predictor variables, explained 78.8% of the environmental dissimilarity, indicating strong explanatory power (Table 1, Supplementary

Material 3). Environmental variables explained 24% of the distribution pattern of ferns and lycophytes in the NAF. Bioclimatic factors accounted for 17% of this pattern, with mean annual cloud cover (10%) and mean monthly precipitation in the coldest quarter (6%) contributing the most to the model. Edaphic factors explained 6%, with soil silt content (3%) and soil water pH (2.5%) being the most influential variables. Topographic factors—including elevation and terrain roughness—only 1% of the model. Geographic distance was the strongest explanatory factor for the patterns obtained in the GDM, accounting for 56% of the observed composition, and in the model, it explained 76% of the pattern.

Group of variables	Percentage of explanation	Variable set percentage contribution
All variables	78.8	100%
Bioclimatic Factors	14.1	17.9%
Edaphic Factors	4.0	5.1%
Topography, Terrain Roughness and Elevation	0.8	1%
Geographical Distance	59.5	75.5%

Table 1: Explanatory Percentages of Environmental Factors in the GDM Model. Bioclimatic factors include temperature seasonality, precipitation of the warmest quarter and the coldest quarter, average annual cloud cover, wind speed, and aridity index. Edaphic Factors include cation exchange capacity at pH 7, clay content, water pH, silt, and soil organic carbon.

The NMDS analysis, based on the composition of ferns and lycophytes in the NAF remnants, yielded a stress value of 0.121, indicating an adequate representation of the dissimilarity among areas. The analysis revealed no clear separation between the sub-regions of the BNs and PEC (Figure 3). However, K-means clustering divided the areas into two groups, as determined by the silhouette method to be the optimal number of clusters. This clustering provided a clearer separation, with the first cluster comprising 50% of areas from each sub-region and the second cluster consisting of 58.82% PEC areas and 41.18% BNs areas.

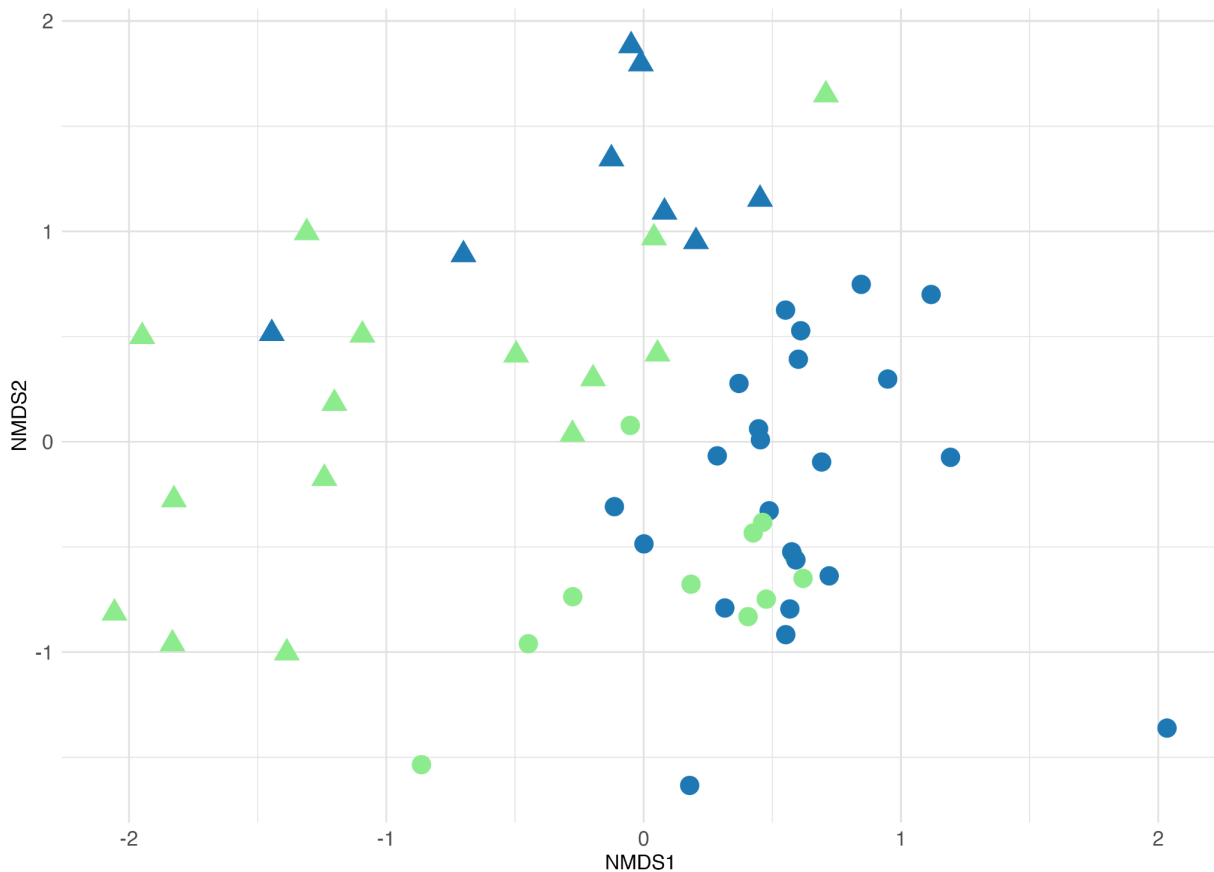


Figure 4. NMDS results illustrating the floristic affinities between the NAF areas. Triangles represent cluster 1; circles represent cluster 2. The green color represents BNs areas and the blue color represents PEC areas.

ANOSIM analysis comparing the BNs and PEC groups showed no significant difference ($R = 0.124$, $p = 0.006$). In contrast, the K-means clusters demonstrated a statistically significant difference ($R = 0.445$, $p < 0,001$). These results suggest that the composition of fern and lycophyte communities is not structured by the sub-region to which they belong.

The classification of NAF areas based on the GDM allowed for an analysis of community composition patterns. Initially, dividing the areas into two classes revealed that Class 1 predominantly grouped coastal areas from Alagoas to Ceará, along with some BNs in Pernambuco, Ceará, and Rio Grande do Norte (Figure 5). When three classes were considered, a clearer separation of the PEC's coastal areas emerged (Figure 5). Class 1 represented the closest coastal strip, while class 2 included more inland forests and BNs in Paraíba and northern Ceará. Class three

grouped most BNs in Pernambuco, the Chapada do Araripe – the southernmost point of Ceará – (fig. 1), and the BNs in Rio Grande do Norte. Finally, in the four-class division, the PEC was further subdivided according to degrees of inland. Class 1 corresponded to a narrow coastal strip, likely representing Restinga and mangrove areas. Class 2 included coastal forest areas and BNs in northern Ceará, while Class 4 covered the most inland portions of the PEC and BNs in Paraíba and Pernambuco near the coast. As in the three-class division, Class 3 grouped most of the BNs in Pernambuco and Chapada do Araripe in Ceará. Overall, the GDM classification highlights that no clear structuring exists between the NAF sub-regions when considering both the environmental variables and ferns and lycophyte communities. In all class divisions, areas from both the BNs and PEC were grouped, reflecting overlapping community compositions.

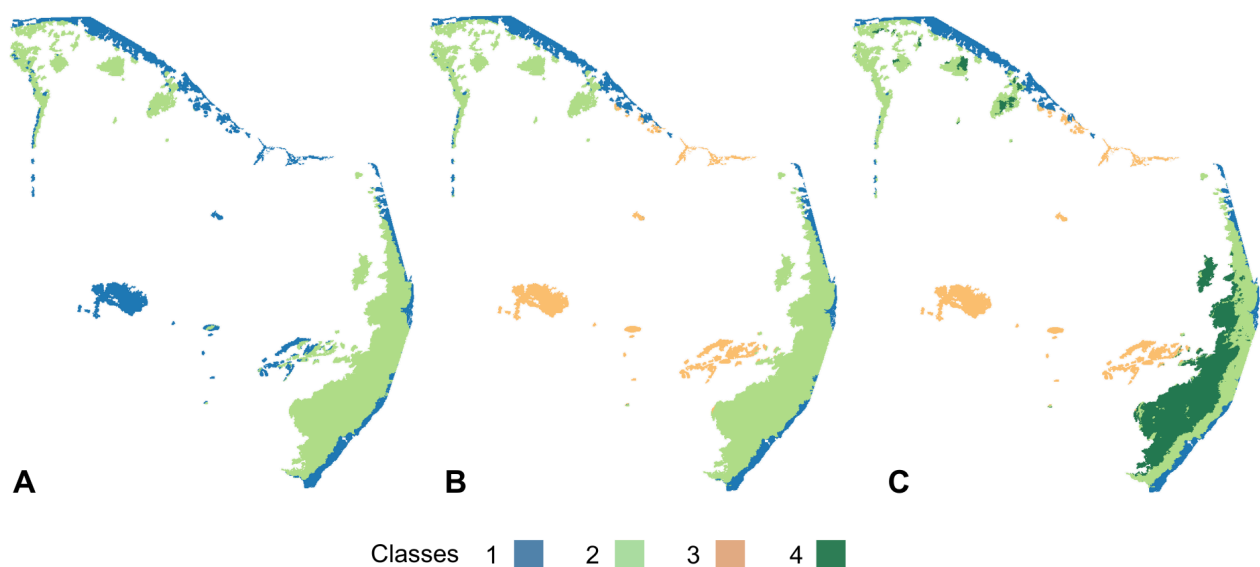


Figure 5. GDM results: analysis indicates that regions of the same color correspond to higher levels of similarity in the composition of ferns and lycophytes within the Northeastern Atlantic Forest. A. Classification in two classes. B. Classification in three classes. C. Classification in four classes

DISCUSSION

This study identified an environmental structure between the biogeographical sub-regions of the Northeastern Atlantic Forest (*Brejos Nordestinos* and Pernambuco Center), based on the analyzed variables (Figure 3). However, this distinction did not extend to the floristic composition of ferns

and lycophytes, as the analyses indicated no clear separation between the plant communities in the BNs and PEC (Figures 4–5). The division of the areas into clusters using the K-means method revealed a significant differentiation in floristic composition, suggesting that the organization of the communities is not directly associated with the geographical boundaries of the sub-regions.

The sub-regions of the NAF exhibit significant environmental distinctions, as evidenced by the positioning of the remnants in the PCA (Figure 3). These distinctions reflect variation in climatic, topographical, and edaphic factors between the BNs and PEC, underscoring the environmental complexity and heterogeneity of the sub-regions. Despite these differences, the composition of the fern and lycophyte communities in the sub-regions remains highly similar, with 71.6% of the taxa shared between them. Although macro-environmental differences can vary, the remnants of both sub-regions share environmental characteristics typical of humid tropical forests (Pôrto et al., 2006). Additionally, the environmental heterogeneity within these remnants creates favorable conditions for a wide diversity of ecological niches, promoting the occurrence of numerous taxa (Weigand et al., 2019; Suissa et al., 2021). The GDM results further identified the key environmental factors contributing to the distribution patterns of fern and lycophyte communities in the NAF (Table 1). These factors likely act as environmental filters, shaping community composition by determining which species successfully go through the gametophyte stage to establish sporophytic populations capable of persisting across generations within these remnants (Haufler et al., 2016).

The classification obtained by GDM does not corroborate the grouping of FAN subregions based on floristic dissimilarity (Figure 5). The classification did not reflect the phytophysionomies, suggesting that other factors weigh on the generated pattern. The GDM divisions were more closely related to the distance of the forests from the coast (Figure 5), likely due to factors such as humidity loss. This pattern does not align with the findings of Lima et al. (2024), who studied the floristic affinities of ferns and lycophytes in the Atlantic Forest. The authors did not include data from the NAF, which might have resulted in a less accurate classification of this section of the Atlantic Forest (Lima et al., 2024).

Geographical distance, according to Hubbell's Neutral Theory (2001), plays a role in shaping the composition of biological communities. The author postulates that Euclidean distance and community similarity are inversely proportional, meaning that the farther apart remnants are, the less similar their biota tends to be (Hubbell, 2001). In the case of ferns and lycophytes in the NAF, as recovered in the study of Lima et al (2024)., geographical distance has emerged as the primary factor explaining the observed dissimilarity in community composition (Table 1). Geographic distance is closely related with environmental changes across the different phytophysiognomies that compose the NAF. The inward placement of the forests could be influencing this strong correlation with geographical distance, as moving farther away from the coast leads to a decrease in humidity and alterations in other environmental conditions. Consequently, these changes affect community structure, which in turn impacts the composition of ferns and lycophytes.

Among the most relevant factors highlighted by the GDM is average annual cloud cover. Previous studies, such as Weigand et al. (2019), have identified this environmental factor as one of the most significant determinants of fern and lycophyte richness at a local scale. Average annual cloud cover is strongly linked to decreased solar irradiation and increased relative humidity (Kanniah et al., 2012), both of which are essential for the growth and reproduction of these plants (Haufler et al., 2016). These conditions are particularly important during the gametophytic phase, where water availability is crucial for successful reproduction (Haufler et al., 2016).

Variables related to soil composition are also highly relevant in the distribution of ferns and lycophytes (Moulatlet et al., 2019). Several studies have demonstrated a strong relationship between edaphic factors and community composition (Moulatlet et al., 2019). For instance, studies in the Ecuadorian Amazon by Tuomisto et al. (2003) indicated soil texture –comprising of silt, sand, and clay–as a significant determinant of fern and lycophyte richness. Similarly, in the NAF, silt was one of the most relevant factors in shaping the observed distribution patterns (Supplementary Material 3). This significance is likely due to its impact on soil texture, which in turn affects water and nutrient retention capacity. Another important variable influencing community composition in the

NAF was the pH of the soil water. Soil pH affects the availability of essential nutrients and regulates various chemical, physical, and biological processes in the soil, including those critical for plant growth and development (Neina, 2019).

Ferns and lycophytes depend on water for reproduction, as their flagellated antherozoids must swim to reach the oosphere during the gametophytic phase (Haufler et al., 2016). Consequently, areas with high rainfall typically exhibit higher species richness, as pointed out in the study by Tuomisto et al. (2014) in the Amazon. Similarly, in the NAF, the average monthly rainfall in the coldest quarter was identified as a key factor influencing the distribution pattern of these communities (Table 1).

The absence of structured fern and lycophyte communities across the sub-regions of the NAF may be linked to the forest's biogeographical history. The current characteristics of the Atlantic Forest are directly influenced by paleoclimatic dynamics during the Quaternary period, particularly the Pleistocene epoch (2.58 Ma - 11.7 Ka) (Lins-e-Silva, 2021). This epoch was characterized by climatic fluctuations, including cycles of glaciation and interglaciation, which profoundly affected vegetation patterns and the distribution of South American biota (Salgado-Labouriau, 1994; Popp, 2017; Narváez-Gómez et al., 2018). The climatic dynamics caused significant fluctuations in the extent of the Atlantic Forest. During glacial periods, the forest contracted into smaller remnants, whereas in interglacial periods, warming and increased humidity allowed it to expand (Lins-e-Silva, 2021). Carnaval & Moritz (2008) have identified regions that remained environmentally favorable for forests during these oscillations, known as refugia, one of which is the PEC (Carnaval & Moritz, 2008).

Silveira et al. (2019) provided deeper insights into the dynamics of NAF retraction and expansion during the Pleistocene. They highlighted that during the Last Glacial Maximum, the BNs expanded their range and established connections with the PEC coastal forest (Silveira et al., 2019). This connection likely re-established gene flow between BN and PEC populations. Notably, the BNs in Pernambuco, Paraíba, and the Chapada do Araripe showed evidence of connectivity with PEC

populations, while the BNs in northern Ceará were more isolated from the other remnants (Silveira et al., 2019). This pattern was partially observed in our results for ferns and lycophytes, except for the BN's from Paraíba (Figure 5)

The lack of geographical barriers between the BNs and the PEC during the Quaternary period (Silveira et al., 2019) likely facilitated the expansion of fern and lycophyte communities through dispersal (Figure 4–5). This historical dynamic may explain the low level of differentiation currently observed between the sub-regions of the NAF, indicating a biogeographical legacy from past climatic and ecological shifts.

The absence of structure of ferns and lycophytes communities in the NAF may also be related to their reproductive biology, particularly the process of spore dispersal. During the sporophytic phase, these propagules are produced in large quantities, with individual plants potentially generating millions or even billions of spores (Haufler et al., 2016). Spores play a fundamental role in colonizing new environments, facilitating gene flow between populations, and enabling broad species occurrence areas (Rose & Dassler, 2017). Although approximately 90% of spores are dispersed within a two-meter radius of the parent plant, a significant portion remain airborne and can be transported by atmospheric currents, potentially traveling long distances. This aerial dispersal occurs at varying locations and times, depending on atmospheric dynamics, extending the range of these plants and influencing their spatial distribution (Peck et al., 1990).

The homogenization of fern and lycophyte communities in the NAF may be influenced by long-distance dispersal facilitated by the atmospheric circulation system of northeastern Brazil (Nimer, 1972), which might help extend the reach of these propagules. This region is characterized by complex atmospheric dynamics, driven by winds that move in different directions due to disturbed currents. These disturbances lead to irregularities in air trajectories, deviating from the typical circulation patterns (Nimer, 1972). This disorganization likely contributes to the long-distance dispersal of spores. The irregularities in atmospheric currents arise from the convergence of trade winds from the northern and southern hemispheres, along with the influence

of climatic phenomena like El Niño and La Niña (Ferreira & Mello, 2005), which alter atmospheric dynamics and drive currents in multiple directions.

In contrast to our findings, studies on angiosperms in the NAF have demonstrated a clear structure between the sub-regions. For instance, Ferraz et al. (2004) examined 742 species of trees and shrubs across 35 localities and observed a division between BNs and PEC. Another study by Nascimento et al. (2012), which included trees, shrubs, and herbaceous species, noted floristic similarities between remnants of different BNs, with a PEC area standing out as the most floristically distinct in the analysis. Similarly, Lopes et al. (2012) reached comparable conclusions. They analyzed a matrix of 1,063 tree species from 34 remnants in Northeastern Brazil and confirmed structuring based on the forest type, including distinctions between the PEC and BNs. These studies on seed plants suggest that such structuring on sub-regions could be related to the dispersal capacities of these lineages, which are generally lower compared to the long-distance dispersal capacity of spores. This results in more geographically restricted distribution patterns for angiosperms compared to ferns and lycophytes.

In conclusion, while environmental factors play a significant role in structuring the sub-regions of the Northeast Atlantic Forest, the floristic composition of ferns and lycophytes appears to be influenced by a more complex interplay of ecological factors and biogeographic history. Future studies at the population level are needed to assess the presence of genetic structuring or gene flow between these plants populations. This will provide a more detailed understanding of the interactions within the communities in the remnants of BNs and PEC. This approach will help elucidate the ecological and evolutionary processes that have shaped these communities. We expect that increased sampling efforts and the application of more robust analytical approaches will provide greater clarity on the distribution pattern of ferns and lycophytes within the Northeastern Atlantic Forest.

Acknowledgments

We thank the Federal University of Pernambuco for support during the research and the Pro-Rectorate for Research and Innovation (Propesqi) for promoting the research, which originated from an undergraduate research project (ID 230221453). We also thank the herbaria curators for their availability. TEA thanks CNPq for the grant (317091/2021–2) awarded. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001 (88887.937988/2024-00) awarded to L.V. Lima.

Author's contributions

DVSS: Conception, data collection, data analysis and interpretation, and preparation of the manuscript draft.

LVL: Data analysis, critical revision, and addition of intellectual content

MPPS: Data analysis, critical revision, and addition of intellectual content

TEA: Conception, data interpretation, manuscript preparation, critical revision, and addition of intellectual content

ACPS: Conception, data interpretation, manuscript preparation, critical revision, and addition of intellectual content

Conflict of interest

The authors declare no conflict of interest.

REFERENCES

- Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes Gonçalves, J. L., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6), 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., & Jetz, W. (2018). A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, 5(1). <https://doi.org/10.1038/sdata.2018.40>

- Andrade-Lima, D. (1953) Notas sobre a dispersão de algumas espécies vegetais no Brasil. *Anais da Sociedade de Biologia de Pernambuco*. 11, 25-49.
- Andrade-Lima, D. (1960) Estudos fitogeográficos de Pernambuco. *Arquivos do Instituto de Pesquisas Agronômicas*. 5, 305-341.
- Andrade-Lima, D. (1982). Present-day forest refuges in northeastern Brazil. *Biological diversification in the tropics*, 245, 251.
- Andrade-Lima, D. (1961). Tipos de florestas de Pernambuco. *Anais da Associação dos Geógrafos brasileiros*, 12(1), 68-95.
- Badger, J. et al. Global wind atlas 3.0. World Bank Group <https://globalwindatlas.info>, 2019.
- Barrington, D. S. Ecological and Historical Factors in Fern Biogeography. *Journal of Biogeography*, v. 20, n. 3, p. 275, May 1993.
- Barrington, D. S. (1993). Ecological and Historical Factors in Fern Biogeography. *Journal of Biogeography*, 20(3), 275. <https://doi.org/10.2307/2845635>
- Bigarella, J.J. Considerações a respeito das mudanças paleoambientais na distribuição de algumas espécies vegetais e animais no Brasil. *An Acad Bras Cienc*, v. 47, p. 411-464, 1975.
- Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, 35(7), 1187–1201. <https://doi.org/10.1111/j.1365-2699.2007.01870.x>
- Castro, D. P., Rodrigues, M., Borges-Leite, M. J., Lima, D. C., & Diva Maria Borges-Nojosa. (2019). Anuran diversity indicates that Caatinga relictual Neotropical forests are more related to the Atlantic Forest than to the Amazon. *PeerJ*, 6, e6208–e6208. <https://doi.org/10.7717/peerj.6208>
- Coimbra-Filho, A. F., & Câmara, I. G. Os limites originais do bioma da Mata Atlântica na Região Nordeste do Brasil.(1996) FBCN. Rio de Janeiro, 86 pp.
- Ferraz, E. M. N., Araújo, E. de L., & da Silva, S. I. (2004). Floristic similarities between lowland and montane areas of Atlantic Coastal Forest in Northeastern Brazil. *Plant Ecology Formerly 'Vegetatio'*, 174(1), 59–70. <https://doi.org/10.1023/b:vege.0000046062.77560.f5>

- Ferreira, A. G., & Giovanni. (2023). Principais sistemas atmosféricos atuantes sobre A Região Nordeste do Brasil e a influência dos Oceanos Pacífico e Atlântico no clima da região. Repositorio.ufc.br. <http://www.repositorio.ufc.br/handle/riufc/72077>
- Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, 13(3), 252–264. <https://doi.org/10.1111/j.1472-4642.2007.00341.x>
- Flora e Funga do Brasil (2025). Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/>
- Fundação SOS Mata Atlântica. (2023). A Mata Atlântica. Itu, São Paulo. Accessed 2024-06-27. <https://cms.sosma.org.br/wp-content/uploads/2023/10/Folheto-sosma-2023-v2digital-1.pdf>.
- Haufler, C. H., Pryer, K. M., Schuettpelz, E., Sessa, E. B., Farrar, D. R., Moran, R., Schneller, J. J., Watkins, J. E., & Windham, M. D. (2016). Sex and the Single Gametophyte: Revising the Homosporous Vascular Plant Life Cycle in Light of Contemporary Research. *BioScience*, 66(11), 928–937. <https://doi.org/10.1093/biosci/biw108>
- Hengl, T. et al. (2017). Soilgrids250m: global gridded soil information based on machine learning. *PLoS One* 122, e0169748.
- Hubbell, S. P. (2001). The unified neutral theory of species abundance and diversity. Princeton University Press, Princeton, NJ. Hubbell, SP (2004) *Quarterly Review of Biology*, 79, 96-97.
- Kanniah, K. D., Beringer, J., North, P., & Hutley, L. (2012). Control of atmospheric particles on diffuse radiation and terrestrial plant productivity. *Progress in Physical Geography: Earth and Environment*, 36(2), 209–237. <https://doi.org/10.1177/0309133311434244>
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4(1). <https://doi.org/10.1038/sdata.2017.122>
- Kornas, J. (1993). The Significance of Historical Factors and Ecological Preference in the Distribution of African Pteridophytes. *Journal of Biogeography*, 20(3), 281. <https://doi.org/10.2307/2845636>

- Lima, V. X., Nogueira-Melo, G. S., Baltazar, J. M., Medeiros, P. S. de, Soares, A. M., Lira, C. R. S. de, & Gibertoni, T. B. (2018). Fungal perspective on neotropical biogeography: poroid fungi (Agaricomycetes: Hymenochaetales and Polyporales) and the Brazilian moist forests. *Fungal Ecology*, 36, 1–7. <https://doi.org/10.1016/j.funeco.2018.06.004>
- Link-Pérez, M. A., & LafNAF, S. W. (2018). Fern and lycophyte diversity in the Pacific Northwest: Patterns and predictors. *Journal of Systematics and Evolution*, 56(5), 498–522. <https://doi.org/10.1111/jse.12430>
- Lins-e-Silva, A. C. B., Ferreira, P. S. M., & Rodal, M. J. N. (2021). The North-Eastern Atlantic Forest: Biogeographical, Historical, and Current Aspects in the Sugarcane Zone. *The Atlantic Forest*, 45–61. https://doi.org/10.1007/978-3-030-55322-7_3
- Lopes, C. G. R., Ferraz, E. M. N., & Araújo, E. de L. (2012). Floristic similarity between seasonal and ombrophilous forests in the Atlantic Forest of Brazil. In A. D. Bezerra & T. S. Ferreira (Eds.), *Evergreens: Types, Ecology and Conservation*. UK Ed. p. 182.
- Moran, R. C. (1995). The importance of mountains to pteridophytes, with emphasis on neotropical montane forests.
- Morrone, J. J., Escalante, T., Rodríguez-Tapia, G., Carmona, A., Arana, M., & Mercado-Gómez, J. D. (2022). Biogeographic regionalization of the Neotropical region: New map and shapefile. *Anais Da Academia Brasileira de Ciências*, 94. <https://doi.org/10.1590/0001-3765202220211167>
- Moulatlet, G. M., Zuquim, G., & Tuomisto, H. (2019). The role of soils for pteridophyte distribution in tropical American forests. *Fern Gazette*, 21(1).
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.
- Naimi, B., & Araújo, M. B. (2016). sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography*, 39(4), 368-375.

- Nascimento, L. M. do, Rodal, M. J. N., & Silva, A. G. da. (2012). Florística de uma floresta estacional no Planalto da Borborema, nordeste do Brasil. *Rodriguésia*, 63(2), 429–440. <https://doi.org/10.1590/s2175-78602012000200015>
- Narváez-Gómez, J., Cabral, A., Frazão, A., Colli-Silva, M., & Santana, P. (2018). Biogeografia Neotropical: história e conceitos. *VIII Botânica no Inverno*, 145-166.
- Neina, D. (2019). The Role of Soil pH in Plant Nutrition and Soil Remediation. *Applied and Environmental Soil Science*, 2019(5794869), 1–9. <https://doi.org/10.1155/2019/5794869>
- Nimer, E. (1972). Climatologia da região Sudeste do Brasil: introdução à climatologia dinâmica-subsídios à geografia regional do Brasil. *Revista Brasileira de Geografia*, 34(1), 3-48.
- Oliveira, U., Soares-Filho, B., Leitão, R. F. M., & Rodrigues, H. O. (2019). BioDinamica: a toolkit for analyses of biodiversity and biogeography on the Dinamica-EGO modelling platform. *PeerJ*, 7, e7213. <https://doi.org/10.7717/peerj.7213>
- Pradhan, P., & Setyawan, A. D. (2021). Filtering multi-collinear predictor variables from multi-resolution rasters of WorldClim 2.1 for Ecological Niche Modeling in Indonesian context. *Asian Journal of Forestry*, 5(2).
- Peck, J. H., Peck, C. J., & Farrar, D. R. (1990). Influences of Life History Attributes on Formation of Local and Distant Fern Populations. *American Fern Journal*, 80(4), 126. <https://doi.org/10.2307/1547200>
- Pereira, A. B. (2009). Mata Atlântica: Uma Abordagem Geográfica. *Nucleus*, 6(1), 27–52. <https://doi.org/10.3738/1982.2278.152>
- Popp, J. H. (2017.) *Geologia Geral*. 7. ed. Rio de Janeiro: LTC Editora. 352 p. ISBN 8521631227.
- Pôrto, K. C., Almeida-Cortez, J. S., Tabarelli, M. (2006). Diversidade biológica e conservação da floresta Atlântica ao norte do Rio São Francisco. Brasília. Ministério do Meio Ambiente, Brasília.
- Pôrto, K. C., CABRAL, J. J. P., Tabarelli, M. (2004). Brejos de altitude em Pernambuco e Paraíba: história natural, ecologia e conservação. Ministério do Meio Ambiente.

- Posit Team (2022). RStudio: integrated development environment for R. Posit Software, PBC, Boston, MA. URL: <http://www.posit.co>.
- PPG I. (2016). A community-derived classification for extant lycophytes and ferns. *Journal of systematics and evolution*, 54(6), 563-603. <https://doi.org/10.1111/jse.12229>
- Prado, J., & Hirai, R. Y. (2014). Biogeography of the Brazilian Atlantic forest: evidence from phylogenetic data sets and perspectives for fern and lycophytes studies. *Fern Gazette*, 19(7), 241-257.
- R Core Team. (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Rodal, M. J. N. (1998). Florestas serranas de Pernambuco: localização e conservação dos remanescentes do brejo de altitude. UFRPE, Imprensa Universitária. 25 p.
- Rodal, M. J. N., Barbosa, M. R. V., & Thomas, W. W. (2008). Do the seasonal forests in northeastern Brazil represent a single floristic unit? *Brazilian journal of biology*, 68, 467-475. <https://doi.org/10.1590/s1519-69842008000300003>
- Rose, J. P., & Dassler, C. L. (2017). Spore Production and Dispersal in Two Temperate Fern Species, With an Overview of the Evolution of Spore Production in Ferns. *American Fern Journal*, 107(3), 136–155. <https://doi.org/10.1640/0002-8444-107.3.136>
- Salgado-Labouriau, M. L. (1994). História ecológica da Terra. Editora Blucher. São Paulo. 307 p.
- Santiago, A. C. P. (2006). Pteridófitas da Floresta Atlântica ao Norte do Rio São Francisco: florística, biogeografia e conservação. Repositorio.ufpe.br. <https://repositorio.ufpe.br/handle/123456789/632>
- SANTIAGO, A. C. P. et al. (2023) Considerações sobre distribuição, diversidade e ecologia de samambaias e licófitas. In: SANTO, Marcelo Guerra; SANTIAGO, Augusto César Pessoa; SYLVESTRE, Lana da Silva (org.). Samambaias e licófitas do Brasil: biologia e taxonomia. Rio de Janeiro: EdUERJ. cap. 6, p. 649-784. ISBN 978-85-7511-584-8.

- Santos, A. M., Cavalcanti, D. R., Silva, J. M. C. da, & Tabarelli, M. (2007). Biogeographical relationships among tropical forests in north-eastern Brazil. *Journal of Biogeography*, 34(3), 437–446. <https://doi.org/10.1111/j.1365-2699.2006.01604.x>
- Santos, V. M., Marcela, & Lücking, R. (2019). Diversity of foliicolous lichens in isolated montane rainforests (Brejos) of northeastern Brazil and their biogeography in a neotropical context. *Ecological Research*, 35(1), 182–197. <https://doi.org/10.1111/1440-1703.12071>
- Silva, J. D., & Casteleti, C. H. M. (2005). Estado da biodiversidade da Mata Atlântica brasileira. *Mata Atlântica: biodiversidade, ameaças e perspectivas*, 1, 43-59.
- Silveira, M. H. B., Mascarenhas, R., Cardoso, D., & Batalha-Filho, H. (2019). Pleistocene climatic instability drove the historical distribution of forest islands in the northeastern Brazilian Atlantic Forest. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 527, 67–76. <https://doi.org/10.1016/j.palaeo.2019.04.028>
- Silvestre, L. C., de Mendonça, J. D. L., da Silva Xavier, S. R., & Jadim, J. G. (2019). Riqueza e similaridade florística de samambaias e licófitas na Floresta Atlântica no Nordeste do Brasil. *Oecologia Australis*, 23(3). <https://doi.org/10.4257/oeco.2019.2303.08>
- Soares-Filho, B., Rodrigues, H., & Follador, M. (2013). A hybrid analytical-heuristic method for calibrating land-use change models. *Environmental Modelling & Software*, 43, 80–87. <https://doi.org/10.1016/j.envsoft.2013.01.010>
- Suissa, J. S., & Sundue, M. A. (2020). Diversity Patterns of Neotropical Ferns: Revisiting Tryon's Centers of Richness and Endemism. *American Fern Journal*, 110(4). <https://doi.org/10.1640/0002-8444-110.4.211>
- Suissa, J. S., Sundue, M. A., & Testo, W. L. (2021). Mountains, climate and niche heterogeneity explain global patterns of fern diversity. *Journal of Biogeography*. <https://doi.org/10.1111/jbi.14076>
- Tabarelli M, Marins JF, Silva JMC. (2002) La biodiversidade brasileira, amenazada. *Investigação e Ciência* 308: 42–49.

- Tabarelli, M., Pinto, L. P., Silva, J. M. C., Hirota, M. M., & Bedê, L. C. (2005). Desafios e oportunidades para a conservação da biodiversidade na Mata Atlântica brasileira. *Megadiversidade*, 1(1), 132-138.
- Tabarelli, M., & Santos, A. M. M. (2004). Uma breve descrição sobre a história natural dos brejos nordestinos. *Brejos de Altitude em Pernambuco e Paraíba, História Natural, Ecologia e Conservação*, 9, 17-24.
- Tabarelli, M., Siqueira Filho, J. A. D., & Santos, A. M. M. (2006). A Floresta Atlântica ao norte do rio São Francisco. *Diversidade biológica e conservação da floresta atlântica ao norte do rio São Francisco*. Ministério do Meio Ambiente, Brasília, 23-37.
- Thiers B. (2024). *Index Herbariorum: a global directory of public herbaria and associated staff*. New York, New York Botanical Garden's Virtual Herbarium. <https://sweetgum.nybg.org/science/ih/>
- Title, P. O., & Bemmels, J. B. (2018). ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, 41(2), 291–307. <https://doi.org/10.1111/ecog.02880>
- Tryon, R. (1986). The biogeography of species, with special reference to ferns. *The Botanical Review*, 52, 117-156.
- Tryon, R. M., & Tryon, A. F. (2012). *Ferns and allied plants: with special reference to tropical America*. Springer Science & Business Media.
- Tuanmu, M.-N., & Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 24(11), 1329–1339. <https://doi.org/10.1111/geb.12365>
- Tuomisto, H., Axel Dalberg Poulsen, Kalle Ruokolainen, Moran, R. C., Quintana, C., Celi, J., & Cañas, G. (2003). Linking Floristic Patterns With Soil Heterogeneity And Satellite Imagery In Ecuadorian Amazonia. *Ecological Applications*, 13(2), 352–371. [https://doi.org/10.1890/1051-0761\(2003\)013\[0352:lfpwsh\]2.0.co;2](https://doi.org/10.1890/1051-0761(2003)013[0352:lfpwsh]2.0.co;2)

Veloso, H. P., Rangel-Filho, A. L. R., & Lima, J. C. A. (1991). Classificação da vegetação brasileira, adaptada a um sistema universal. IBGE.

Weigand, A., Abrahamczyk, S., Aubin, I., Bitá-Nicolae, C., Helge Bruelheide, Carvajal-Hernández, C. I., Cicuzza, D., Cavalcante, L., János Csiky, Dengler, J., de, L., Guerin, G. R., Haider, S., Hernández-Rojas, A., Jandt, U., Johan Reyes-Chávez, Dirk Nikolaus Karger, Phyo Kay Khine, Kluge, J., & Thorsten Krömer. (2019). Global fern and lycophyte richness explained: How regional and local factors shape plot richness. *47(1)*, 59–71. <https://doi.org/10.1111/jbi.13782>

Wilson, A. M., & Jetz, W. (2016). Remotely Sensed High-Resolution Global Cloud Dynamics for Predicting Ecosystem and Biodiversity Distributions. *PLOS Biology*, *14(3)*, e1002415. <https://doi.org/10.1371/journal.pbio.1002415>

Wolf, P. G., Schneider, H., & Ranker, T. A. (2001). Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? *Journal of Biogeography*, *28(2)*, 263–270. <https://doi.org/10.1046/j.1365-2699.2001.00531.x>

Zomer, Robert; Trabucco, Antonio (2019). Global Aridity Index and Potential Evapotranspiration (ET0) Database: Version 3. Figshare.com. <https://doi.org/10.6084/m9.figshare.7504448.v6>

SUPPLEMENTARY MATERIAL

Supplementary Material 1. Northeastern Atlantic Forest areas used for analysis.

Supplementary Material 2. Ferns and Lycophytes from the analyzed areas of the Northeastern Atlantic Forest

Supplementary Material 3. Explanatory Percentages of Each Environmental Variable in the GDM Model

Data Accessibility Statement

The scripts to run the analyses, as well as the datasets, are available on Github (<https://github.com/xxxxxxx>).

This preprint was submitted under the following conditions:

- The authors declare that they are aware that they are solely responsible for the content of the preprint and that the deposit in SciELO Preprints does not mean any commitment on the part of SciELO, except its preservation and dissemination.
- The authors declare that the necessary Terms of Free and Informed Consent of participants or patients in the research were obtained and are described in the manuscript, when applicable.
- The authors declare that the preparation of the manuscript followed the ethical norms of scientific communication.
- The authors declare that the data, applications, and other content underlying the manuscript are referenced.
- The deposited manuscript is in PDF format.
- The authors declare that the research that originated the manuscript followed good ethical practices and that the necessary approvals from research ethics committees, when applicable, are described in the manuscript.
- The authors declare that once a manuscript is posted on the SciELO Preprints server, it can only be taken down on request to the SciELO Preprints server Editorial Secretariat, who will post a retraction notice in its place.
- The authors agree that the approved manuscript will be made available under a [Creative Commons CC-BY](#) license.
- The submitting author declares that the contributions of all authors and conflict of interest statement are included explicitly and in specific sections of the manuscript.
- The authors declare that the manuscript was not deposited and/or previously made available on another preprint server or published by a journal.
- If the manuscript is being reviewed or being prepared for publishing but not yet published by a journal, the authors declare that they have received authorization from the journal to make this deposit.
- The submitting author declares that all authors of the manuscript agree with the submission to SciELO Preprints.