

Woody vegetation in Atlantic Forest inselbergs: floristic similarity, patterns of richness, pollination/dispersal syndromes, and influence of climatic variables

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Abstract: Forest ecosystems established on developed soils occupy the most significant territorial extension in the Atlantic Forest and are historically the most studied environments in this domain. However, woody vegetation on granitoid rock outcrops (inselbergs) has been historically neglected. The objective of this study was to analyze the composition of the woody flora of inselbergs in the Monumento Natural do Maciço das Andorinhas (MONAMA), a southern region of Espírito Santo state, and evaluate its similarity with other inselbergs studied in southeastern Brazil. Based on field expeditions and literature data, we recorded a total of 27 species, 25 genera, and 16 families. The families Fabaceae and Myrtaceae, along with the genus *Eugenia*, were the richest in species diversity. The predominant pollination and dispersal syndromes were entomophily and zoochory, respectively. Furthermore, *Erythroxylum deciduum*, *Ficus cyclophylla*, *Pseudobombax petropolitanum*, *Trigoniodendron spiritusantense*, and *Wunderlichia azulensis* are listed as endangered species. *Pseudobombax petropolitanum*, *Tabebuia reticulata* and *Wunderlichia azulensis* are endemic to inselbergs of the Atlantic Forest. Species endemic to the Atlantic Forest and species with wide geographic distribution across Brazilian phytogeographical domains predominated. Regarding environmental variables, the CCA indicated a strong correlation between woody species and elevation, maximum temperature of the warmest month, mean diurnal range, and precipitation in the driest month. MONAMA has more species shared with inselbergs in southern Espírito Santo due to geographic distance. This study provides an essential contribution to the knowledge of the woody vegetation of inselbergs, which has been historically neglected in the Atlantic Forest domain.

Keywords: Conservation; environmental variables; rock outcrop; rupicolous flora; saxicolous flora.

Vegetação lenhosa em inselbergs de Mata Atlântica: similaridade florística, padrões de riqueza, síndromes de polinização/dispersão e influência de variáveis climáticas

Resumo: Ecossistemas florestais estabelecidos em solos desenvolvidos ocupam a extensão territorial mais significativa na Mata Atlântica e são historicamente os ambientes mais estudados neste domínio. No entanto, a vegetação lenhosa em afloramentos rochosos granitoides (inselbergs) tem sido historicamente negligenciada. O objetivo deste estudo foi analisar a composição da flora lenhosa de inselbergs no Monumento Natural do Maciço das Andorinhas (MONAMA), uma região ao sul do estado do Espírito Santo, e avaliar sua similaridade com outros inselbergs estudados no sudeste do Brasil. Com base em expedições de campo e dados da literatura, registramos um total de 27 espécies, 25 gêneros e 16 famílias. As famílias Fabaceae e Myrtaceae, juntamente com o gênero *Eugenia*, foram as mais ricas em diversidade de espécies. As síndromes predominantes de polinização e dispersão foram entomofilia e zoocoria, respectivamente. Além disso, *Erythroxylum deciduum*, *Ficus cyclophylla*, *Pseudobombax petropolitanum*, *Trigoniodendron spiritusantense* e *Wunderlichia azulensis* estão listadas como espécies ameaçadas de extinção. *Pseudobombax petropolitanum*, *Tabebuia reticulata* e *Wunderlichia azulensis* são endêmicas de inselbergs da Mata Atlântica. Espécies endêmicas da Mata Atlântica e espécies com ampla distribuição geográfica nos domínios fitogeográficos brasileiros predominaram. Em relação às variáveis ambientais, a CCA indicou forte correlação entre espécies lenhosas e altitude, temperatura máxima do mês mais quente, amplitude média diurna

e precipitação no mês mais seco. MONAMA possui mais espécies compartilhadas com inselbergs no sul do Espírito Santo devido à distância geográfica. Este estudo fornece uma contribuição essencial para o conhecimento da vegetação lenhosa de inselbergs, que tem sido historicamente negligenciada no domínio da Mata Atlântica.

Palavras-chave: *Conservação; variáveis ambientais; afloramento rochoso; flora rupícola; flora saxícola.*

Introduction

Inselbergs, rocky outcrops of granite and/or gneiss, stand out as centers of plant diversity, especially in tropical and subtropical regions (Porembski et al. 1997, Porembski and Barthlott 2000b). In Brazil, these ecosystems predominate in the Caatinga and Atlantic Forest, being particularly common in the southeastern region, where the most diversity and variability of plants in Brazilian inselbergs is concentrated (Safford and Martinelli 2000, Porembski 2007, de Paula et al. 2020, Azevedo et al. 2024). These ecosystems, recognized as terrestrial islands (Porembski and Barthlott 2000a, Porembski and Barthlott 2000b), are strongly influenced by environmental filters, such as thermal variations, winds, shallow, impermeable, and overheated soil, limiting the fixation of roots, seeds, and propagules (Larson et al. 2000, Porembski and Barthlott 2000a). These characteristics result in ecologically isolated ecosystems that are prone to harboring endemic, specialized, and threatened species (Porembski and Barthlott 2000b, Porembski 2007, de Paula et al. 2016, Couto et al. 2016, 2017, Francisco et al. 2018). However, they face threats, especially from mining, invasive grasses, fires, tourism, goat farming, and the extraction of ornamental plants, resulting in loss of biodiversity and degradation of ecosystem services (Porembski et al. 2016, Francisco et al. 2023).

Different habitat types have been recognized in tropical inselbergs, which include cryptogam crust, epilithic vascular vegetation, monocol mats, rock pools, shallow depressions, crevices, ephemeral vegetation, vertical rock walls, woody vegetation, and forest islands (Porembski et al. 1997, Porembski and Barthlott 2000b, Porembski 2007, Couto et al. 2023, 2025). Woody vegetation of inselbergs is characterized by woody individuals of short stature, adapted to shallow soils and high light intensity (Porembski et al. 1997, Couto et al. 2025). Although there is an increase in studies on the flora of Atlantic Forest inselbergs, the understanding of the woody flora in these ecosystems is still limited (Sarhou et al. 2003, Ottaviani et al. 2016, Francisco et al. 2018, Couto et al. 2022, 2025), as well as their pollinators and seed dispersers, harming conservation efforts. Species pollinated by insects (entomophily) are predominant in Neotropical ecosystems (Bawa 1990), while dispersal by vertebrates assumes great relevance in tropical forests (Almeida-Neto et al. 2008). In contrast, the dispersal pattern found in open ecosystems, such as inselbergs, is predominantly abiotic, that is, driven by the wind (Porembski et al. 1998, Silva Costa et al. 2015).

Furthermore, our understanding of the abiotic factors that influence diversity, that is, species composition on rocky ecosystems, is still limited. For example, it is widely recognized that the biological diversity of the Atlantic Forest is shaped by geographic, geological, pedological, and climatic variability. This domain spans a broad latitudinal range (3°S–30°S), altitudinal range (from sea level to nearly 3,000 meters), and precipitation levels, resulting in the development of different types of vegetation, including dense rainforests, deciduous and semideciduous forests, and open vegetation formations, such as coastal restingas and rocky outcrops (Stehmann et al. 2009). Among these variables,

lithology, i.e., rock type, plays a fundamental role in the beta diversity of lithophytes plant communities in eastern Brazil, with distinct floras hosted in areas of granite and/or gneiss outcrops (inselberg), limestone outcrops, quartzite rocky grasslands, and ironstone rocky grasslands (Azevedo et al. 2024). In addition to lithology, climatic variables influence the species composition of inselbergs in eastern Brazil, distinguishing, for example, the flora of coastal inselbergs of the Atlantic Forest from those located further inland (de Paula et al. 2021), as well as the inselbergs of the Atlantic Forest in comparison to those situated in the dry diagonal of Brazil, with a semi-arid climate within the Caatinga domain (Azevedo et al. 2024). Among the most critical climatic variables in the structuring of plant communities on rocky outcrops are the variables related to temperature and precipitation (Pinto-Junior et al. 2020a, de Paula et al. 2021, Azevedo et al. 2024). These climatic variables indicate that the dependence on moisture and adaptations to seasonality are likely essential characteristics of the plants that elucidate their distributions in the Brazilian inselbergs (de Paula et al. 2019). Therefore, it is crucial to learn about the woody community of inselbergs and understand how these ecological processes affect the species composition in these environments.

In this study, we conducted an inventory of woody species in a complex of inselbergs within the “Monumento Natural do Maciço das Andorinhas”, in the state of Espírito Santo, southeastern Brazil. Furthermore, we evaluated the floristic similarity of the woody species from MONAMA with other inselbergs from southeastern Brazil, expecting that geographically closer inselbergs would present more similar communities of woody species. We analyzed the relationships between the woody flora and the respective influence of environmental variables among the inselbergs, assuming these variables affect the species composition. Finally, we verified which pollination and dispersal syndromes are most frequent in the woody species of the inselbergs of MONAMA, expecting that the results follow the general pattern found for vegetation on rocky outcrops (entomophily and anemochory/autochory).

Material and Methods

1. Study site

The study was carried out in a rocky complex of dome-shaped lowland inselbergs, located in the Monumento Natural Maciço das Andorinhas (hereafter MONAMA) (20°47' S, 41°21' W), a protected area located in the municipalities of Jerônimo Monteiro and Cachoeiro de Itapemirim, in the southern region of Espírito Santo state (Figure 1). The geological formation of MONAMA is mainly composed of granite and/or gneissic rocks, the climate in the region has been classified as Cwa (Alvares et al. 2013), with dry winters and rainy summers, the mean annual temperature is about 24°C, the mean annual rainfall is 1,450 mm, situated along an elevation gradient ranging from 150 to 500 m a.s.l. (Couto et al. 2016, Covre et al. 2021).

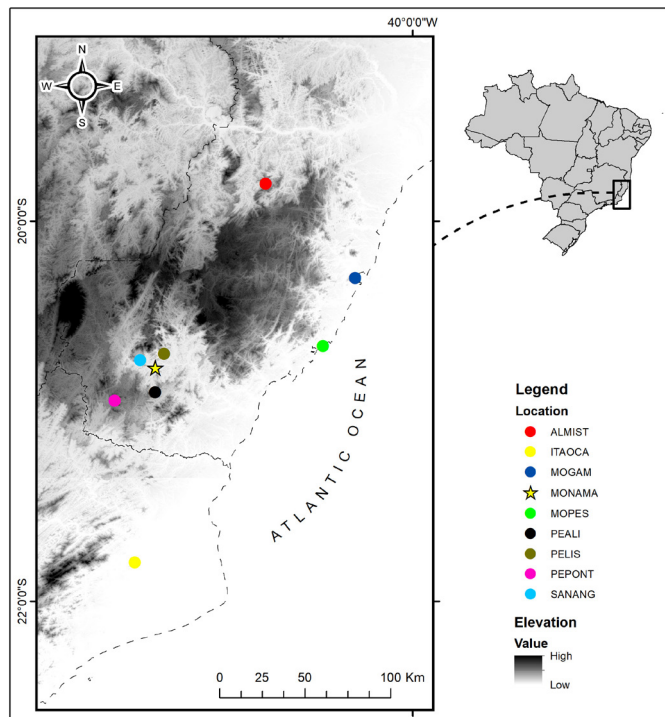


Figure 1. Location of the “Monumento Natural do Maciço das Andorinhas” (MONAMA), in the municipality of Jerônimo Monteiro, Espírito Santo, Brazil, and the inselbergs used in the floristic similarity (See Table 1)

MONAMA was initially surrounded by the submontane Semideciduous Seasonal Forest (Veloso et al. 1991). However, currently, it is surrounded by a mosaic formed by remnants of seasonal forests and anthropic areas, with a predominance of crops (coffee, eucalyptus, and orange plantations), livestock farming, in addition to urban areas and ornamental rock mining (Covre et al. 2021). The main recurring impacts under MONAMA are mining and weed invasion, two of the leading global threats to inselbergs (de Paula et al. 2015, Porembski et al. 2016). Published data on MONAMA's rupicolous flora showed high richness, threatened and endemic species (see Covre et al. 2021), including new species to science that were described in the last two decades through samples collected in this location (Martinelli and Forzza 2006, Versieux and Wanderley 2007, Coelho and Valadares 2019, Couto et al. 2020). These facts corroborate MONAMA as being of biological importance, as already evidenced by other authors (Martinelli 2007, Couto et al. 2016, Manhães et al. 2016).

2. Data collection

Sampling efforts took place in the MONAMA inselbergs, known locally as Pedra da Parada Cristal (20°47.51' S, 41°22.21' W), Pedra das Três Irmãs (20°47.21' S, 41°21.47' W), and Pedra das Andorinhas (20°46.54' S, 41°21.27' W). To expand the MONAMA floristic list of woody species (Covre et al. 2021), ten excursions were carried out over a year (2019–2020), through random walks (Filgueiras et al. 1994), when samples were collected fertile and processed following the usual procedures in floristic surveys (Mori et al. 1989), and subsequently deposited in the Capixaba Herbarium (CAP), of the Department of

Forestry and Wood Sciences at the Federal University of Espírito Santo (acronym follows Thiers 2022, constantly updated). Specimen identification was carried out using taxonomic keys, monographs, comparisons with herbarium collections, and consultations with specialists from specific taxonomic groups. Subsequently, the list was complemented with data available in the literature on the MONAMA flora (Covre et al. 2021).

The circumscription of angiosperm families followed the Angiosperm Phylogeny Group (APG IV 2016). Abbreviations of authors' names, currently accepted names, synonyms, and the geographic distribution of taxa follow Flora and Funga do Brasil (<http://floradobrasil.jbrj.gov.br/>), and rare species were categorized according to Giulietti et al. (2009). The species were classified into five geographic distribution patterns: 1) wide distribution (occur in more than three phytogeographic domains); 2) endemic to Atlantic Forest (Ma); 3) Amazon; 4) Caatinga; 5) Cerrado. Species threatened were cited by the National List of Threatened Species (MMA 2022) and the State List of Threatened Flora of Espírito Santo (Espírito Santo 2022), according to IUCN criteria (VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

The pollination syndromes of the species were characterized based on the criteria proposed by Faegri and Van Der Pijl (1913), classifying the species into abiotic (Anemophily – wind) or biotic (Entomophily – insects, Ornithophily – birds and Chiropterophily – bats) syndromes. Regarding dispersal syndrome, the species were classified as anemochoric, zoochoric, and autochoric, according to Van Der Pijl (1982).

The recorded species were categorized according to their occupation in the different types of habitats found in rocky outcrops, without taking into account microhabitats occurring on a smaller scale (Porembski 2007). Following this assumption, the habitat types were classified into two large groups: (a) vegetation islands - classified as circular or ellipsoidal vegetation patches surrounded by bare rock, which are evidenced by rupicolous trees that vegetate directly on the rock, concomitant with the formation of monocotyledon mats (Porembski 2007), and (b) woody thicket - transitional vegetation between the outcrop and the vegetation of the surrounding matrix, without the presence of monocotyledon mats (Rizzini 1997).

Nine areas of inselbergs in the Atlantic Forest, including the area studied here - MONAMA, were selected (Table 1). To select the inselbergs, we analyzed the floristic lists where woody vegetation (shrubs/trees) was sampled. To create the matrix, we included 87 species of shrubs and trees, collectively referred to as woody vegetation. Also, for each inselberg, 19 bioclimatic variables (Supplementary Table S1) were obtained from the Worldclim 2.1 database (available at www.worldclim.org), with a spatial resolution of 30 arc seconds (Fick and Hijmans 2017). From here on, bioclimatic variables will be referred to as environmental variables.

3. Data analysis

Canonical correspondence analysis (CCA) (Ter Braak 1986) was used to examine the relationship between woody species on the nine inselbergs and environmental variables. Before running the CCA, we performed correlation testing and collinearity diagnosis to select the most significant variables and remove redundancies (Legendre and Legendre 2012). The correlation between variables was assessed

Table 1. Areas of inselbergs in the Atlantic Forest that were used for the analysis. (Spp. = number of species, Gen. = number of genera, Fam. = number of families).

Acronym	Location (state)	Spp.	Gen.	Fam.	Latitude (S)	Longitude (W)	Elevation (m)	Reference
MONAMA	Monumento Natural do Maciço das Andorinhas - Jerônimo Monteiro (ES)	27	25	16	20°46'19"	41°21'12"	150–500	This study
ALMIST	Alto Misterioso - São Roque do Canaã e Itaguaçu (ES)	27	21	17	19°48'10"	40°46'19"	850–1143	Esgario et al. (2009)
MOGAM	Morro da Gameleira - Vitória (ES)	12	12	10	20°17'58"	40°18'5"	20–107	Santos et al. (2010)
MOPES	Morro da Pescaria - Guarapari (ES)	12	12	10	20°39'27"	40°28'15"	0–75	Dal Col and Thomaz (2016)
PEPONT	Pedra dos Pontões - Mimoso do Sul (ES)	17	13	10	20°56'43"	41°34'05"	700–1400	Couto et al. (2017)
PEALI	Pedra da Aliança - Muqui (ES)	10	10	5	20°54'05"	41°21'15"	200–450	Couto et al. (2025)
PELIS	Pedra Lisa - Cachoeiro de Itapemirim (ES)	10	10	7	20°41'55"	41°18'28"	180–300	Couto et al. (2025)
SANANG	Pedra Santa Angélica - Alegre (ES)	12	12	11	20°43'55.3"	41°25'59.3"	150–300	Couto et al. (2025)
ITAOCA	Morro do Itaoca - Campos dos Goytacazes (RJ)	12	12	11	21°47'48"	41°27'41"	10–170	Couto et al. (2021)

using Spearman's Correlation. We included in the analysis only variables in which the correlation with other variables was less than 0.7 (Supplementary Figure S1). Collinearity between variables was assessed using the variance inflation factor (VIF). VIF values > 10 indicated significant collinearity (Zuur et al. 2010). Four variables were selected: elevation, maximum temperature of the warmest month, mean diurnal range, and driest month precipitation. The significance of the variation in woody species explained by environmental variables was tested in ANOVA-like Monte Carlo with 999 permutations.

The influence of spatial autocorrelation on the composition of woody species was analyzed using the Mantel test (Legendre and Legendre 2012). For this, a spatial matrix was created based on the geographic coordinates of the inselbergs. The inclusion of geographic distance between areas as a component aimed to verify the contribution of space to floristic similarity. The statistical significance test for the Mantel correlation was based on 10,000 permutations. The analyses were carried out using the *corrplot* (Wei and Simko 2017) and *vegan* (Oksanen et al. 2019) packages in the R software (R Core Team 2023). To enhance the robustness of the analyses, only species identified at a specific taxonomic level were included in the dataset. Species with dubious identifications ("affinis" [aff.] or "conferatum" [cf.]) were excluded, and different subspecies and varieties were considered as the same species.

The floristic similarity between the inselbergs was assessed using cluster and ordination analyses. Cluster analysis used the Jaccard similarity index (Magurran 1988), based on the matrix of presence and absence of woody species using the UPGMA clustering algorithm (unweighted pair group method with arithmetic mean). To determine whether the cluster adequately represents the original similarity matrix, the cophenetic correlation coefficient (Borcard et al. 2011) was

calculated by performing a Pearson correlation between the original similarity matrix and the cophenetic matrix. Cluster analysis was performed using the Paleontological Statistics - PAST v. 1.89 software (Hammer et al. 2001).

Results

1. Floristics

Twenty-seven woody species were recorded for MONAMA, distributed in 25 genera and 16 families (Figure 2; Table 2). The most representative families in terms of the number of species were Fabaceae (five species, 19%), Myrtaceae (four species, 15%), followed by Anacardiaceae (8%), Malvaceae (8%) and Verbenaceae (8%), with two species each. These families represented 56% of the total recorded species richness. The genus *Eugenia* (Myrtaceae) was represented by three species, while the others were represented by only one.

Through our field observations, it was possible to discriminate between two types of habitats with woody vegetation (vegetation island and woody thicket) on the slopes of the inselbergs. The vegetation island habitat was evidenced by the rupicolous trees that vegetate directly on the exposed rock, such as *Pseudobombax petropolitanum* A. Robyns, *Tabebuia reticulata* A.H. Gentry and *Wunderlichia azulensis* Maguire & G.M. Barroso. Together with these tree species, there were formations of monocotyledon mats represented mainly by *Alcantarea patriae* Versieux & Wand., *Pitcairnia azouryi* Martinelli & Forzza, and *Vellozia plicata* Mart., which resulted in a mosaic-shaped structure. This habitat was classified as shallow depressions, according to Porembski (2007). The second habitat (woody thicket) was composed predominantly of saxicolous species that grow on thin and poorly developed soil, such as *Pilocarpus spicatus* A. St.-Hil., *Calliandra harrisii* (Lindl.) Benth.,

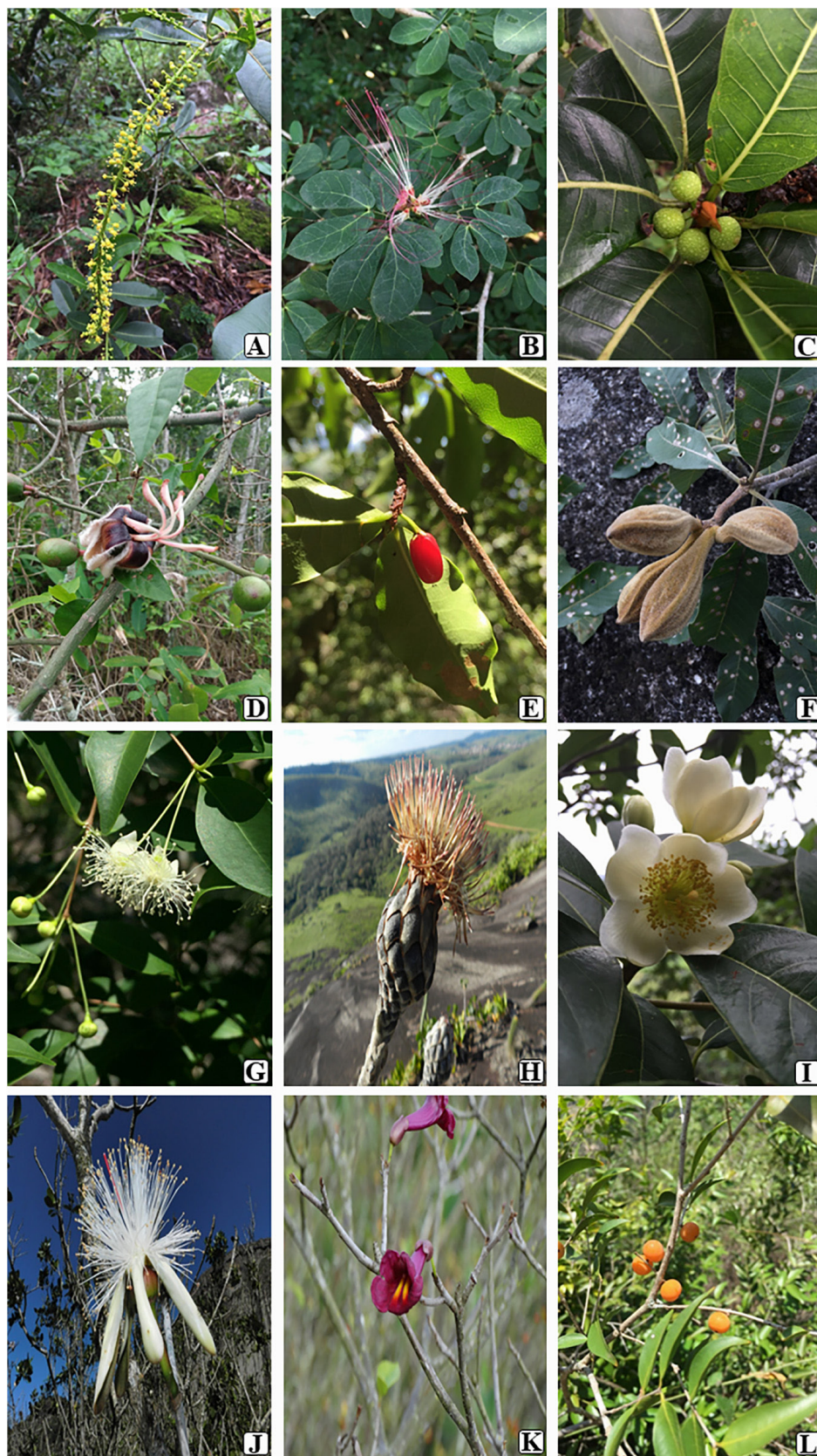


Figure 2. Woody species recorded for the “Monumento Natural do Maciço das Andorinhas” (MONAMA). A. *Pilocarpus spicatus* (Rutaceae); B. *Calliandra harrisii* (Fabaceae); C. *Ficus cyclophylla* (Moraceae); D. *Ceiba erianthos* (Malvaceae); E. *Erythroxylum deciduum* (Erythroxylaceae); F. *Aspidosperma gomezianum* (Apocynaceae); G. *Eugenia punicifolia* (Myrtaceae); H. *Wunderlichia azulensis* (Asteraceae); I. *Kielmeyera membranacea* (Calophyllaceae); J. *Pseudobombax petropolitanum* (Malvaceae); K. *Tabebuia reticulata* (Bignoniaceae); L. *Myrciaria floribunda* (Myrtaceae)

Table 2. Woody species recorded in inselbergs of the “Monumento Natural do Maciço das Andorinhas”, Espírito Santo, Southeast Brazil. Pollination syndrome (PS): Ent = entomophily, Orn = ornithophily, Qui = chiropterophily; Dispersal syndrome (DS): Ane = anemochory, Zoo = zoochory, Aut = autochory; Phytogeographical Domain (DF): AD = wide distribution (occur in more than three phytogeographical domains in Brazil and/or outside Brazil), Am = Amazon, Ca = Caatinga, Ce = Cerrado, EN = endemic to the Atlantic Forest (Ma). Iv = islands of vegetation, Tw = woody thicket. “*” = species restricted to rocky outcrops. Voucher: Covre = João Mário Comper Covre. “—” = not applicable.

Family/Species	PS	DS	DF	Rocky habitat types	Voucher (herbarium)
ANACARDIACEAE (2)					
<i>Astronium graveolens</i> Jacq.	Ent/Ane	Ane	AD	Tw	Covre 236 (CAP)
<i>Spondias mombin</i> L.	Ent	Zoo	Am/Ce/Ma	Tw	Covre 242 (CAP)
APOCYNACEAE (1)					
<i>Aspidosperma gomezianum</i> A.DC.	Ent	Ane	EN	Iv	Covre 243 (CAP)
ASTERACEAE (1)					
<i>Wunderlichia azulensis</i> Maguire & G.M.Barroso*	Ent	Ane	Ca/Ma	Iv	Covre 246 (CAP)
BIGNONIACEAE (1)					
<i>Tabebuia reticulata</i> A.H.Gentry*	Ent/Orn	Ane	EN	Iv	Covre 237 (CAP)
CALOPHYLLACEAE (1)					
<i>Kielmeyera membranacea</i> Casar.	Ent	Ane	EN	Iv	Covre 247 (CAP)
ERYTHROXYLACEAE (1)					
<i>Erythroxylum deciduum</i> A.St.-Hil.	Ent	Zoo	Am/Ce/Ma	Tw	Covre 244 (CAP)
EUPHORBIACEAE (1)					
<i>Cnidoscolus oligandrus</i> (Müll.Arg.) Pax	Ent	Aut	Ca/Ma	Tw	Covre 238 (CAP)
FABACEAE (5)					
<i>Albizia polycephala</i> (Benth.) Killip ex Record	Ent	Aut	Ca/Ce/Ma	Tw	Covre 235 (CAP)
<i>Anadenanthera peregrina</i> (L.) Speg.	Ent	Aut	AD	Tw	Covre 245 (CAP)
<i>Andira legalis</i> (Vell.) Toledo	Ent	Zoo	EN	Tw	Covre 251 (CAP)
<i>Calliandra harrisii</i> (Lindl.) Benth.	Ent	Aut	Ca/Ce/Ma	Tw	Covre 234 (CAP)
<i>Deguelia costata</i> (Benth.) A.M.G.Azevedo & R.A.Camargo	Ent	Ane	EN	Tw	Covre 252 (CAP)
MALVACEAE (2)					
<i>Ceiba erianthos</i> (Cav.) K.Schum.	Qui	Ane	Ca/Ma	v	Covre 239 (CAP)
<i>Pseudobombax petropolitanum</i> A.Robyns*	Qui/Orn	Ane	EN	Iv	Covre 250 (CAP)
MELASTOMATACEAE (1)					
<i>Pleroma heteromallum</i> (D.Don) D.Don	Ent	Ane	Ce/Ma	Iv	Covre 98 (CAP)
MORACEAE (1)					
<i>Ficus cyclophylla</i> (Miq.) Miq.	Ent	Zoo	EN	Tw	Covre 198 (CAP)
MYRTACEAE (4)					
<i>Eugenia punicifolia</i> (Kunth) DC.	Ent	Zoo	AD	Iv/Tw	Covre 240 (CAP)
<i>Eugenia pyriformis</i> Cambess.	Ent	Zoo	Ce/Ma	Tw	Covre 248 (CAP)
<i>Eugenia bahiensis</i> DC.	Ent	Zoo	EN	Tw	Covre 249 (CAP)
<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	Ent	Zoo	AD	Iv/Tw	Covre 183 (CAP)
RUTACEAE (2)					
<i>Esenbeckia grandiflora</i> Mart.	Ent	Aut	AD	Tw	Covre 48 (CAP)
<i>Pilocarpus spicatus</i> A.St.-Hil.	Ent	Aut	Ca/Ce/Ma	Tw	Covre 241 (CAP)
TRIGONIACEAE (1)					
<i>Trigoniodendron spiritusanctense</i> E.F.Guim. & Miguel	—	Zoo	EN	Tw	Covre 254 (CAP)
URTICACEAE (1)					
<i>Urera baccifera</i> (L.) Gaudich. ex Wedd.	Ane	Zoo	AD	Tw	Covre 54 (CAP)
VERBENACEAE (2)					
<i>Lantana camara</i> L.	Ent	Zoo	AD	Tw	Covre 154 (CAP)
<i>Lippia origanoides</i> Kunth	Ent	Aut	AD	Iv	Covre 46 (CAP)

Erythroxylum deciduum A.St.-Hil. and *Kielmeyera membranacea* Casar., forming denser woody vegetation without monocotyledon mats. Other species such as *Albizia polycephala* (Benth.) Killip ex Record, *Astronium graveolens* Jacq., *Cnidoscolus oligandrus* (Müll.Arg.) Pax, *Deguelia costata* (Benth.) A.M.G.Azevedo & R.A.Camargo and *Spondias mombin* L., were also recorded in this habitat.

Three species found in this study are on the official national list of species of the national flora threatened with extinction, namely: *W. azulensis*, listed as Vulnerable (VU), *P. petropolitanum*, and *Trigoniodendron spiritusanctense* E.F.Guim. & Miguel, listed as Endangered (EN); and three registered species are on the State list of threatened flora of Espírito Santo, namely: *Ficus cyclophylla* (Miq.) Miq. and *T. spiritusanctense*, cited as VU, and *E. deciduum*, as EN.

2. Geographic distribution

When we analyzed the geographic distribution, species endemic to the Atlantic Forest (nine spp., 33%) and those with wide geographic distribution among Brazilian phytogeographic domains (eight spp., 30%) predominated. Five species (19%) were shared between the Amazon/Cerrado and the Atlantic Forest; three species (11%) were disjunct between Caatinga/Atlantic Forest, and two species (7%) were disjunct between the Cerrado/Atlantic Forest (Table 2).

3. Pollination/dispersal syndromes

Pollination strategies showed the dominance of entomophily syndrome, recorded for 84% of the species (22 spp.), followed by chiropterophily, ornithophily, and anemophily, with two representative species for each. The species *A. graveolens*, *T. reticulata*, and *P. petropolitanum* presented more than one pollination syndrome.

Regarding dispersal syndrome, zoochoric was the most frequent (42% of species, $n = 11$ spp.), followed by anemochoric (31% of species, $n =$ eight spp.) and autochoric (27% of species, $n =$ seven spp.). Among the families sampled, Fabaceae was the only one that presented the three types of syndromes (Table 2).

4. Environmental variables

The first axis (CCA1) explained 29.6% (eigenvalue, 0.8313, $p = 0.001$) of this constrained variation, and the second axis (CCA2) explained 29.16% (eigenvalue, 0.8193, $p = 0.012$). Together, the two axes explained 58.8% of total inertia, which was highly significant at $p = 0.001$ (Monte Carlo Permutation test, $n = 999$; $F = 1.74$), indicating a strong correlation between woody species and elevation, maximum temperature of warmest month, mean diurnal range and precipitation of driest month (Table 3).

Elevation had a more significant influence on CCA1 in a positive direction (Elev, $F = 1.6155$, $p = 0.017$). In comparison, the maximum temperature of the warmest month had a more significant influence in a negative direction ($F = 1.89$, $p = 0.001$). The mean diurnal range influenced the CCA2 axis in the negative direction (Table 3) and showed a high correlation with the CCA1 axis (Figure 3).

The inselbergs of Pedra dos Pontões (PEPONT) and Morro da Pescaria (MOPES) were positively correlated with elevation and negatively with the Maximum Temperature of the Warmest Month (Figure 3). Morro do Itaoca (ITAOCA), Pedra Santa Angélica (SANANG), Pedra Lisa (PELIS), MONAMA and Alto Misterioso (ALMIST) were positively correlated with variables related to

Table 3. Correlations of environmental variables with the first two axes of canonical ordination of woody species from nine inselbergs areas in Brazil.

Environmental variables	Correlation coefficients	
	CCA1	CCA2
Elev	0.3365	0.3454
Mean.diur.range	0.6792	-0.4836
Max.temp.warm.month	-0.7600	-0.6350
Precip.driest.month	-0.2501	0.9657

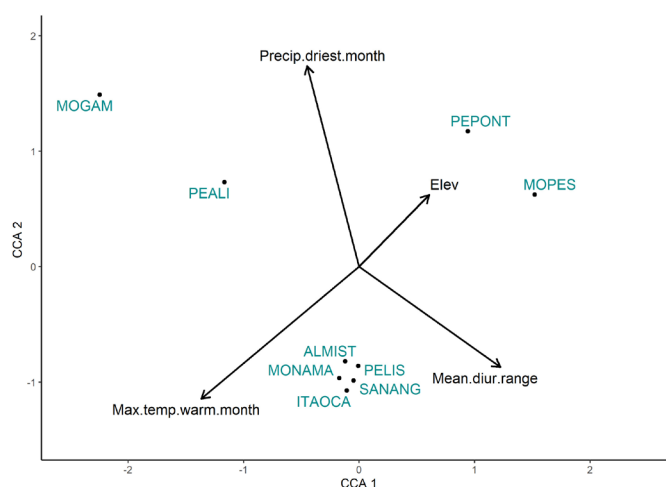


Figure 3. Canonical correspondence analysis (CCA) illustrating the relationship between the nine inselberg areas in southeastern Brazil based on the occurrence matrix of 87 woody species. Elev (Elevation); Max.temp.warm.month (Maximum temperature of the hottest month); Mean.diur.range (Mean Diurnal Range (Monthly average (maximum temperature - minimum temperature))); Precip.driest.month (Precipitation of the driest month)

temperature and negatively correlated with precipitation of driest month. In comparison, Morro da Gameleira (MOGAM) and Pedra da Aliança (PEALI) were more influenced by precipitation (Figure 3).

5. Similarity

The similarity dendrogram showed the formation of three largest groups (Figure 4). The inselbergs located in the south of Espírito Santo, under the influence of the Submontane Semideciduous Seasonal Forest (MONAMA, Pedra da Aliança, Pedra Lisa and Pedra Santa Angélica), formed a group with the highest similarity index (0.24). The species shared between MONAMA and Pedra da Aliança were: *A. polycephala*, *Aspidosperma gomezianum* A.DC., *Ceiba erianthos* (Cav.) K.Schum., *D. costata*, *K. membranacea*, *P. petropolitanum*, and *T. reticulata*. The species shared between MONAMA and Pedra Lisa were: *A. gomezianum*, *C. erianthos*, *Eugenia puniceifolia* (Kunth) DC., *Myrciaria floribunda* (H.West ex Willd.) O.Berg, *P. petropolitanum*, *T. reticulata*, and *W. azulensis*. Finally, the species shared between MONAMA and Pedra Santa Angélica were: *A. gomezianum*, *C. erianthos*, *C. oligandrus*, *Eugenia bahiensis* DC., *K. membranacea*, *P. petropolitanum*, and *T. reticulata*. Only four species were shared

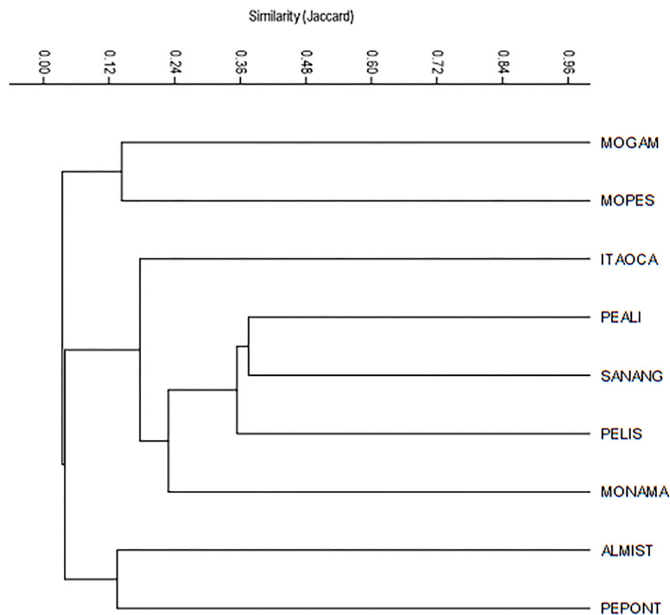


Figure 4. Similarity dendrogram (Jaccard index) obtained through the analysis of 86 species of shrubs and trees in nine inselberg areas in southeastern Brazil. Cophenetic correlation coefficient = 0.9363

between the areas: *A. gomezianum*, *C. erianthos*, *P. petropolitanum*, and *T. reticulata*. Despite having a lower similarity index (0.18), Itaoca is also part of this group, sharing six species with MONAMA: *A. polycephala*, *A. graveolens*, *K. membranacea*, *Pleroma heteromallum* (D.Don), *P. petropolitanum*, and *T. reticulata*.

The second largest group was formed by the inselbergs Pedra dos Pontões (PEPONT) and Alto Misterioso (ALMIST), which shared four species: *Clusia criuva* Cambess., *Eremanthus crotonoides* (DC.) Sch.Bip., *Myrsine venosa* A.DC., and *P. heteromallum*. Three species were shared between MONAMA and ALMIST: *W. azulensis*, *Lantana camara* L., and *P. heteromallum*. Two species were shared between MONAMA and PEPONT: *P. petropolitanum* and *P. heteromallum*.

The third largest group was formed by the inselbergs Morro da Gameleira (MOGAM) and Morro da Pescaria (MOPES), which share three species: *Clusia spiritu-sanctensis* G.Mariz & B.Weinberg, *Ruehssia loniceroides* (Hook.) F.Esp.Santo & Rapini, and *Schinus terebinthifolia* Raddi. Two species were shared between MONAMA and MOPES: *Lippia origanoides* Kunth and *P. heteromallum*. Only one species was shared between MONAMA and MOGAM: *K. membranacea*.

Of the 86 woody species analyzed, 12 were exclusive to MONAMA: *Anadenanthera peregrina* (L.) Speg., *Andira legalis* (Vell.) Toledo, *C. harrisii*, *C. oligandrus*, *E. deciduum*, *Esenbeckia grandiflora* Mart., *Eugenia pyriformis* Cambess., *F. cyclophylla*, *P. spicatus*, *S. mombin*, *T. spiritusanctense*, and *Urera baccifera* (L.) Gaudich. ex Wedd. No species were shared among all inselbergs. The cophenetic correlation coefficient was 0.9363, indicating little distortion between the matrix and the dendrogram obtained in the analysis. The Mantel test indicated a positive and significant spatial correlation between the geographic distance of inselbergs and the composition of woody species (Mantel test, $r = 0.4625$; $P = 0.015$).

Discussion

This study provides an essential contribution to the knowledge of the woody vegetation of inselbergs, which has been historically neglected in the Atlantic Forest domain (see Couto et al. 2025). We presented data on species composition, pollination and dispersal syndrome, geographic distribution, and conservation, in addition to conducting analyses of floristic groupings with other woody floras from inselbergs in southeastern Brazil. This information is essential for developing public policies aimed at biodiversity conservation, restoration, and the management of remaining areas (Chaves et al. 2013).

The richness of woody species found for MONAMA ($n = 27$ spp.) is within the range (10 to 27 spp.) and at the upper limit of the values observed in several floristic surveys carried on inselbergs of the Atlantic Forest (Esgario et al. 2009, Santos et al. 2010, Dal Col and Thomaz 2016, Couto et al. 2017, 2021, 2025). These comparisons must be interpreted with caution due to some factors such as the size of the inselbergs, isolation, and habitat heterogeneity, which affects species richness (Porembski 2007), in addition to the sampling effort on this group of plants.

In this study, the richest family in terms of the number of species was Fabaceae, characterized by more significant variations in survival strategies in drier environments (Porto et al. 2008), such as efficiency in association with nitrogen-fixing bacteria (Queiroz 2009). This result follows a trend when we analyze the leading families of woody species recorded for inselbergs from the Atlantic Forest (Santos et al. 2010, Pena et al. 2017, Araújo et al. 2022, Couto et al. 2021, 2022, 2025) and the Caatinga (Araújo et al. 2008, Porto et al. 2008, Lopes-Silva et al. 2019), in which the Fabaceae family is among the most representative in terms of the number of species. Other studies on inselbergs in Africa and Venezuela also indicate that Fabaceae is among the richest in species and highlight the effectiveness of this family's adaptation to rocky environments (Gröger 1994, 2000, Porembski and Brown 1995, Gröger and Barthlott 1996, Porembski and Barthlott 2000b).

Myrtaceae was the second most species-rich family in MONAMA, represented by the genus *Eugenia* ($n = 3$ spp.). This family stands out among the richest on the woody flora of inselbergs in French Guiana (Sarhou et al. 2003) and also for inselbergs in the Atlantic Forest (Pires et al. 2014, Pena et al. 2017, Araújo et al. 2022, Couto et al. 2017, 2022, 2025). In studies on woody vegetation on rocky outcrops in the Cerrado (cerrado rupestre), Myrtaceae is also among the richest in number of species, highlighting its importance for rocky environments (Pinto et al. 2009, Lima et al. 2010). The adaptation capacity of Myrtaceae species to edaphoclimatic restrictions has been noted in other works on inselbergs in French Guiana (Granville 1978, Larpin 2001). It is also recognized for its essential relationship with wildlife, guaranteeing necessary food resources (fleshy fruits) and establishing crucial biotic interactions (Gomes et al. 2016, Couto et al. 2025).

The existence of endangered species in MONAMA, *F. cyclophylla*, *P. petropolitanum*, *T. spiritusanctense*, and *W. azulensis*, reinforces the relevance of this conservation unit for protecting Brazilian threatened flora. Furthermore, the species *T. reticulata* (Bignoniaceae) was cited as rare for the Brazilian flora (Giulietti et al. 2009), demonstrating the area's importance for Espírito Santo biodiversity.

When we analyzed the species shared between the Atlantic Forest and other Brazilian phytogeographic domains, Caatinga and Cerrado

were the most representative, with 14 species each. Thus, because they have island characteristics, inselbergs have significant phytogeographic contributions to regional diversity, acting as shelter for xeric vegetation from other phytogeographic domains of the Brazilian dry diagonal (Ratter et al. 1997).

Of the 26 species recorded, only *P. petropolitanum*, *T. reticulata*, and *W. azulensis* are restricted to rocky outcrops, corroborating the pattern for woody vegetation on inselbergs (Couto et al. 2025), and indicating that the high endemism cited for lowland inselbergs is more associated with the herbaceous-subshrub stratum, represented by the families Bromeliaceae, Orchidaceae, Asteraceae and Melastomataceae (de Paula et al. 2020), a stratum not sampled in this study. Also, these data corroborate previous studies that highlight the importance of the surrounding matrix as a source of species for the colonization of inselbergs (Couto et al. 2016, 2021, 2022, Sarthou et al. 2017, Francisco et al. 2018, 2023).

The woody individuals that vegetate on thin and poorly developed soil in inselbergs (saxicolous plants) are concentrated in microhabitats existing in cracks and depressions in the rocks where the conditions for establishment are more favorable. The variety of microhabitats in these environments allows the establishment of species with different requirements, which promotes more species richness in these areas (Safford and Martinelli 2000). Although the flora of inselbergs is mainly characterized by herbs and shrubs (Porembski 2007, Couto et al. 2017), rupicolous trees are also important (Francisco et al. 2018, Couto et al. 2016, 2022, 2025, Jerônimo Júnior et al. 2025). For example, the rupicolous tree *P. petropolitanum* is suggested as an essential, nurse plant in the Atlantic Forest inselbergs (Couto et al. 2016, 2019). Their morphological characteristics favor the colonization of a diversity of epiphytes, allowing inselbergs to function as biodiversity refuges (Couto et al. 2016, 2019, 2022, Francisco et al. 2018, 2023).

Insect pollination syndrome (entomophily), the most important for the recorded species, occupies a prominent position among pollinating agents in Semideciduous Seasonal Forests (Kinoshita et al. 2006, Yamamoto et al. 2007) as well as on tropical inselbergs, sandstone and ironstone outcrops (Biedinger et al. 2000, Conceição et al. 2007, Jacobi and Carmo 2011). This highlights the ecological importance of this group of pollinators, mainly represented by bees, known as the most versatile and active pollinators, obtaining resources from plants with a wide range of floral attributes (Faegri and Van Der Pijl 2013). Notably, the Myrtaceae family is one of the most important for beekeeping in Brazil, standing out for its pollen, which is the central attractive resource, possibly associated with the presence of nectar (Gressler et al. 2006).

As for dispersal syndrome, zoochoric was the most evident among the woody species of MONAMA, a typical pattern found in tropical environments (Howe and Smallwood 1982, Martins et al. 2007), in seasonal tropical forests (Morellato and Leitão-Filho 1992, Kinoshita et al. 2006), and inselberg woody vegetation (Couto et al. 2025). A more significant number of autochoric and anemochoric species were expected, strategies often associated with open areas, such as rocky outcrops (Conceição et al. 2007, Jacobi and Carmo 2011, Silva Costa et al. 2015). However, these works focus on all vegetation, unlike this study, which emphasizes woody species. Generally, autochoric and anemochoric plants produce smaller propagules, facilitating the colonization of new sites (Howe and Smallwood 1982). However, smaller propagules tend to have higher mortality than larger ones

during the early stages of plant development (Westoby 1998, Díaz et al. 2016). Thus, zoochoric plants, which produce fleshy fruits, and seeds with greater mass, that can persist viable for longer, increase the chance of locating suitable sites for seedling establishment and survival (Howe and Smallwood 1982, Schupp et al. 2010). The Myrtaceae family significantly influenced this result, as all Brazilian species in this family produce fleshy fruits whose seeds are potentially dispersed by frugivorous vertebrates (Landrum and Kawasaki 1997). The Fabaceae family presented three types of dispersal, which can be explained by the great morphological diversity, resulting in a wide variety of fruits (Queiroz 2009). This result attests to the importance of the inselbergs' woody vegetation as a vital source of food resources for maintaining wildlife.

Our results indicated the relative influence of environmental factors on the species composition of the analyzed inselbergs, which are environments with extreme microclimatic influences (Larson et al. 2000, Gröger and Huber 2007). Elevation has a strong influence on species composition, causing changes in the floristic and structure of the plant community, as demonstrated in other studies (França and Stehmann 2004, Sarthou et al. 2017, Lucena et al. 2020, Pinto-Junior et al. 2020a). Another critical environmental variable is temperature, which includes the maximum temperature of the warmest month and the mean diurnal range. Inselbergs, due to their mosaic vegetation and the presence of exposed rocks, are more susceptible to high temperatures and significant daily temperature variations (Szarzynski 2000). These conditions affect the composition of the vegetation (Porembski and Barthlott 2000b). Due to their shallow soils and low water retention capacity (Porembski 2007), water availability on inselbergs is a limiting factor for much of the vegetation; therefore, precipitation that occurs in the driest months helps survival and alters species composition in these xeric environments (Sarthou et al. 2017).

We observed that the low similarity values influenced by the small number of species shared between areas—even those that are geographically close—reflect the intrinsic floristic particularities of each location (Sarthou et al. 2017, Yates et al. 2019, de Paula et al. 2019, 2021). This supports the great diversity of species influenced by environmental heterogeneity resulting from differences in latitude, altitude, or the presence of barriers to species migration (Porembski 2007). The results from the Mantel test indicated that geographic distance influences floristic similarity between inselbergs, with geographically close inselbergs tending to be more similar to one another (Pinto-Junior et al. 2020b). Although the PEPONT inselberg, close to MONAMA, was grouped with ALMIST, which is more geographically distant. This result is related mainly to the difference in elevation between ALMIST and MONAMA. The ALMOST/PEPONT and MOPES/MOGAM groups probably differed due to their distance from the coastal region and elevation. Some inselbergs in the state of Espírito Santo exhibited low similarities, which seems to be a result of the proximity to the coast (Morro da Gameleira, Morro da Pescaria), higher altitudes (Pedra dos Pontões, Alto Misterioso), the difference in the size of the inselbergs or the sampling effort, affecting the richness of species that colonize these environments.

Finally, the state of Espírito Santo is recognized as one of the most prominent explorers of ornamental rocks in the world (Sardou Filho et al. 2013), and this activity represents the most significant global threat

to the biodiversity of inselbergs (Porembski et al. 2016). Therefore, this study provides data that can be useful in public conservation policies and also brings a critical perspective on the woody vegetation of inselbergs, a group often neglected in the phytogeographic domain of the Atlantic Forest.

Supplementary Material

The following online material is available for this article:

Figure S1 - Graphical display of the correlation matrix using the R package 'corrplot'; Spearman correlations between elevation and bioclimatic variables. The blue color represents the positive correlation, and the red color represents the negative correlation, and the darker the color, the stronger the correlation. The size of the square represents the strength of the correlation and the larger the square, the stronger the correlation. These values are correlation coefficients.

Table S1 - Bioclimatic variables obtained from the Worldclim 2.1 database, with a spatial resolution of 30 arc seconds.

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Marcelo Trindade Nascimento: writing – original draft, writing – review & editing.

Henrique Machado Dias: supervision, writing – original draft, writing – review & editing.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

Supporting data are available at: <https://doi.org/10.48331/scielodata.5TXHDF>

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