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Original Article

So close no matter how far: The floristic affinities of the Serra do Papagaio ferns and lycophytes within the Atlantic Forest

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ABSTRACT

We discuss the importance of fern and lycophyte species in the Atlantic Forest ecosystem as well as the need for floristic inventories to understand their distribution and conservation status. We focus on the Serra do Papagaio region in southeastern Brazil, which is known for its high plant diversity but lacks comprehensive inventories of ferns and lycophytes. In this study, we conducted a floristic inventory of Serra do Papagaio and identified 172 fern and 29 lycophyte species. Our findings reveal 21 threatened species and two new records for Minas Gerais State. Additionally, we compared the floristic composition of Serra do Papagaio with that of other areas within the Atlantic Forest using non-metric multidimensional scaling (NMDS) and generalized dissimilarity modeling (GDM) analyses. The results highlight distinct clusters of areas based on elevation and geographic location. We emphasize the need for further sampling and conservation efforts in Serra do Papagaio as well as provide valuable insights into the drivers of fern and lycophyte diversity in the Atlantic Forest.

Keywords: Floristic survey, hotspot, Serra da Mantiqueira, southeastern Brazil mountains.

Introduction

The Atlantic Forest is a biodiversity hotspot located mainly along eastern South America and extends from northeastern Brazil to Argentina and Paraguay (Myers *et al.,* 2000; Marques *et al.,* 2021). Ferns and lycophytes are important components of the Atlantic Forest ecosystem (Sharpe *et al.*,2010; Souza *et al*., 2021), comprise a significant proportion of the understory flora in this region, and exhibit high levels of endemism (Souza *et al.,* 2021; Suissa *et al.,* 2021). These plants are known for their limited ability to acclimate to microclimate changes. This is attributed to their slow growth, intolerance to high luminosity, and sensitivity to changes in humidity, although some species have higher tolerance to environmental heterogeneity (Page, 2002). These traits make them exceptional bioindicators

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of environmental changes in tropical forests (Lawrence *et al.,* 2010). Understanding the distribution patterns of ferns and lycophytes species within the Atlantic Forest can provide valuable insights into ecological processes and aid in conservation efforts to preserve the biodiversity of this region (Kessler, 2010; Heringer *et al.,* 2020; Souza *et al.,* 2021).

Historically, the Atlantic Forest has experienced significant habitat loss and fragmentation due to human activities, such as logging, agriculture, and urbanization (Scarano & Ceotto, 2015; Carlucci *et al.,* 2021). As a result, many fern and lycophyte species within this ecosystem have become threatened or endangered (Prado *et al.,* 2015; Blair *et al.,* 2016; Portaria MMA nº 148/2022; CNCFlora, 2024). Floristic inventories are critical tools for monitoring plant diversity in tropical regions like the Atlantic Forest (Jayakumar *et al.,* 2011). They provide a comprehensive understanding of the distribution and abundance of plant species, making it easier to evaluate conservation priorities and develop effective strategies for managing regional biodiversity (Barbosa *et al.,* 2021). However, neotropical ecosystems still have large sampling gaps (Oliveira *et al.* ,2016), and there is a need for additional floristic studies of fern and lycophyte species within the Atlantic Forest to identify new populations, investigate factors affecting their distribution, and inform conservation efforts (Almeida & Salino, 2016; Gasper *et al.,* 2016).

The Atlantic Forest exhibits a remarkable environmental heterogeneity. This is due to the presence of lowland and mountainous areas, a gradient ranging from rainforest to deciduous forests, a transition from coastal to inland regions, and diverse geological origins (Oliveira-Filho & Fontes, 2000; Miranda *et al.,* 2018). This complex mosaic of habitats offers a unique opportunity for comparative studies, particularly in relation to ferns and lycophytes (Tryon, 1972; Page ,2002; Moran, 2008). By conducting comparative studies between different areas within the Atlantic Forest, we can gain valuable insights into the ecological patterns and processes that shape the distribution, diversity, and conservation of ferns and lycophytes, contributing to our understanding of the broader dynamics of this globally significant phytogeographic domain (Paciencia & Prado, 2005).

Serra do Papagaio is a mountain range in southeastern Brazil, within the Mantiqueira Range. It has been identified as one of the richest areas in terms of plant diversity within the Atlantic Forest (Souza *et al*., 2012; Mendonça, 2017; Souza *et al*., 2021). Until now, no inventory of fern and lycophyte species within Serra do Papagaio had been carried out. Exploring the diversity of ferns and lycophytes in the region can provide valuable insights into this understudied area of the Atlantic Forest. Furthermore, when analyzing the floristic data comparatively with geographically and environmentally close areas, we may obtain valuable information on the ecological factors that influence plant distribution and abundance within different habitats. This approach could also aid in identifying potential threats to regional biodiversity.

The present study conducted an inventory of the fern and lycophyte species in Serra do Papagaio, analyzed the floristic affinities of this region in the Atlantic Forest, and investigated potential relationships with environmental factors that could influence the composition of the species. Our goals were (I) to inventory the ferns and lycophytes of Serra do Papagaio and (II) compare the species composition between it and geographically and environmentally closely related areas in the Atlantic Forest.

Material and methods

Sampled areas

Two protected areas were sampled in the Serra do Papagaio mountain range, Parque Estadual da Serra do Papagaio (Serra do Papagaio State Park) and Reserva Particular do Patrimônio Natural do Matutu – RPPN (Matutu Private Natural Heritage Reserve), which are both referred to in this study as Serra do Papagaio. Serra do Papagaio State Park is a protected area located in the Serra da Mantiqueira region, in southern Minas Gerais State, southeastern Brazil (Fig. 1). It was created in 1998, as a protected area of approximately 22,917 ha, through the state decree 39793/98, and expanded to 25,888 ha in 2021 through the state law 23774/2021 (IEF, 2021). The park is in the municipalities of Aiuruoca, Alagoa, Baependi, Itamonte, and Pouso Alto. The main types of vegetation present are *Araucaria* forests (mainly along watercourses in moist soil, between 1,600 and 1,700 m) and montane tropical rain forests and cloud forests interspersed with widely distributed high-altitude grasslands (*campos de altitude*) (Santiago *et al.,* 2018; Santana *et al.,* 2020). The altitude of Serra do Papagaio ranges from 1,180m to 2,359m, and the climate in the region is classified as Cwb (highland tropical) (Alvares *et al.,* 2013), with warm and moist summers, cold and dry winters, and frost occurring in the colder months of the year. The annual mean temperature ranges from 18–19 C°, and the mean annual rainfall is 1500 mm (Simas *et al.,* 2005; Alvares *et al.,* 2013).

Reserva Particular do Patrimônio Natural do Matutu - RPPN (Matutu Private Natural Heritage Reserve) covers an area of approximately 348 ha and was created through the IEF-MG Directive 105/2008 (IEF, 2021). It is a protected area adjacent to the eastern part of Serra do Papagaio State Park. It has an elevation of approximately 1,400 m and the same types of vegetation and mean temperature and rainfall described above.

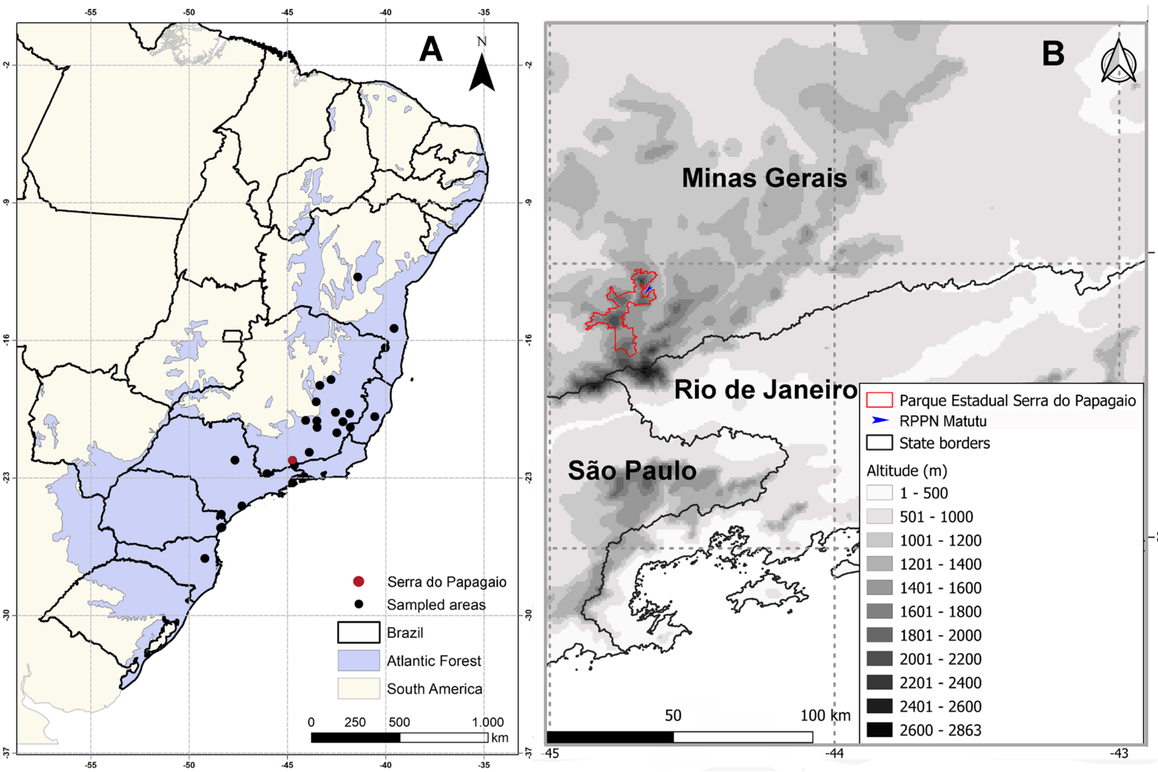

Figure 1. A. Map showing the areas location used in the comparative analysis of the Serra do Papagaio flora. **B.** Map showing the Serra do Papagaio location.

Dataset assembly

For the floristic inventory, collections were made by the authors from August 2003 to March 2015 in the municipalities of Aiuruoca, Baependi, and Alagoa, using the walking survey method (Filgueiras *et al.*, 1994). The collections were deposited in two main herbaria: BHCB and CESJ (herbarium codes follow Thiers, 2022). Other previously collected specimens were examined in the BHCB, CESJ, and RB herbaria. The sampled material was identified with the Flora e Funga do Brasil (2023) and additional specialized literature. For the conservation status of the recorded species, we followed Portaria MMA nº 148, June 7th, 2022, and the CNC Flora (2024) for national status and Biodiversitas (2007) for Minas Gerais State. Additionally, we classified the species life form following Chen *et al.* (2022). The information regarding preferred substrates was compiled from available specimen data.

Floristic affinities analysis

A dataset with 26 inventories of ferns and lycophytes distributed throughout the Atlantic Forest was built (Tab. 1, Fig. 1). We used the Atlantic Forest *sensu lato* concept presented by Muylaert *et al.* (2018). We followed the PPG I (2016) and the Flora e Funga do Brasil (2023) to update the species and genera names accordingly. Each name was manually verified and vouchers were consulted whenever necessary.

To analyze the floristic data, we used two different approaches. Non-metric multidimensional scaling (NMDS) was used to visualize the ordination of areas based on the floristic composition. Generalized dissimilarity modeling (GDM) was used to model the relationship between species composition and environmental variables. GDM allowed us to examine the effects of multiple environmental variables on the floristic composition (Ferrier *et al.*, 2007).

The NMDS was conducted using the Bray-Curtis dissimilarity index in the Vegan package in the software R (Oksanen *et al*., 2022). The GDM was made using the BioDinamica toolset (Oliveira *et al.*, 2019) in the software Dinamica Ego (Soares-Filho *et al.*, 2013). The GDM was adjusted to the provided data and geographical distance among the areas using Euclidian distance, in the model. Aiming to evaluate the major patterns of ferns and lycophytes community distribution in the Atlantic Forest, we used the Clara method to classify the GDM output into seven classes, as implemented in BioDinamica. As environmental input, we used the 19 Bioclimatic variables from CHELSA 2.1 (Karger *et al.*, 2018), annual cloud mean and cloud seasonality (Wilson & Jetz, 2016), dissimilarity and range from the enhanced vegetation index (EVI) (Tuanmu & Jetz, 2015), elevation (World Clim SRTM derived, Fick & Hijmans, 2017), potential evapotranspiration (PET),

Table 1. Atlantic Forest areas used for floristic analysis.

Location	State	Area (ha)	Altitude (m.s.m.)	Dominant vegetation	Species richness	Reference
Serra do Cuscuzeiro	SP	584	800-1050	FES/CE	113	Salino, 1996
A.P.A. Fernão Dias	MG	180,373	1000-2068	FOD/FOM/FES	173	Melo & Salino, 2007
P.E. do Jacupiranga	SP	150,000	10-1310	FOD/RES	207	Salino & Almeida, 2008
Maciço da Juréia	SP	84,225	30-1250	FES	86	Prado (2004)
P.N. da Serra de Itajaí	SC	57,475	150-940	FOD	185	Gasper & Sevegnani, 2010
P.N. da Chapada Diamantina	BA	50,610	200-1800	CE/CR/FOD/CAA	124	Nonato, 2005
P.E. do Rio Doce	MG	35,973	230-515	FES	116	Melo & Salino, 2002
A.P.A. Cairuçu	RJ	33,800	0-1320	FOD /MG/ RES	115	Sylvestre, 1997
P.N. do Caparaó	MG/ES	31,853	1000-2891	FOD/CA	301	Moreira *et al.*, 2020
P. N. Itatiaia	MG/RJ	30,000	500-2789	FOD/CA	141	Condack, 2006
Cariri	MG/BA	19,264	800-1000	FOD	154	Salino *et al.* (Unpublished data)
Serra do Mar Paranaense	PR	18,000	0-1889	FOD/RES	166	Paciencia (2008)
Serra Negra	MG	13,654	900-1698	FOD/FES/FAM/ CR	203	Souza *et al.* (2012)
P. E. da Serra do Intendente (Tabuleiro)	MG	13,518	685-1300	CE, CR, FOD	221	Salino *et al.* (Unpublished data)
P. E. da Serra do Brigadeiro	MG	13,210	800-1870	FOD, FES, CA	144	Salino *et al.* (Unpublished data)
P. E. do Rio Preto	MG	12,184	700-1826	FES	189	Salino *et al.* (Unpublished data)
Serra do Caraça	MG	10,187	750-2072	FES/FOD/CR	234	Viveros, 2010
P.E. Itacolomi	MG	7,000	660-1760	FES/CR	170	Rolim, 2007
Reserva Biológica Augusto Ruschi	ES	4,000	800-1100	FOD	126	Aquije & Santos (2007)
Ilha do Mel	PR	2,894	0-148	Formações campestres, RE, Floresta	114	Salino *et al.*, 2005
A.P.A. Sul RMBH	MG	2,280	790-1420	FES/CE	190	Figueiredo & Salino, 2005
R.P.P.N. Serra Bonita	BA	2,000	300-1080	FES/CR	182	Matos *et al.* (2010)
P.E. Ibitipoca	MG	1,488	1200-1784	CR/FES/FOM	169	Salino *et al.* (Unpublished data)
Reserva Rio das Pedras	RJ	1,260	20-1050	FOD/RES	114	Mynssen & Windisch, 2004
Estação Biológica de Caratinga	MG	880	400-680	FES	102	Melo & Salino, 2002
P. E. da Serra do Papagaio	MG	25,880	1100-2360	FOD, CA	181	Present work
R.P.P.N. Mata do Sossego	ES	180	1100-1650	FOD	151	Souza & Salino (Unpublished data)

States: BA: Bahia; ES: Espírito Santo; MG: Minas Gerais; PR: Paraná; RJ: Rio de Janeiro; SC: Santa Catarina; SP: São Paulo. Vegetation types: CAA: Caatinga. CA: Campos de Altitude. CE: Cerrado. CR: Campos Rupestres. FES: Seasonal Semideciduous Forest. FOD: Dense Rainforest. FOM: Mixed Ombrophilous Forest. MG: Mangrove. RES: Restinga. A.P.A.: Environmental Protection Area; P.E.: State park; P.N.: National park; R.P.P.N.: Private Natural Heritage Reserve.

and terrain roughness index (Title & Bemmels, 2018). All layers were used at a resolution of 30-arc seconds (1 km). To avoid multicollinearity, we ran a Pearson correlation test using a threshold of 0.7. The selected environmental layers were mean annual air temperature, mean diurnal air temperature range, isothermality, precipitation amount of the driest month, precipitation seasonality, mean monthly precipitation amount of the warmest quarter, mean monthly precipitation amount of the coldest quarter respectively (CHELSA 1, 2, 3, 14, 15, 18, 19), cloud seasonality, EVI dissimilarity, elevation, and terrain roughness index. We used jackknife to test the impact of subsets of predictor variables. We divided the variables into four groups (1 - bioclimatic variables, 2 - elevation and terrain roughness, 3 - cloud mean and seasonality, and 4 - EVI range and dissimilarity) and ran independent analyses with three out of the four groups. We also ran a multiple regression analysis to evaluate the relationship among elevation, area size, and species number. The analyses were performed in R (R Core Team, 2022), implemented in R Studio (Posit Team, 2022). We explored a range of class cut thresholds, generating classification maps with two to ten classes. The classes in GDM reflect an environmental classification constrained by predicted biological dissimilarity (Ferrier *et al.*, 2007)

Results

Serra do Papagaio inventory

We found 201 species, of which 172 are ferns and 29 are lycophytes (Table S1) (Fig. 2). Polypodiaceae (32 species), Lycopodiaceae (25), and Dryopteridaceae (24) are the richest families (Table S1). The richest genera are *Phlegmariurus* Holub *a* (14 species), *Elaphoglossum* Schott ex J.Sm. (12), *Amauropelta* Kunze (10), and *Cyathea* Sm. and *Asplenium* L. (nine species each). Regarding the preferential substrate, 122 species (61.2% of the total) are exclusively terrestrial, 48 species (23.88%) are exclusively epiphytes, 16 species (7.96%) are exclusively rupestral, five species (2.49%) are facultatively terrestrial or epiphytic, four species (1.99%) occupy all the substrates, four species (1.99%) occur as terrestrial or rupestral plants, and one species (0.5%) is facultatively rupestral or epiphytic.

We found 25 threatened species, 10 at the national level and 22 at the state level (Table S1). We also found two new records for Minas Gerais State. *Ceradenia glaziovii* (Baker) Labiak, according to Labiak *et al.* (2013), has not been collected for the last 50 years and was presumed to be extinct in the wild. The species was previously known only from São Paulo State (Labiak 2020). The other new record is *Rumohra glandulosissima* Sundue & J.Prado. It was only known from the states of Rio de Janeiro and São Paulo (Prado *et al.* 2020). The following species are known only from Serra do Papagaio in Minas Gerais: *Diphasiastrum falcatum* B.Øllg. & P.G.Windisch, *Hymenophyllum viridissimum* Fée, and *Cyathea glaziovii* (Fée) Domin. *Polystichum auritum* (Fée) Yatsk. is restricted to Parque Nacional do Caparaó and Serra do Papagaio, *Phlegmariurus hemleri* (Nessel) B. Øllg. is known only from Serra do Papagaio and Parque Estadual da Serra do Brigadeiro, and *Austrolycopodium erectum* (Phil.) Holub, and *Lellingeria tamandarei* (Rosenst.) A.R.Sm. & R.C.Moran occur only in Caparaó, Itatiaia, and Serra do Papagaio (the last species was previously recorded only from the part of the park in Rio de Janeiro State). *Ophioglossum crotalophoroides* Walter is cited for a protected area in Minas Gerais for the first time (Serra do Papagaio) and is known only from two other collections in the state, including one made in 1904. *Phlegmariurus rostrifolius* (Silveira) B.Øllg. (*Silveira 179*, herbarium R – photo) stands out because it is known only from the type, which was collected in 1897 in the region (Øllgaard & Windisch, 2019).

Floristic affinities

The NMDS analysis reveals three distinct patterns. The first pattern encompasses areas situated, on average, at elevations above 1000 meters (including Ibitipoca, Sossego, Sul BH, Brigadeiro, Fernão Dias, Rio Preto, Caraça, Intendente, Caparaó, and Papagaio – see Tab. 1). The second pattern comprises areas below 1000 meters elevation and that are situated more than 60 km from the coastline in a straight line (such as Itajaí, Jacupiranga, Cariri, Serra Bonita, and Serra do Mar). The third pattern is defined by coastal lowland areas (below 1000 meters elevation), situated within 60 km of the coastline (including Augusto Ruschi, Juréia, Ilha do Mel, Cairuçu, and Rio das Pedras), alongside two inland areas from the Rio Doce basin (Rio Doce and Caratinga). Despite being at lower elevations, these inland areas are over 200 km away from the sea (see Fig. 3). There are three outliers in this NMDS analysis. The first two are Chapada Diamantina, in the Espinhaço Range (Bahia State), and Cuscuzeiro (São Paulo State), which are a mosaic of phytophysiognomies (a Cerrado and Atlantic Forest ecotone). The third outlier is Itatiaia, which did not group with geographically neighboring areas, such as Serra do Papagaio (Fig. 3).

We observed a significant relationship between mean elevation and area size with the number of species present. The model yielded an adjusted R-squared of 0.2996, indicating that approximately 30% of the variance in the number of species can be explained by mean altitude and area size. The F-test had a value of 6.346 with a p-value of 0.006386, suggesting that the model is statistically significant at a significance level of 0.05. Additionally, the residual standard error was 41.1, indicating the model had a good fit to the data (Fig. 4).

In the GDM results, we observed the percentage of deviance explained by the model with all predictor variables was 65.7%, suggesting that the model can explain most of the data variation (Fig. 4). The intercept was 0.3406, which means that when all other variables are held constant, the average expectation of the response variable is that value. The model that included all environmental variables explained 65.7% of the variation in the data, indicating a good fit for the provided data (Tab. 2). When we analyzed subset 1, in which the bioclimatic variables were removed from the model, the percentage of explanation decreased to 56.7%, with a variable set percentage contribution of 13.6%. Similarly, excluding the cloud variables resulted in a slightly lower percentage of explanation compared to the model that had all variables (63.41%), with a smaller variable set percentage contribution of 3.4%. Removing the EVI (enhanced vegetation index) from the model slightly reduced the percentage of explanation to 64.5%, with a variable set percentage contribution of 1.7%. Excluding elevation and terrain roughness from the model resulted in a decrease in the percentage of explanation to 59.71%, with a variable set percentage contribution of 9%. When the distance variable was removed from the model, there was a substantial drop in the percentage of explanation to 18.3%, with a significantly higher variable set percentage

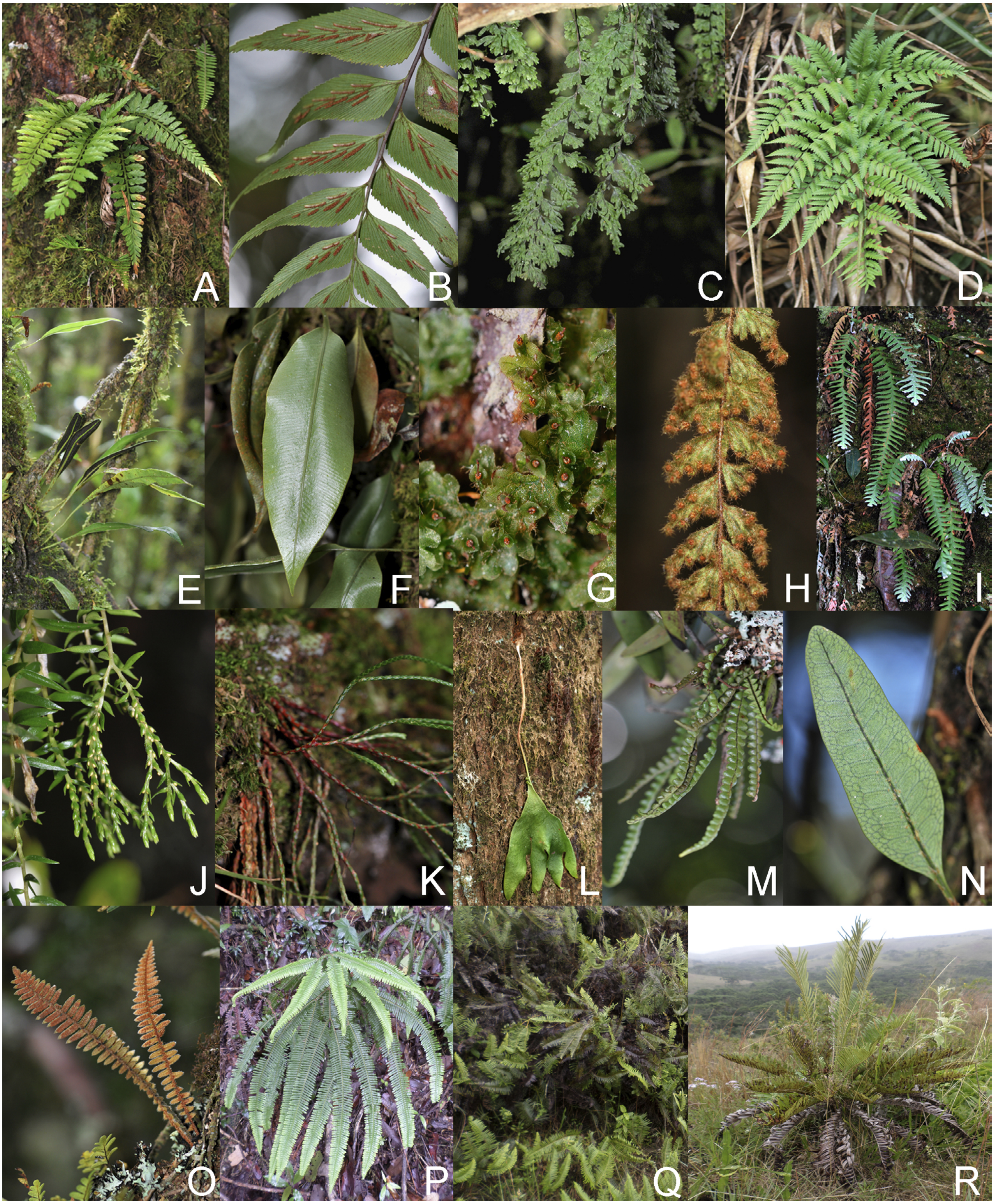

Figure 2. Images of some ferns and lycophytes found in Serra do Papagaio. **A.** *Asplenium auritum* Sw. **B.** *Asplenium serra* Langsd. & Fisch. **C.** *Hymenophyllum polyanthos* (Sw.) Sw. **D.** *Rumohra adiantiformis* (G.Forst.) Ching. **E.** *Elaphoglossum gayanum* (Fée) T.Moore. **F.** *Elaphoglossum vagans* (Mett.) Hieron. **G.** *Trichomanes polypodioides*. **H.** *Hymenophyllum pulchellum* L. **I.** *Ceradenia albidula Rosenst* L. **J.** *Phlegmariurus biformis* (Hook.) B.Øllg. **K.** *Phlegmariurus fontinaloides* (Spring) B.Øllg. **L.** *Cheiroglossa palmatum* (L.) C.Presl. **M.** *Melpomene flabelliformis* (Poir.) A.R.Sm. & R.C.Moran **N.** *Microgramma squamulosa* (Kaulf.) de la Sota. **O.** *Pleopeltis hirsutissima* (Raddi) de la Sota. **P.** *Sticherus squamosus* (Fée) J. Gonzales. **Q.** *Dicranopteris nervosa* (Kaulf.) Maxon. **R.** *Lomariocycas schomburgki* (Klotzsch) Gasper & A.R.Sm.

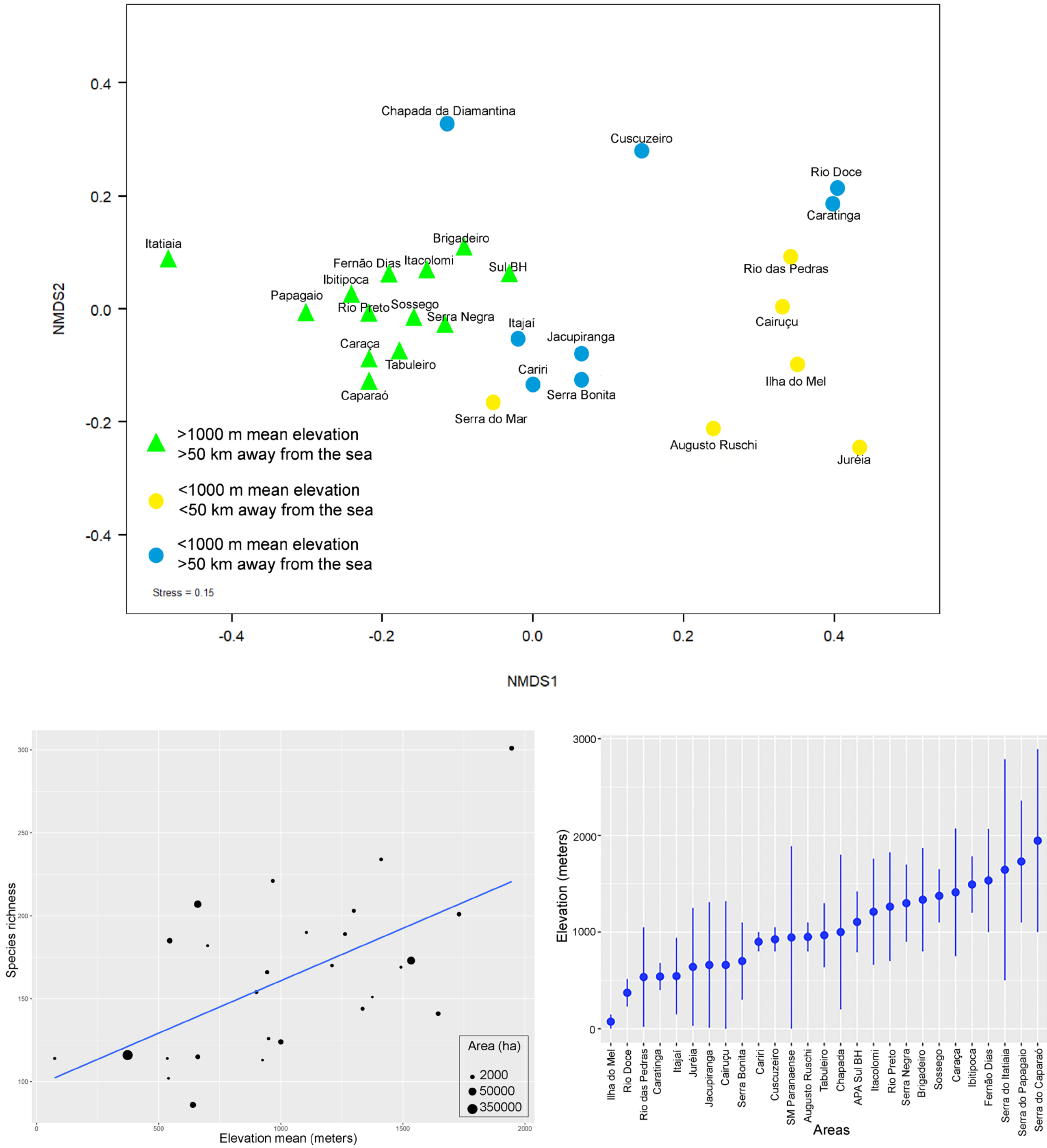

Figure 3. A. NMDS. Green triangles representing areas with elevation means above 1000 m and more than 50 km away from the sea in a straight line. Yellow circles representing areas with elevation means lower than 1000 m and less than 50 km away from the sea. Blue circles representing areas with elevation means lower than 1000 m and more than 50 km away from the sea. **B.** Multiple regression showing the relationship of areas sizes, species richness, and elevation. **C.** Areas' elevation range.

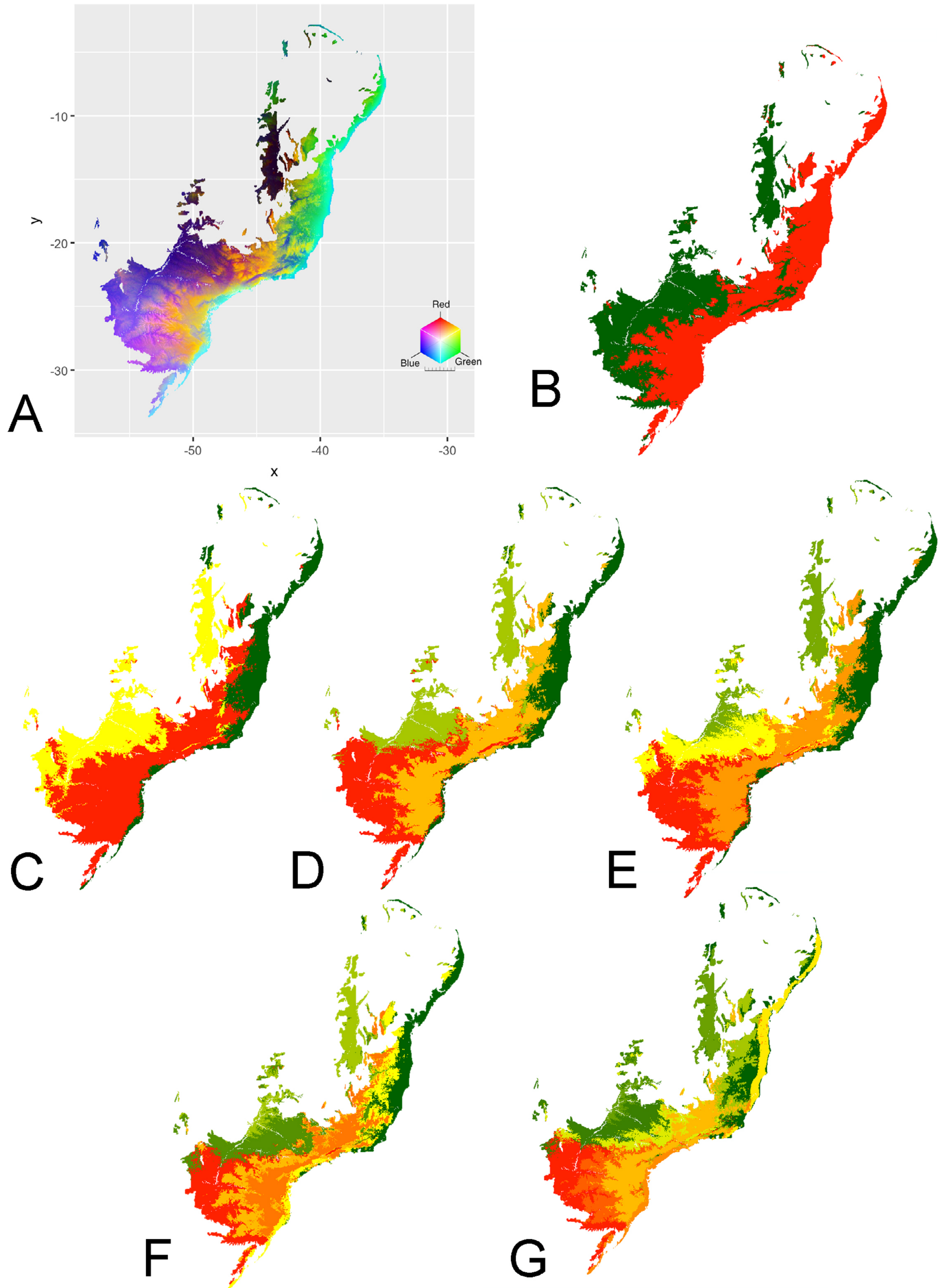

Figure 4. GDM results. **A.** RGB Map showing similar colors representing similar fern and lycophyte composition in Atlantic Forest. **B.** Classification in two classes. **C.** Classification in three classes. **D.** Classification in four classes. **E.** Classification in five classes. **F.** Classification in seven classes. **G.** Classification in ten classes.

Table 2. Results of the independent GDM runs.

Subset	Run type	Percentage of explanation	Variable set percentage contribution
–	With all Variables	65.65	100
1	Without Bioclimatic	56.71	13.61
2	Without Cloud	63.41	3.41
3	Without EVI	64.52	1.72
4	Without Elevation and Terrain Roughness	59.71	9.04
5	Without distance	18.25	72.20

contribution of 72.2%. (Tab. 2). Classification into two groups indicated a separation between western and eastern regions (Fig. 4B). When classifying into three classes (Fig. 4C), a clear separation is observed between northeastern (Fig. 4C, green) and central/southern regions of the Atlantic Forest (Fig. 4C, red), as well as a more inland area (Fig. 4C, yellow). Notably, a gradient from coast to inland is observed when dividing the area into four to ten classes (Fig. 4D-G).

Discussion

Serra do Papagaio has high species richness compared to other sampled areas in the Atlantic Forest in Brazil (Tab. 1). Parque Nacional do Itatiaia, with 342 species (Carrijo *et al*., 2018), Parque Nacional do Caparaó, with 301 species (Carrijo *et al*., 2020), Serra dos Órgãos, with 286 species (Rizzini, 1954), Parque Estadual Turístico do Alto Ribeira, with 250 species (Mazziero *et al.,* 2018), Reserva Biológica do Alto da Serra de Paranapiacaba, with 214 species (Prado & Labiak, 2009), Parque Estadual do Jacupiranga, with 207 species (Salino & Almeida, 2008), Serra Negra, with 209 species (Souza *et al.,* 2012), and Reserva Natural Guaricica (Matos *et al.,* 2020), with 204 species, are sampled areas with more species than Serra do Papagaio. These are all in southeastern Brazil, except for Guaricica. Serra do Papagaio is the second richest inventoried area for ferns and lycophytes located exclusively in Minas Gerais State, after Serra Negra. It contains 27.2 % of all species of ferns and lycophytes recorded in the state (738 spp. in total, according to Flora e Funga do Brasil, 2023).

Although our results indicate a remarkable richness in Serra do Papagaio, the species additional sampling could result in new records of species. It is well documented for various taxonomic groups, including ferns and lycophytes, that the neotropical region is undersampled, primarily due to sampling bias (Almeida & Salino, 2016; Oliveira *et al.,* 2016), and sampling efforts are positively related to richness (Almeida & Salino, 2016; Oliveira *et al.,* 2021; Suissa *et al.* ,2021). Compared to other mountain ranges in southeastern Brazil, such as Serra do Itatiaia and Serra do Caparaó, Serra do Papagaio has a relatively shorter history of intensive fern and lycophyte sampling. For instance, *Phlegmariurus rostrifolius* is known only from a single type specimen collected in 1867. This may indicate the presence of microendemism but also highlights the need for more exhaustive sampling in Serra do Papagaio to better understand its fern and lycophyte diversity.

Mountain ranges can serve as refuges for ancient diverged lineages that benefit from more stable geological and climatic conditions (Cronk, 1997; Fjeldsa *et al.,* 1999; Tang *et al.,* 2018). They can also promote speciation through climatic heterogeneity across elevational gradients and strong seasonal stability within these gradients (Tang *et al.*, 2018). This leads to the emergence of species with limited ranges and niche sizes that, consequently, restrict dispersal and gene flow (Janzen, 1967; Polato *et al.,* 2018; Rangel *et al*., 2018). Considering these environmental conditions, it is expected that the region would exhibit remarkable species richness and endemism. These findings align with the recognition of Serra da Mantiqueira as a hotspot for the abundant diversity of ferns and lycophytes, including numerous endemic species (Souza *et al.,* 2021). Notably, Serra do Papagaio emerges as a key area within the Serra da Mantiqueira Range, given its unique flora, endemic species, and limited historical sampling.

The NMDS ordination suggested that elevation may play a role in or influence the floristic similarity (Fig. 3), which is in accordance with the GDM results. The first pattern, comprising areas with elevations above 1000 meters, may reflect assemblages with species that prefer colder and more humid environments. In fact, such areas are mostly covered by more humid phytophysiognomies, such as ombrophilous forest (Tab. 1). These areas are known as one of the richest formations regarding ferns and lycophytes in the Atlantic Forest (Flora do Brasil, 2023; Salino & Almeida, 2009). On the other hand, the second pattern consists of inner areas below 1000 meters and may be associated with species that prefer warmer and drier environments. These areas are mostly in seasonal deciduous or semideciduous forests in the Atlantic Forest domain (Tab. 1). In these formations within the Atlantic Forest, the seasonality of the dry period may act as a species filter in the community assemblages, resulting in lower species richness compared to humid ombrophilous formations (Flora do Brasil, 2023; Salino & Almeida, 2009). The third pattern, encompassing lowland areas near the ocean, may reflect the influence of the sea on the availability of water, which can affect the distribution of species (Qian *et al.,* 2023). It has been demonstrated that the heterogeneity of habitats promoted by elevational gradients is a key factor in fern and lycophytes species richness and composition (Kessler *et al.,* 2016; Suissa *et al.,* 2021; Umair *et al.,* 2023).

The multiple regression results suggest that elevation and area size are important factors influencing species diversity in the study area (Fig. 3). Elevation had a positive correlation with richness, while area size had a negative correlation. Large and small areas at low elevations had lower species richness, while areas of small and medium size, but at higher elevations, had higher richness. This pattern may be associated with environmental heterogeneity and niche specialization distributed along an elevational gradient (Kessler *et al.,* 2011; 2016), which are known strong drivers of fern and lycophyte diversification (Suissa *et al.,* 2021; Suissa & Sundue, 2020).

Serra do Itatiaia, one of closest areas to Papagaio, appears as an outlier. This raises the question whether dissimilarity in fern and lycophyte assemblages in the Atlantic Forest is driven more by geographic or environmental distance. GDM operates as a beta-diversity analysis, focusing on dissimilarities among communities rather than considering species in isolation. In this context, our results suggest that, among the investigated environmental variables, the geographic distances between studied communities contribute significantly to explaining dissimilarities in fern and lycophyte composition within the Atlantic Forest (Fig. 4). Such results suggest that distance plays a crucial role in the distribution of fern and lycophyte communities in the Atlantic Forest, potentially due to niche specificity or environmental filtering, or even limitations in dispersal. Climate and altitude contributed significantly to the remaining variation. Taking into consideration a comprehensive global study that explored the drivers of fern and lycophyte hotspots using a large dataset (Suissa & Sundue, 2020), it becomes evident that additional factors must be considered. These factors include phytophysiognomies and soil types because they are directly intertwined with the distribution of ferns and lycophytes (Karst *et al*., 2005; Andrade *et al*., 2017; Viana & Dalling, 2022).

The GDM analysis output shows that regions with similar compositions of ferns and lycophytes display similar color patterns (Fig. 4). The patterns identified in the GDM results suggest a potential relationship between environmental characteristics and the observed patterns found in the NMDS analysis (Fig. 4A). The classification method used allowed the identification of breakpoints in the dissimilarity distribution of fern and lycophyte communities in the Atlantic Forest. The two-class classification (Fig. 4B) distinguishes the Atlantic Forest broadly (*sensu lato*) from a stricter definition (*sensu stricto*), possibly reflecting climate-based differences between the coastal and inner areas impacting fern and lycophyte communities. The three-class classification (Fig. 4C) highlights clear distinctions, the northeastern region in green, central/southern regions in red and an inland zone in yellow, which may have been influenced by the elevation and latitude since they are known to be associated with fern and lycophyte distributions (Suissa & Sundue, 2020; Testo *et al*., 2019). A coast-to-inland gradient emerges in four to seven classes (Fig. 4D-F), revealing the role of continentality as humidity decreases. Additional factors could play a role in the diversity of fern and lycophyte communities, including edaphic factors, which might significantly influence the formation of diversity gradients within tropical rainforests (*e.g.*, Tuomisto & Poulsen, 1996; Zuquim *et al*., 2009; Pansonato *et al*., 2013; Tuomisto *et al*., 2014; Moulatlet *et al*., 2019; Tuomisto *et al*., 2019; Viana *et al*., 2021; Michael *et al*., 2023). Additionally, the different phytophysiognomies within the Atlantic Forest, characterized by distinct microclimatic conditions, can significantly impact the community structure of ferns and lycophytes due to seasonality, luminosity, humidity, and other ecological filters (Kessler *et al.,* 2016). Biotic interactions, such as competition and facilitation among species, can also shape the composition of ferns and lycophytes (Kluge & Kessler, 2011). For example, certain ferns, such as members of Gleicheniaceae may exhibit competitive advantages over others, leading to differences in their abundance and distribution patterns (Yang *et al.,* 2021). On the other hand, facilitative interactions, such as the provision of shade or shelter by certain plant species, can create favorable microhabitats for fern and lycophyte establishment and growth (Gould *et al.,* 2013; Wan *et al.*, 2014; Zhang *et al.,* 2017). Understanding the complex interplay between these environmental and biotic factors is essential to comprehend the dynamics of fern and lycophyte communities within the Atlantic Forest and to develop effective conservation strategies (Carvajal-Hernández *et al.,* 2017).

Our findings support the hypothesis that the presence of coastal mountain ranges in the Brazilian Atlantic Forest, such as Serra do Mar and Serra da Mantiqueira, plays a crucial role in enhancing rainfall and retaining humidity by creating a physical barrier to the Atlantic air masses (Oliveira-Filho & Fontes, 2000). The resulting microhabitats, which favor forest growth, ensure a consistent level of humidity and temperature stability. For instance, the high-elevation dwarf forests in Serra do Papagaio, Serra do Itatiaia, and Serra do Caparaó are ecosystems that thrive at high elevations and rely on consistent cloud cover to maintain the necessary humidity. These formations are known for their high levels of endemism, abundance of epiphytes, and presence of rare species (Campos *et al.,* 2018; Carrijo *et al.,* 2018; 2020). On the other hand, in inland areas the elevation tends to be lower. In northeastern Brazil, the Atlantic Forest is predominantly found in coastal areas, while inland areas are characterized by semiarid to arid formations. In such cases, the oceanic moisture is hindered by orographic barriers, limiting its reach inland. These findings align with the hypothesis previously proposed (Tryon, 1972; Tryon & Tryon,1982; Suissa & Sundue, 2020) about the distribution of fern and lycophyte diversity in tropical regions.

The species diversity in the mountain ranges in southeastern Brazil is predominantly influenced by allopatric speciation driven by climate and environmental heterogeneity (Safford, 2007). The impact of climatic and topographic variations becomes apparent when comparing the border region between the states of Espírito Santo and Rio de Janeiro. Souza *et al.* (2021) found a notable reduction in species richness in this region, which the authors attributed to the Serra do Mar's departure from the coastal zone and the presence of lowland areas, usually characterized by lower humidity levels and a more open vegetation structure. The GDM results revealed variations in the composition of fern and lycophyte communities, which aligns with the disparities observed in species richness reported by the authors (Fig. 5).

Lower coastal areas sampled had low species richness (Cariaçu with 115 spp., Ilha do Mel with 114 spp., and Rio das Pedras with 114 spp.) compared to other sampled areas. They are areas with high levels of humidity but low species richness compared to areas at higher elevations. Interestingly, areas at lower elevations that are more than 200 km from the ocean also had low species richness, although some are large. For example, Rio Doce has 116 species distributed in 35,973 ha and an elevation range of 230–515m (Tab. 1, Fig. 4). Nevertheless, these observations might be primarily linked to local factors, such as soil types, temperature, humidity, and the biogeographic history of the area. In this case, low species richness may be related to the predominance of semideciduous formations in the areas and the dry seasonality effect acting as an ecological filter of the species composition.

When analyzing the GDM results, we observe that Serra do Itatiaia and Serra do Papagaio are in a region with a similar composition, although this conflicts with the result from the NMDS. Two possible explanations can be considered. First, Itatiaia has a higher sampling effort, and it has been demonstrated that sampling bias had a strong negative impact on documenting species richness (Almeida & Salino, 2016; Carrijo *et al.,* 2018; Suissa & Sundue, 2020). Second, Serra do Itatiaia harbors a considerable number of microendemics. The NMDS analysis is sensitive to species absences, and unique occurrences can potentially influence Itatiaia as an outlier.

Therefore, we hypothesize that the uniqueness of Serra do Itatiaia may be attributed to its significant range elevation (Fig. 8), which potentially offers a broader spectrum of environments with diverse niche conditions that lead to higher species richness. Studies have shown that the more humid sides of mountains tend to host a greater abundance of ferns, which aligns with the niche requirements of these plant lineages (Suissa & Sundue, 2020).

We underscore the biological importance of Serra do Papagaio in the Atlantic Forest. Our results highlight the significance of preserving areas at higher elevations because they contribute significantly to species diversity. Elevation is an important factor influencing the composition of ferns and lycophytes, while spatial heterogeneity plays a crucial role in shaping species distribution patterns. Distinct phytophysiognomies can lead to isolated groups of ferns and lycophytes, even in geographically close regions. These findings emphasize the need to consider spatial heterogeneity when designing effective conservation strategies, as it plays a pivotal role in maintaining biodiversity. We highlight the complex interplay between environmental factors and species diversity, as well as the importance of considering multiple variables in conservation planning. We also emphasize the need for additional research and conservation efforts to fully understand the richness and diversity of species in the Serra da Mantiqueira region. Overall, our results contribute to a better scientific understanding of the Atlantic Forest ecosystem and provide essential insights that can guide conservation strategies. This work highlights the need to incorporate spatial heterogeneity and environmental factors in conservation planning efforts to ensure the long-term preservation of biodiversity in the region.

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Author Contributions

LVL: Contributions to the conception and design of the study, data collection, data analysis and interpretation, preparation of the manuscript draft, contribution to the critical revision, and the addition of intellectual content; AS: Contributions to manuscript preparation, data collection, critical revision, and the addition of intellectual content; VAOD: Contributions to manuscript preparation, data collection, preparation of the manuscript draft, critical revision, and the addition of intellectual content; SGF: Contributions to data collection, manuscript preparation, critical revision, and the addition of intellectual content; LMN: Contributions to data collection, manuscript preparation, critical revision, and the addition of intellectual content; TEA: Contributions to the conception and design of the study, data collection, data analysis and interpretation, preparation of the manuscript draft, contribution to the critical revision, and the addition of intellectual content.

Conflict of Interest

The authors declare no conflict of interest.

Supplementary Material

The following online material is available for this article:

Table S1 – Species list of ferns and lycophytes from the Serra do Papagaio.

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