Acta Botanica Brasilica - 34(4): 645-661. October-December 2020.
doi: 10.1590/0102-33062020abb0129

The pattern of high plant diversity of Neotropical inselbergs: highlighting endemic, threatened and unique species

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Received: February 4, 2020
Accepted: July 27, 2020

ABSTRACT

Understanding how multiple drivers shape plant community diversity across environmental gradients is one of the most important issues in plant ecology and biodiversity conservation. We aimed to analyse plant community structure and diversity in four inselbergs in Espírito Santo State, Brazil. We evaluated species diversity, floristic composition and similarity, phytosociological structure, occurrence, and conservation status of rupicolous flora in the inselberg communities. We used field expeditions and plant inventory data from 370 sampling units. We estimated floristic similarity and compared diversity indexes among inselbergs. We observed marked differences in community structure and diversity among inselbergs, where the southern region had the highest number of taxa and higher values of diversity indices. There were also notable differences in floristic composition and phytosociological structure, with a decrease in similarity as geographical distance increased. This finding demonstrated the existence of differences in the patterns of dominance and vegetation cover along the latitudinal gradient, as well as differences in endemic, threatened, and exclusive species, and represents a first step toward establishing criteria for biodiversity conservation for inselbergs in Espírito Santo State.

Keywords: alpha diversity, Atlantic Forest, biodiversity conservation, floristic composition, latitudinal gradient, phytosociological structure, rock outcrop

Introduction

Inselbergs are usually rocky granite outcrops that emerge abruptly from their surrounding ecosystems, such as savannah and forests, representing isolated terrestrial islands (Porembski & Barthlott 2000; Parmentier & Hardy 2009). These rocky outcrops are common around the world, occurring in America, Africa, Asia, and Australia (Carlucci *et al*. 2014), and form important landscape elements that play a role in the maintenance of biodiversity (Porembski *et al*. 2016). Inselbergs *lato sensu* are found throughout the east of Brazil, from the north-eastern semi-arid region to the cloudy and cold highlands of Rio Grande do Sul (Safford & Martinelli 2000). Although these granite outcrops are recognised by 75 % of the Brazilian population, they are still poorly studied; neither the floristic characteristics nor the ecological and biogeographical features of the flora are widely known (Safford & Martinelli 2000). Even with a few studies, the inselbergs in south-eastern Brazil, mainly in the states of Espírito Santo, Minas Gerais, and Rio de Janeiro,

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have the greatest expression of vegetation variability (Moura *et al*. 2011; de Paula *et al.* 2020).

The most-studied domains with inselbergs in Brazil are the Atlantic Forest, the Cerrado, and the Caatinga. These areas have a mosaic of vegetation types, where the union between biotic and physical factors results in the most diverse and heterogeneous inselbergs (Safford & Martinelli 2000). In this context, the sharing of flora among inselbergs will depend on their specific environmental conditions and the degree of isolation (Porembski 2007), which can change over relatively short distances (Schut *et al*. 2014) and provide heterogeneity to support plant diversity (Yates *et al*. 2019). Even with few and specific studies carried out in Espírito Santo State (Esgario *et al*. 2009; Couto *et al*. 2016; 2017; 2019; Francisco *et al*. 2018; Pena & Alves-Araújo 2017; Pinto-Junior *et al*. 2020), the granitic inselbergs were listed as priority areas for conservation (Martinelli 2007), and have been described as vegetation relicts and ecological refuges (IBGE 2012). However, these inselbergs are threatened, mostly due to exploration and trading ornamental rocks (Campello 2000).

Despite the recognized value for conservation, granitic inselbergs also have characteristics such as reduced dispersability (Hopper *et al*. 2009), high numbers of localized rare/endemics species (Porembski 2007) and strongly differentiated population systems (Hmeljevski *et al*. 2017), which can assist to develop hypotheses explaining the ecology, evolution and best conservation practices for very old, climatically buffered and infertile landscapes (Ocbil theory) (Hopper *et al*. 2016). Thus, there are still large gaps in our knowledge regarding the flora and ecological processes of various mountain regions throughout the Brazilian territory, including the inselbergs (Meirelles *et al*. 1999; Martinelli 2007).

Understanding how multiple drivers shape plant community diversity across environmental gradients is one of the most important issues in plant ecology and biodiversity conservation (Lavergne *et al*. 2010). However, how the plant community is structured on tropical inselbergs remains unknown; data on species diversity and phytosociological structure are especially sparse. The geological, geomorphological and microenvironmental characteristics of inselbergs provide extreme environmental conditions (*i.e.* low nutrient or water availability, high radiation levels and large temperature amplitude); only certain plant species, with morphological and ecophysiological adaptations, can tolerate such conditions (Lüttge 1997; Bremer & Sander 2000; Biedinger *et al*. 2000; Porembski 2007). These species consequently have a restricted geographic distribution with a considerable number being endemics (Barthlott *et al*. 1993; Porembski *et al*. 2000a; Seine *et al*. 2000; Porembski 2007) and predominantly create patchy vegetation formations (Porembski 2007; de Paula *et al*. 2016; Villa *et al*. 2018b).

In this study, we aimed to analyze the plant community structure and diversity in four inselbergs in Espírito Santo State, south-eastern Brazil. Specifically, we evaluated the plant species diversity, floristic composition and similarity, phytosociological structure, and the occurrence and conservation status of rupicolous flora on inselbergs. As a consequence, our knowledge of plant community structure and diversity patterns on the inselbergs can be used to increase the likelihood of success in defining conservation criteria.

Materials and methods

Study areas

This study was performed on four inselbergs located in the Atlantic Forest matrix in Espírito Santo State, south-eastern Brazil (Fig. 1, Tab. 1). This rupicolous vegetation is typical of Espírito Santo, being associated with granitic and gneissic inselbergs, and can be found between 0 and 1,480 m a.s.l. The vegetation is mainly associated with plant communities formed by monocotyledonous mats of Bromeliaceae, Cyperaceae, and Velloziaceae distributed in patches and/or shrubs (Porembski *et al*. 2000a; Porembski 2007).

Vegetation sampling

The line intercept transect method was used to measure coverage for all plants (Mueller-Dombois & Ellenberg 2002; Herrick *et al*. 2017; Morgan & Salmon 2019). The cover was measured along a line intercept transect, by noting the point along with the tape where the cover began and the point at which it ended (Elzinga *et al*. 2001). In each inselberg, ten parallel 100 m lines, systematically spaced at 10 m, were used for recording plant coverage. Every intercept was divided into 10 m intervals to determine the beginning and the end of each sampling unit, and then, the frequency of occurrence of each species (Elzinga *et al*. 2001; Mueller-Dombois & Ellenberg 2002; Herrick *et al*. 2017). Sampling points with bare rock were removed from the analysis.

Floristic survey

The floristic survey consisted of the collection of fertile specimens and was conducted between April 2015 and July 2019, with successive field expeditions to encompass the different seasons. All fertile botanical material was collected and processed according to the usual techniques for vascular plants (Fidalgo & Bononi 1989). Taxonomic identification of botanical material was carried out by using the Flora do Brasil 2020 em construção (2020), taxonomic literature, herbarium data, and expert taxonomists. All botanical material was deposited in the herbariums of the Universidade Federal do Espírito Santo (SAMES, CAP, and VIES), Instituto Nacional da Mata Atlântica (INMA/

MBML) and Universidade Federal de Viçosa (VIC), with duplicate samples sent to the herbarium of Jardim Botânico do Rio de Janeiro (RB). The spelling of names, synonymy, and authors follow Flora do Brasil 2020 em construção 2020 (JBRJ 2019) with APG IV (2016) circumscription for angiosperm families, and PPG I (2016) for monilophytes and lycophytes. Species life forms were classified according to Raunkiaer (1934).

Quantification of biodiversity indexes

Measurements of taxonomic diversity indices were calculated in each sampling area along the climatic gradient. Measurements included species richness, Shannon-Wiener and Pielou evenness index (Magurran 2004). Species richness refers to the total number of species recorded at each sampled area. The Shannon-Wiener index (*H'*) and Pielou evenness index (*J*) were calculated using the following equations:

$$H' = -\sum pi.ln(pi)$$

and

$$J = H'/H'max$$

where *pi* is the absolute coverage of each species; *ln* is the natural logarithm; *H'max* is *ln* of *S* and *S* is the total number of species at a sampling area. These indices incorporate the species richness and the proportion of each species within each sample (Magurran 2004). All diversity indices were calculated using the 'vegan' package (Oksanen *et al*. 2019) in R software 4.0.3 (R Development Core Team 2020).

Data analyses

To test the floristic similarity between the four sampled areas, a Cluster Analysis was performed using a matrix of presence and absence data, using Sørensen Distance as the coefficient and UPGMA as the algorithm. The inclusion criterion of individuals in the matrix was the identification at the species level. The cluster analysis was represented by a similarity matrix and was evaluated by the Cophenetic Correlation Coefficient (CCC).

Measures of alpha diversity were calculated for each sampling area by site using species richness, Pielou evenness and Shannon-Wiener diversity index. To compare the means of cover and alpha diversity metrics, we performed the

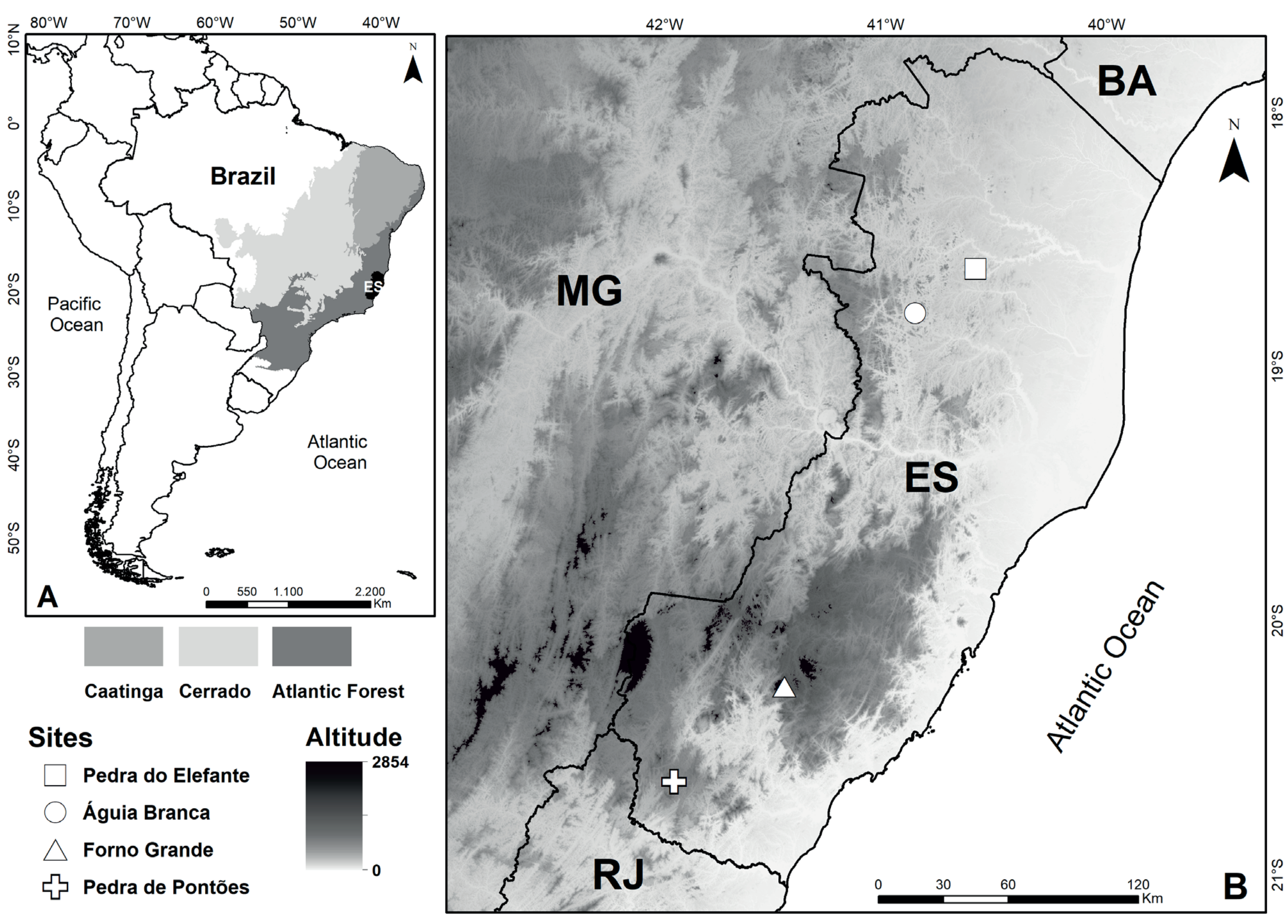

Figure 1. Location and general aspects of the study area. **A** – Location of the study area in relation to South America and **B** – in relation to Brazil and Espírito Santo State (ES). Border states: BA – Bahia, MG – Minas Gerais and RJ – Rio de Janeiro. Study area: white square – Pedra do Elefante, white circle – Águia Branca (north), white triangle – Forno Grande and white cross – Pedra de Pontões (south).

Kruskal-Wallis test (for non-normally distributed data), followed by Dunn's multiple comparison test (Dinno 2017). Variables were tested for normal distribution with the Shapiro-Wilk test and by evaluating the Q-Q plot (Crawley 2012). All these analyses were performed using the *'ade4'*, *'car'*, *'cluster'*, *'dunn.test'*, *'gclus'*, *'permute'* and *'vegan'* packages (Hurley 2019; Maechler *et al*. 2018; Oksanen *et al*. 2019; Simpson 2019; Dinno 2017; Dray & Dufour 2007; Fox & Weisberg 2019) in the R 4.0.3 software environment (R Development Core Team 2020).

Phytogeography, endemism and threatened species

The distribution of species and endemism were analysed using the literature and online databases, as Flora do Brasil 2020 em construção 2020 (JBRJ 2019), Herbário Virtual da Flora e de Fungos (INCT 2019) and JABOT (JBRJ/Jabot 2019). Information on threatened species was obtained through the 'Lista Nacional Oficial de Espécies da Flora Ameaçadas de Extinção' (MMA 2014), 'Livro Vermelho da Flora do Brasil' (Martinelli & Moraes 2013) and 'Espécies da Flora Ameaçadas de Extinção no Estado do Espírito Santo' (Simonelli & Fraga 2007).

Results

Floristic composition

Based on 228 records, a total of 168 species of vascular plants were found belonging to 51 families and 114 genera, including 1 lycophyte, 13 pteridophytes, and 154 angiosperms (six magnoliids, 59 monocots, and 89 eudicots) (Tab. 2). The richest family was Orchidaceae with 13 species, followed by Asteraceae and Bromeliaceae (12 spp. each), Melastomataceae (11 spp.), Cyperaceae (eight spp.), Araceae (seven spp.), Clusiaceae, Euphorbiaceae, Fabaceae, Malvaceae and Velloziaceae (six spp. each) and Cactaceae (five spp.). The richest genera were *Anthurium* (Araceae) and *Clusia* (Clusiaceae) with six species each, followed by *Pleroma* (Melastomataceae) with five, *Alcantarea* (Bromeliaceae) and *Peperomia* (Piperaceae) with four species each. Also, five species from the inselbergs studied were recently described as new to science, and eight were new records for the Espírito Santo State. The life-form spectrum showed a predominance of phanerophytes (67 spp. – 40 %), followed by chamaephytes (47 spp. – 28 %), hemicryptophytes (39 spp. – 23.2 %) and cryptophytes (12 spp. – 7.1 %) (more details List S1 in supplementary material).

Phytosociological structure

Regarding species richness, the southern areas, located at higher altitudes, were richer than the northern areas; the number of genera and families also followed this pattern, but with less-significant differences (Tab. 3).

Among the families richest in species, Cyperaceae and Velloziaceae stand out in three studied areas, and Asteraceae, Melastomataceae, Orchidaceae, and Poaceae, in two southern areas. The percentage of genera with only one species exceeded 90% in Águia Branca and Pedra do Elefante, and reached its highest value in Forno Grande; for families with only one species, the highest percentage was observed in Pedra de Pontões (Tab. 3). The total vegetation sampled from 1,000 linear meters was higher in the southern sites; consequently, the highest values for bare rock were recorded to northern areas of Espírito Santo State.

The four plant communities were organized in an oligarchic structure, where a few species dominant account more than 50 % of the Importance Value (IV). In Águia Branca three species totaled 75.68 % of IV, *Vellozia plicata*, *Trilepis lhotzkiana* and *Alcantarea nigripetala*, and also recorded the highest values for relative coverage and frequency (Tab. S1 in supplementary material). *Alcantarea trepida* as the dominant species and codominant *Pleroma cucullatum* represented 67.44 % of IV in the Pedra do Elefante (Tab. S2 in supplementary material). In the two southern sampled areas, five species formed the dominant group; *Melinis minutiflora*, *Cyperus pohlii*, mosses, *Pleroma heteromallum*, *Alcantarea extensa* totaled 54 % (Tab. S3 in

Table 1. General descriptions of four Neotropical inselbergs selected in Espírito Santo State, south-eastern Brazil.

	Águia Branca	Pedra do Elefante	Forno Grande	Pedra de Pontões
Climate (Alvares *et al*. 2013)	Aw – Tropical zone with dry winter	Aw – Tropical zone with dry winter	Cwb – Humid subtropical zone with dry winter and temperate summer	Cwb – Humid subtropical zone with dry winter and temperate summer
Region	North	North	South	South
Mean annual temperature (Incaper 2016)	23 °C	24 °C	15 °C	19.5 °C
Mean annual precipitation (Incaper 2016)	1,175 mm	1,125 mm	1,325 mm	1,375 mm
Forest matrix (Veloso *et al*. 1991)	Seasonal Semideciduous Forest	Seasonal Semideciduous Forest	Dense Ombrophylous Forest Montane	Seasonal Semideciduous Forest
Elevation	260 m asl	675 m asl	1,480 m asl	980 m asl
Municipalities	Águia Branca	Nova Venécia	Castelo	Mimoso do Sul
Geographic Coordenates	18° 58' 26.1'' S 40° 42' 26.9'' W	18° 46' 07.3'' S 40° 27'2 4.1'' W	20° 30 '40.1'' S 41° 05' 26.5'' W	20° 56' 25.4'' S 41° 32' 46.7'' W
Status	Private	Environmental Protection Area	State Park	Private

Table 2. List of species recorded in four Neotropical inselbergs in Espírito Santo State, southeastern Brazil. Life-forms: Th – therophyte, Cr – cryptophyte, Hc – hemicryptophytes, Ch – chamephytes, Ph – phanerophayte. Phytogeographic Domains: Am – Amazônia, Ca – Caatinga, Ce – Cerrado, MA – Mata Atlântica (Atlantic Forest), Pam – Pampa and Pan – Pantanal. * – exclusive occurrence to inselbergs, ! – endangered species. In bold endemic species of Espírito Santo State.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
ÁGUIA BRANCA			
Pteridophytes and Lycophytes			
ANEMIACEAE			
Anemia retroflexa Brade	Hc	MA	H.V. Pinto Junior 204
PTERIDACEAE			
Cheilanthes geraniifolia (Weath.) R.M.Tryon & A.F.Tryon	Hc	Ce, MA	H.V. Pinto Junior 359
Doryopteris collina (Raddi) J.Sm.	Hc	Am, MA	N.S.S. Braga 125
SELAGINELACEAE			
Selaginella convoluta (Arn.) Spring	Ch	Ca, Ce, MA	H.V. Pinto Junior 225
Magnoliid			
ARISTOLOCHIACEAE			
Aristolochia gracilipedunculata F.González	Hc	MA	H.V. Pinto Junior 222
PIPERACEAE			
Peperomia incana (Haw.) Hook.	Ch	MA	H.V. Pinto Junior 165
Peperomia warmingii C.DC.	Ch	Ce, MA	H.V. Pinto Junior 230
Monocots			
ARACEAE			
Anthurium marcusianum Theófilo, L. Kollmann & Sakur.*	Ch	MA	H.V. Pinto Junior 228
Anthurium aff. *parasiticum* (Vell.) Stellfeld	Ch	MA	H.V. Pinto Junior 232
Philodendron edmundoi G.M.Barroso	Ch	MA	H.V. Pinto Junior 193
Anthurium mucuri E.G.Gonç. & L.F.A. de Paula	Ch	MA	H.V. Pinto Junior 171
ARECACEAE			
Syagrus ruschiana (Bondar) Glassman*!	Ph	MA	H.V. Pinto Junior 380
BROMELIACEAE			
Alcantarea nigripetala Leme & L.Kollmann*	Hc	MA	H.V. Pinto Junior 153
Encholirium horridum L.B.Sm.*!	Ch	MA	H.V. Pinto Junior 155
Pitcairnia barbatostigma Leme & A.P.Fontana*	Ch	MA	H.V. Pinto Junior 170
Vriesea vellozicola Leme & J.A.Siqueira	Hc	MA	H.V. Pinto Junior 146
CYPERACEAE			
Scleria sp.	Hc	All domains	H.V. Pinto Junior 203
Trilepis lhotzkiana Nees ex Arn.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 150
DIOSCOREACEAE			
Dioscorea campestris Griseb.	Cr	Ca, Ce, MA e Pam	H.V. Pinto Junior 379
ORCHIDACEAE			
Cyrtopodium glutiniferum Raddi*	Hc	Am, MA	H.V. Pinto Junior 227
Oeceoclades maculata (Lindl.) Lindl.	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 231
Pseudolaelia vellozicola (Hoehne) Porto & Brade!	Ch	Ce, MA	H.V. Pinto Junior 169
Vanilla bahiana Hoehne	Ch	Ca, Ce, MA	H.V. Pinto Junior 206
VELLOZIACEAE			
Barbacenia purpurea Hook.	Ch	MA	L.F.T. Menezes 2176
Vellozia candida J.C.Mikan	Ph	Ca, MA	H.V. Pinto Junior 215
Vellozia plicata Mart.	Ph	Ca, Ce, MA	H.V. Pinto Junior 214
Eudicots			
APOCYNACEAE			
Mandevilla fistulosa M.F.Sales et al.*	Cr	Ca, MA	H.V. Pinto Junior 158
Mandevilla grazielae M.F.Sales et al.*	Cr	Ca, MA	H.V. Pinto Junior 168
ASTERACEAE			
Cololobus argenteus M.Monge & Semir*!	Ph	MA	H.V. Pinto Junior 156
BIGNONIACEAE			
Tabebuia reticulata A.H.Gentry*	Ph	MA	H.V. Pinto Junior 201

Table 2. Cont.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
Cuspidaria sp.	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 223
CACTACEAE			
Coleocephalocereus pluricostatus Buining & Brederoo*	Ph	MA	H.V. Pinto Junior 154
CALLOPHYLACEAE			
Kielmeyera rupestris Duarte*!	Ph	MA	H.V. Pinto Junior 499
CLUSIACEAE			
Clusia cf. *fluminensis* Planch. & Triana	Ph	MA	H.V. Pinto Junior 356
EUPHORBIACEAE			
Cnidoscolus hamosus Pohl	Ph	Ca, MA	H.V. Pinto Junior 174
Manihot pohlii Wawra	Ph	MA	H.V. Pinto Junior 501
FABACEAE			
Platypodium sp.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 177
Aeschynomene sp.	Ch	All domains	H.V. Pinto Junior 179
GESNERIACEAE			
Paliavana prasinata (Ker Gawl.) Benth.	Ph	MA	L.F.T. Menezes 2182
Sinningia aghensis Chautems*!	Cr	MA	H.V. Pinto Junior 167
Sinningia brasiliensis (Regel & Schmidt) Wiehler & Chautems	Cr	Ca, MA	H.V. Pinto Junior 224
MALVACEAE			
Ceiba erianthos (Cav.) K.Schum.	Ph	Ca, MA	H.V. Pinto Junior 503
Sida cf. *cordifolia* L.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 157
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 357
Pseudobombax petropolitanum A.Robyns	Ph	MA	L.F.T. Menezes 2181
MELASTOMATACEAE			
Merianthera burlemarxii Wurdack*!	Ph	MA	H.V. Pinto Junior 216
Pleroma cucullatum F.S.Mey., Fraga & R.Goldenb.*!	Ph	MA	H.V. Pinto Junior 264
Pleroma heteromallum (D. Don) D.Don	Ph	Ce, MA	H.V. Pinto Junior 220
Pleroma fissinervium Schrank et Mart. ex DC.	Ph	Ce, MA	H.V. Pinto Junior 377
MYRTACEAE			
Campomanesia anemonea Landrum	Ph	MA	J. Luber 223
Campomanesia eugenioides (Cambess.) D.Legrand ex Landrum	Ph	Ca, Ce, MA	J. Luber 219
Eugenia astringens Cambess.	Ph	MA	H.V. Pinto Junior 500
PLANTAGINACEAE			
Achetaria crenata (Ronse & Philcox) V.C.Souza	Ph	Ca, Ce, MA	H.V. Pinto Junior 271
TRIGONIACEAE			
Trigonia nivea Cambess.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 152
TURNERACEAE			
Turnera rubrobracteata Arbo	Ch	MA	H.V. Pinto Junior 378
VERBENACEAE			
Lantana sp.	Ch	Am, Ca, Ce, MA, Pan	H.V. Pinto Junior 175
APA PEDRA DO ELEFANTE			
Pteridophytes			
PTERIDACEAE			
Cheilanthes geraniifolia (Weath.) R.M.Tryon & A.F.Tryon	Hc	Ce, MA	H.V. Pinto Junior 268
Doryopteris collina (Raddi) J.Sm.	Hc	Am, MA	H.V. Pinto Junior 250
POLYPODIACEAE			
Pleopeltis bradei (de la Sota) Salino	Hc	MA	H.V. Pinto Junior 384
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	Hc	MA	H.V. Pinto Junior 385
Magnoliid			
PIPERACEAE			
Peperomia incana (Haw.) Hook.	Ch	MA	H.V. Pinto Junior 240
Peperomia rotundifolia (L.) Kunth	Ch	Am, MA	H.V. Pinto Junior 266

Table 2. Cont.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
Monocots			
ARACEAE			
Anthurium microphyllum (Raf.) G.Don	Ch	MA	H.V. Pinto Junior 495
Anthurium parasiticum (Vell.) Stellfeld	Ch	MA	H.V. Pinto Junior 269
Philodendron edmundoi G.M.Barroso	Ch	MA	H.V. Pinto Junior 362
BROMELIACEAE			
Alcantarea trepida Versieux & Wand.*	Hc	MA	H.V. Pinto Junior 372
Dyckia trichostachya Baker	Ch	Ce, MA	L.F.T. Menezes 2167
Encholirium horridum L.B.Sm.*!	Ch	MA	H.V. Pinto Junior 370
Orthophytum foliosum L.B.Sm.*!	Hc	MA	H.V. Pinto Junior 361
Vriesea procera (Mart. ex Schult. & Schult.f.) Wittm.	Hc	Ca, Ce, MA	H.V. Pinto Junior 364
CACTACEAE			
Pereskia aculeata Mill.	Ph	Ca, Ce, MA	L.F.T. Menezes 2168
CALLOPHYLACEAE			
Kielmeyera rupestris Duarte*!	Ph	MA	L.F.T. Menezes 2170
COMMELINACEAE			
Dichorisandra paranaensis Maia, Cervi & Tardivo	Ch	MA	H.V. Pinto Junior 366
CYPERACEAE			
Bulbostylis truncata (Nees) M.T.Strong	Hc	Am, Ce, MA	H.V. Pinto Junior 244
Cyperus pohlii (Nees) Steud.	Hc	Ca, Ce, MA, Pan, Pam	H.V. Pinto Junior 247
Scleria sp.	Hc	All domains	H.V. Pinto Junior 248
Scleria latifolia Sw.	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 369
Trilepis lhotzkiana Nees ex Arn.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 270
IRIDACEAE			
Trimezia aff. *juncifolia* (Klatt) Benth. & Hook.	Hc	Ce, MA	H.V. Pinto Junior 245
ORCHIDACEAE			
Acianthera prolifera (Herb. ex Lindl.) Pridgeon & M.W.Chase	Hc	Ca, Ce, MA	H.V. Pinto Junior 260
Cyrtopodium glutiniferum Raddi*	Hc	Am, MA	H.V. Pinto Junior 233
Prescottia plantaginifolia Lindl. ex Hook.	Hc	Ce, MA	H.V. Pinto Junior 205
Pseudolaelia citrina Pabst*!	Ch	MA	H.V. Pinto Junior 389
POACEAE			
Melinis minutiflora P. Beauv.	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 368
VELLOZIACEAE			
Vellozia candida J.C.Mikan	Ph	Ca, MA	H.V. Pinto Junior 249
Vellozia variegata Goethart & Henrard	Ph	Ca, MA	H.V. Pinto Junior 236
Eudicots			
APOCYNACEAE			
Mandevilla fistulosa M.F.Sales et al.*	Cr	Ca, MA	L.F.T. Menezes 2576
ASTERACEAE			
Baccharis serrulata (Lam.) Pers.	Ph	Ca, Ce, MA	H.V. Pinto Junior 242
Borreria capitata (Ruiz & Pav.) DC.	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 376
Lepidaploa cotoneaster (Willd. ex Spreng.) H.Rob.	Ph	Ce, MA	H.V. Pinto Junior 243
BEGONIACEAE			
Begonia ibitiocensis E.L.Jacques & Mamede!	Ph	MA	H.V. Pinto Junior 265
Begonia lossiae L. Kollmann*	Ph	MA	H.V. Pinto Junior 267
BIGNONIACEAE			
Lundia corymbifera (Vahl) Sandwith	Hc	Am, MA	H.V. Pinto Junior 238
CACTACEAE			
Coleocephalocereus pluricostatus Buining & Brederoo*	Ph	MA	H.V. Pinto Junior 374
Pilosocereus brasiliensis subsp. *ruschianus* (Buining & Brederoo) Zappi	Ph	MA	H.V. Pinto Junior 375
CLUSIACEAE			
Clusia melchiorii Gleason	Ph	Ca, MA	H.V. Pinto Junior 383

Table 2. Cont.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
Clusia nemorosa G.Mey.	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 234
CONVOLVULACEAE			
Evolvulus ericifolius Mart. ex Schrank	Ch	Ca, Ce, MA	H.V. Pinto Junior 259
Jacquemontia martii Choisy	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 239
Bonamia agrostopolis (Vell.) Hallier f.	Hc	Ce, MA	H.V. Pinto Junior 386
ERYTHROXYLACEAE			
Erythroxylum subrotundum A.St.-Hil.	Ph	Ca, Ce, MA	H.V. Pinto Junior 246
EUPHORBIACEAE			
Cnidoscolus urens (L.) Arthur	Ph	Am, Ca, Ce, MA, Pan	H.V. Pinto Junior 235
Stillingia argutedentata Jabl.	Ph	MA	H.V. Pinto Junior 255
FABACEAE			
Centrosema coriaceum Benth.	Ph	Ca, Ce, MA	H.V. Pinto Junior 252
Dalbergia aff. *frutescens* (Vell.) Britton	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 253
GESNERIACEAE			
Sinningia aghensis Chautems*!	Cr	MA	H.V. Pinto Junior 371
Sinningia brasiliensis (Regel & Schmidt) Wiehler & Chautems	Cr	Ca, MA	H.V. Pinto Junior 254
LOASACEAE			
Aosa parviflora (Schrad. ex DC.) Weigend	Ch	MA	H.V. Pinto Junior 261
MALPIGHIACEAE			
Byrsonima nitidifolia A.Juss.	Ph	Ca, Ce, MA	H.V. Pinto Junior 251
Niedenzuella acutifolia (Cav.) W.R.Anderson	Hc	Am, Ce, MA	H.V. Pinto Junior 237
MALVACEAE			
Sida spinosa L.	Ph	Ca, Ce, MA	H.V. Pinto Junior 241
MELASTOMATACEAE			
Pleroma cucullatum F.S.Mey., Fraga & R.Goldenb.*!	Ph	MA	H.V. Pinto Junior 264
Pleroma venetiense F.S.Mey., L.Kollmann & R.Goldenb.*!	Ph	MA	H.V. Pinto Junior 258
PLANTAGINACEAE			
Achetaria crenata (Ronse & Philcox) V.C.Souza	Ph	Ca, Ce, MA	H.V. Pinto Junior 257
PORTULACACEAE			
Portulaca hirsutissima Cambess.	Ch	Ca, Ce, MA	H.V. Pinto Junior 419
RUBIACEAE			
Bradea cf. ***montana*** Brade*!	Ch	MA	H.V. Pinto Junior 263
Bradea sp. nov.	Ph	MA	H.V. Pinto Junior 373
SOLANACEAE			
Solanum hexandrum Vell.	Ch	MA	H.V. Pinto Junior 496
TURNERACEAE			
Turnera rubrobracteata Arbo	Ph	MA	H.V. Pinto Junior 256
PARQUE ESTADUAL FORNO GRANDE			
Pteridophytes			
ASPLENIACEAE			
Asplenium sp.	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 310
DENNSTAEDTIACEAE			
Pteridium arachnoideum (Kaulf.) Maxon	Cr	All domains	H.V. Pinto Junior 301
PTERIDACEAE			
Doryopteris collina (Raddi) J.Sm.	Hc	Am, MA	H.V. Pinto Junior 311
Magnoliid			
MONIMIACEAE			
Mollinedia glabra (Spreng.) Perkins	Ph	MA	H.V. Pinto Junior 331
PIPERACEAE			
Peperomia galioides Kunth	Ch	Ca, Ce, MA	H.V. Pinto Junior 273
Monocots			
AMARYLLIDACEAE			

Table 2. Cont.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
Hippeastrum aulicum (Ker Gawl.) Herb.	Cr	MA	H.V. Pinto Junior 297
ARACEAE			
Anthurium fragae Nadruz	Ch	MA	H.V. Pinto Junior 277
Philodendron edmundoi G.M.Barroso	Ch	MA	H.V. Pinto Junior 287
BROMELIACEAE			
Alcantarea extensa (L.B.Sm.) J.R.Grant*	Hc	MA	H.V. Pinto Junior 300
CYPERACEAE			
Bulbostylis sp.	Hc	All domains	H.V. Pinto Junior 321
Cyperus pohlii (Nees) Steud.	Hc	Ca, Ce, MA, Pan, Pam	H.V. Pinto Junior 280
Scleria sp.	Hc	All domains	H.V. Pinto Junior 336
Scleria latifolia Sw.	Hc	All domains	H.V. Pinto Junior 342
Trilepis lhotzkiana Nees ex Arn.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 289
ORCHIDACEAE			
Brasiliorchis picta (Hook.) R.B.Singer et al.	Ch	Ce, MA	H.V. Pinto Junior 278
Cyrtopodium glutiniferum Raddi*	Hc	Am, MA	H.V. Pinto Junior 320
Epidendrum secundum Jacq.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 295
Octomeria crassifolia Lindl.	Ch	Am, Ce, MA	H.V. Pinto Junior 284
Prescottia plantaginifolia Lindl. ex Hook.	Hc	Ce, MA	H.V. Pinto Junior 335
Zygopetalum maculatum (Kunth) Garay	Hc	Ce, MA	H.V. Pinto Junior 276
POACEAE			
Melinis minutiflora P. Beauv.	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 325
Panicum sp.	Cr	All domains	H.V. Pinto Junior 330
SMILACACEAE			
Smilax elastica Griseb.	Hc	Ce, MA	H.V. Pinto Junior 333
VELLOZIACEAE			
Barbacenia pabstiana L.B.Sm. & Ayensu	Ch	MA	H.V. Pinto Junior 272
Vellozia candida J.C.Mikan	Ph	Ca, MA	H.V. Pinto Junior 281
Vellozia variegata Goethart & Henrard	Ph	Ca, MA	H.V. Pinto Junior 274
VERBENACEAE			
Lantana fucata Lindl.	Ch	Ca, Ce, MA	H.V. Pinto Junior 305
Eudicots			
APOCYNACEAE			
Ditassa nitida Decne.	Ch	MA	H.V. Pinto Junior 341
ASTERACEAE			
Baccharis platypoda DC.	Ph	Ca, Ce, MA	H.V. Pinto Junior 288
Baccharis serrulata (Lam.) Pers.	Ph	Ca, Ce, MA	H.V. Pinto Junior 316
Bidens segetum Mart. ex Colla	Th	Ce, MA	H.V. Pinto Junior 315
Cyrtocymura scorpioides (Lam.) H.Rob.	Ph	Am, Ce, MA	H.V. Pinto Junior 294
Cololobus rupestris (Gardner) H.Rob.*!	Ph	MA	H.V. Pinto Junior 343
Hebeclinium macrophyllum (L.) DC.	Ph	Am, Ce, MA	H.V. Pinto Junior 309
Vernonanthura discolor (Spreng.) H.Rob.	Ph	Ce, MA	H.V. Pinto Junior 282
BEGONIACEAE			
Begonia valdensium A.DC.!	Ph	MA	H.V. Pinto Junior 318
CACTACEAE			
Coleocephalocereus pluricostatus Buining & Brederoo*	Ph	MA	H.V. Pinto Junior 334
Hatiora cylindrica Britton & Rose	Ch	MA	H.V. Pinto Junior 306
CLUSIACEAE			
Clusia mexiae P.F.Stevens	Ph	Ce, MA	H.V. Pinto Junior 290
Clusia organensis Planch. & Triana!	Ph	MA	H.V. Pinto Junior 317
ERICACEAE			
Gaylussacia pallida Cham.	Ph	Ce, MA	H.V. Pinto Junior 328
EUPHORBIACEAE			
Sapium glandulosum (L.) Morong	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 329

Table 2. Cont.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
FABACEAE			
Collaea speciosa (Loisel.) DC.	Ph	Ca, Ce, MA	H.V. Pinto Junior 319
Senna neglecta (Vogel) H.S.Irwin & Barneby	Ph	Ca, Ce, MA	H.V. Pinto Junior 303
GESNERIACEAE			
Paliavana prasinata (Ker Gawl.) Benth.	Ph	MA	H.V. Pinto Junior 293
Sinningia sceptrum (Mart.) Wiehler!	Cr	Ce, MA	H.V. Pinto Junior 296
LYTHRACEAE			
Cuphea origanifolia Cham. & Schlecht.	Ch	MA, Pam	H.V. Pinto Junior 308
MELASTOMATACEAE			
Chaetogastra cf. *cerastifolia* (Naudin) P.J.F.Guim. & Michelang.	Ph	Ce, MA	H.V. Pinto Junior 291
Miconia cf. *tristis* Spring	Ph	Ce, MA	H.V. Pinto Junior 326
Pleroma castellense (Brade) P.J.F.Guim. & Michelang.!	Ph	MA	H.V. Pinto Junior 275
Pleroma heteromallum (D. Don) D. Don	Ph	Ce, MA	H.V. Pinto Junior 283
PRIMULACEAE			
Myrsine umbellata Mart.	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 286
SOLANACEAE			
Solanum aff. *didymum* Dunal	Ph	Am, Ce, MA	H.V. Pinto Junior 324
PEDRA DE PONTÕES			
Pteridophytes and Lycophytes			
ANEMIACEAE			
Anemia retroflexa Brade	Hc	MA	D.R. Couto 1641
ASPLENIACEAE			
Asplenium serra Langsd. & Fisch.	Hc	Am, MA	D.R. Couto 2113
BLECHNACEAE			
Telmatoblechnum serrulatum (Rich.) Perrie, D.J. Ohlsen & Brownsey	Cr	Am, Ce, MA	H.V. Pinto Junior 426
DENNSTAEDTIACEAE			
Pteridium arachnoideum (Kaulf.) Maxon	Cr	All domains	H.V. Pinto Junior 101
LOMARIOPSIDACEAE			
Nephrolepis exaltata (L.) Schott	Cr	Am, MA, Pan	D.R. Couto 1348
POLYPODIACEAE			
Microgramma squamulosa (Kaulf.) de la Sota	Ch	Ce, MA	H.V. Pinto Junior 439
Pleopeltis lepidopteris (Langsd. & Fisch.) de la Sota	Hc	MA	H.V. Pinto Junior 425
PTERIDACEAE			
Doryopteris rediviva Fée!	Hc	MA	H.V. Pinto Junior 420
SELAGINELACEAE			
Selaginella convoluta (Arn.) Spring	Ch	Ca, Ce, MA	H.V. Pinto Junior 100
Monocots			
BROMELIACEAE			
Alcantarea patriae Versieux & Wand.*	Hc	MA	D.R. Couto 1792
Pitcairnia decidua L.B.Sm.!	Hc	Ce, MA	H.V. Pinto Junior 424
Pitcairnia flammea Lindl.	Hc	Ce, MA	H.V. Pinto Junior 434
CYPERACEAE			
Bulbostylis sp.	Hc	All domains	H.V. Pinto Junior 93
Cyperus odoratus L.	Hc	All domains	H.V. Pinto Junior 422
Cyperus pohlii (Nees) Steud.	Hc	Ca, Ce, MA, Pam, Pan	H.V. Pinto Junior 181
Rhynchospora exaltata Kunth	Th	Am, Ca, Ce, MA	H.V. Pinto Junior 182
Trilepis lhotzkiana Nees ex Arn.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 16
ORCHIDACEAE			
Bifrenaria tyrianthina (Lodd.) Rchb.f.!	Ch	Ce, MA	D.R. Couto 83
Cyrtopodium glutiniferum Raddi*	Hc	Am, MA	H.V. Pinto Junior 183
Epidendrum secundum Jacq.	Ch	Am, Ca, Ce, MA	H.V. Pinto Junior 95
Habenaria parviflora Lindl.	Hc	Am, Ca, Ce, MA	D.R. Couto 1090

Table 2. Cont.

SITE FAMILY Species	Life-form	Phytogeographic Domains	Voucher
Octomeria crassifolia Lindl.	Hc	Am, Ce, MA	H.V. Pinto Junior 451
Prescottia plantaginifolia Lindl. ex Hook.	Hc	Ce, MA	H.V. Pinto Junior 111
Zygopetalum maculatum (Kunth) Garay	Hc	Ce, MA	H.V. Pinto Junior 128
POACEAE			
Apochloa sp.	Th	Am, Ca, Ce, MA	D.R. Couto 1563
Imperata cf. *brasiliensis* Trin.	Th	All domains	H.V. Pinto Junior 123
Melinis minutiflora P. Beauv.	Hc	Am, Ca, Ce, MA	H.V. Pinto Junior 99
SMILACACEAE			
Smilax aff. *rufescens* Griseb.	Hc	Am, Ce, MA	H.V. Pinto Junior 127
VELLOZIACEAE			
Barbacenia tomentosa Mart.	Ch	Ce, MA	H.V. Pinto Junior 92
Vellozia candida J.C.Mikan	Ph	Ca, MA	H.V. Pinto Junior 208
Vellozia plicata Mart.	Ph	Ca, Ce, MA	H.V. Pinto Junior 88
Vellozia variegata Goethart & Henrard	Ph	Ca, MA	H.V. Pinto Junior 94
Eudicots			
APOCYNACEAE			
Mandevilla atroviolaceae (Stadelm.) Woodson	Cr	Ce, MA	H.V. Pinto Junior 440
ASTERACEAE			
Baccharis crispa Spreng.	Ch	Ca, Ce, MA, Pam	H.V. Pinto Junior 429
Baccharis platypoda DC.	Ph	Ca, Ce, MA	H.V. Pinto Junior 109
Cololobus rupestris (Gardner) H.Rob.*!	Ph	MA	H.V. Pinto Junior 114
Cyrtocymura scorpioides (Lam.) H.Rob.	Ph	Am, Ce, MA	H.V. Pinto Junior 90
Eremanthus crotonoides (DC.) Sch.Bip.	Ph	Ce, MA	H.V. Pinto Junior 108
Lepidaploa cotoneaster (Willd. ex Spreng.) H.Rob.	Ph	Ce, MA	H.V. Pinto Junior 107
CACTACEAE			
Coleocephalocereus pluricostatus Buining & Brederoo*	Ph	MA	H.V. Pinto Junior 213
Hatiora cylindrica Britton & Rose	Ch	MA	H.V. Pinto Junior 444
Rhipsalis sp.	Ch	Am, Ca, Ce, MA, Pan	H.V. Pinto Junior 433
CLUSIACEAE			
Clusia criuva Cambess.	Ph	Ce, MA	D.R. Couto 1246
Clusia mexiae P.F.Stevens	Ph	Ce, MA	H.V. Pinto Junior 437
Clusia organensis Planch. & Triana!	Ph	MA	H.V. Pinto Junior 449
CRASSULACEAE			
Kalanchoe fedtschenkoi Raym.-Hamet & H.Perrier	Ch	MA	H.V. Pinto Junior 453
EUPHORBIACEAE			
Croton floribundus Spreng.	Ph	MA	H.V. Pinto Junior 96
GESNERIACEAE			
Sinningia brasiliensis (Regel & Schmidt) Wiehler & Chautems	Cr	Ca, MA	H.V. Pinto Junior 442
MALVACEAE			
Pseudobombax grandiflorum (Cav.) A.Robyns var. *grandiflorum*	Ph	MA	H.V. Pinto Junior 91
MELASTOMATACEAE			
Trembleya sp.	Ph	Ce, MA	D.R. Couto 561
Miconia polyandra Gardner	Ph	MA	H.V. Pinto Junior 119
Miconia sp.	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 430
Pleroma castellense (Brade) P.J.F.Guim. & Michelang.!	Ph	MA	H.V. Pinto Junior 1
Pleroma heteromallum (D. Don) D. Don	Ph	Ce, MA	H.V. Pinto Junior 102
PORTULACACEAE			
Portulaca hirsutissima Cambess.	Ch	Ca, Ce, MA	H.V. Pinto Junior 445
PRIMULACEAE			
Myrsine umbellata Mart.	Ph	Am, Ca, Ce, MA	H.V. Pinto Junior 112

Table 3. Table containing the results of phytosociological structure of the four communities studied in Espírito Santo State, Brazil.

	Águia Branca	Pedra do Elefante	Forno Grande	Pedra de Pontões
Number of species	27	27	47	50
Number of genera	25	25	39	38
Number of families	18	20	23	27
Number of endemic species	5	6	3	2
Number of threatened species	8	9	5	6
Number of rock outcrops exclusive species	15	13	4	4
Richest Families	Bromeliaceae (3) Velloziaceae (3)	Cyperaceae (3)	Asteraceae (6) Cyperaceae (4) Melastomataceae (4) Orchidaceae (3) Poaceae (3) Velloziaceae (3)	Asteraceae (8) Melastomataceae (5) Orchidaceae (5) Poaceae (4) Cyperaceae (3) Velloziaceae (3)
Genera with one specie	92 %	92 %	95 %	92 %
Family with one specie	61 %	70 %	65 %	74 %
Vegetation sampled (m)	336.7	183.5	1,000	881.5
Bare rock (m)	662.5	816.5	213.19	381.45
Shannon Index (*H'*)	0.95	0.89	2.66	2.48
Evenness (*J*)	0.27	0.26	0.69	0.63

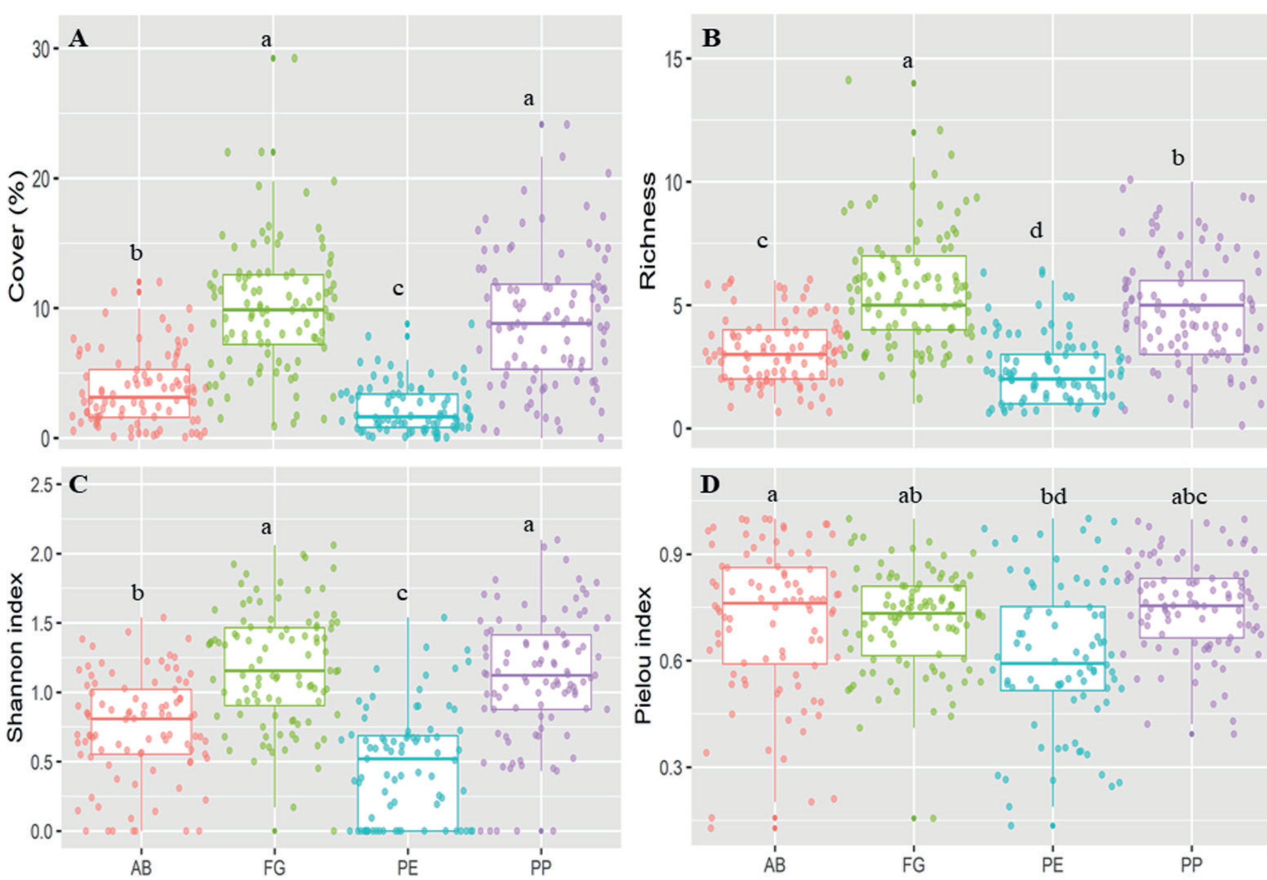

Figure 2. Differences in plant coverage (**A**), species richness (**B**), Shannon index (**C**) and Pielou's evenness index (**D**) along climatic gradient in the north-south axis, Espírito Santo, Brazil. Different letters indicate significant differences (*Dunn test*) among the inselbergs: AB – Águia Branca, PE – Pedra do Elefante, FG – Forno Grande and PP – Pedra de Pontões.

supplementary material) and *V. plicata*, *M. minutiflora*, *Pteridium arachnoideum*, *Eremanthus crotonoides*, *Epidendrum secundum* accounted for 53.19 % of this parameter (Tab. S4 in supplementary material), in Forno Grande and Pedra de Pontões, respectively (more details in the List S2 in supplementary material).

Floristic similarity

Floristically, the four inselbergs can be considered unique due to the low similarity (43 %) observed between the highest similarity inselbergs (Forno Grande and Pedra de Pontões), sites located in the south of Espírito Santo. Among northern inselbergs (Águia Branca and Pedra do Elefante) the similarity decreases to 30 %. When we compare inselbergs between regions the similarities decrease even more. Águia Branca presented similarity values of 16 % and 17 % with Forno Grande and Pedra de Pontões, respectively; and Pedra do Elefante presented similarity values of 22 % and 19 % with Forno Grande and Pedra de Pontões, respectively. From a total of 152 species, 110 species (72.3 %) occurred in only one of the four inselbergs studied, 30 species (19.7 %) in two, eight species (5.3 %) in three inselbergs and four species (*Coleocephalocereus pluricostatus*, *Cyrtopodium glutiniferum*, *T. lhotzkiana* and *Vellozia candida*) occurred in all four inselbergs, representing 2.6 % of the total. The CCC was 0.982.

Changes in community diversity and coverage

In terms of diversity measured by the Shannon Index (*H'*), the sampled areas in southern Espírito Santo presented the highest *H'* values and evenness (all results can be seen in Tab. 3).

We observed significant differences in coverage ($Chi^2 = 120.5$, df = 3, $p < 0.001$, Fig. 2A) and species richness (Kruskal-Wallis test: $Chi^2 = 170.4$, df = 3, $p < 0.01$, Fig. 2B) among sites when we analysed them at the sampling unit scale (Fig. 2). Species richness, cover, and Shannon index maintained similar patterns by region, with the highest values occurring in southern sites (Forno Grande and Pedra de Pontões). The Shannon-Wiener index showed a marked increase along the climatic gradient North-South, being significantly higher in southern sites (Fig. 2C). Conversely, Pielou evenness index showed a similar pattern between sites ($Chi^2 = 12.03$, df = 3, $p < 0.01$, Fig. 2D).

Phytogeography, endemism and threatened species

The distribution of inselberg flora showed that most species (37 %) were distributed exclusively in the Atlantic Forest phytogeographic domain. When we analyzed the distribution between domains, species shared exclusively with the Cerrado represented 17.2 %, with the Caatinga representing 4.76 % and Amazonia 3 %. The species occurring in the Atlantic Forest, Cerrado and Caatinga domains represented 12 %, adding the Amazon domain this value raises to 12.5 %.

Regarding the endemic species of Espírito Santo State, we found 13 species identified as endemic to rocky outcrops, and our survey also identified the presence of 24 species with occurrence exclusively on rocky outcrops. In relation to threatened species, we observed 21 species distributed among Red List categories (IUCN 2012): Vulnerable (33.3 %), Endangered (42.9 %), and Critically Endangered (23.8 %). When we analyzed by region the inselbergs of northern Espírito Santo had nine threatened species (69 %) identified as endemics of rocky outcrops while the southern inselbergs recorded four species (31%). The same patterns were observed for exclusive and threatened species: 21 spp. (84 %) and four spp. (16 %) were exclusive species; and 13 spp. (62 %) and 8 spp. (38 %) were threatened species for north and south inselbergs, respectively (more details in List S3 in supplementary material).

Discussion

This study demonstrated differences in floristic similarity, phytosociological structure, species richness, plant coverage, and Shannon diversity index among Brazilian inselberg with different elevational and climate conditions. Overall, the life-forms were similar among inselbergs, the number of endemic and/or threatened species was high, while the number of species shared with other phytogeographic domains was low.

The richest families and genera have been well represented in other studies of inselberg neotropical flora (França *et al*. 2005; Alves *et al*. 2007; Caiafa & Silva 2007; Porembski 2007; Ribeiro *et al*. 2007; Esgario *et al*. 2009; de Paula *et al*. 2017). These families and genera, common between regions and different inselbergs sites, probably are linked to habitat filtering, such as low nutrient, water availability, high radiation levels, and large temperature amplitude (Biedinger *et al*. 2000; Porembski 2007). Thus, only taxons with specific adaptive traits, as morphological (i.e. caulescent rosette, succulence, and tank-forming) (Biedinger *et al*. 2000; Porembski 2007), anatomical (*i.e.* pseudostems, adventitious roots, sclerophylly, pachycaulous and caudiciformous species) (Biedinger *et al*. 2000), physiological (*i.e.* desiccation tolerance) (Kluge & Brulfert 2000) and functional attributes associated with life history (*i.e.* life-form, resource acquisition, growth, reproduction, and dispersal) (Biedinger *et al*. 2000) will be able to occur. The high floristic richness in the inselbergs studied is evident when we compared with other studies (*i.e.* Porembski *et al*. 1998; Meirelles 1999; Caiafa 2002), and due to a large number of families with only one species, a characteristic pattern of places with high floristic richness (Ratter *et al*. 2003).

Regarding the phytosociological structure and physiognomy, we found a higher number of rare species than other studies focused on rocky outcrops (Meirelles 1996; Conceição 2003; Caiafa & Silva 2007), characteristic that demonstrates the oligarchism present in the rupicolous communities (Scarano 2002). Therefore, Velloziaceae and Bromeliaceae families were observed to be extremely important in the inselbergs studied, due to the higher occurrence and relative importance of a single species from each family. This pattern was also found to be common to the rocky outcrops located in the Cerrado domain (Conceição & Giulietti 2002) and the Atlantic Forest (Ribeiro & Medina 2002), where Velloziaceae and Bromeliaceae families are most common mat-formers.

Some authors also report the high abundance (Conceição 2003; Conceição & Pirani 2007) and adaptations (Kluge & Brulfert 2000) of Velloziaceae family on rocky outcrops are related to poikilohydric adaptation to water stress (Dinakar *et al*. 2012). Thus, during dry periods poikilohydric species tend to dehydrate, returning to a hydrated state with the rains, which is why they are also called "resurrection plants" (Porembski & Barthlott 2000). This adaptation to water stress (desiccation tolerance) represents an important ecophysiological adaptation, influencing community structure and composition (Rietkerk & Koppel 2008; Meloni *et al*. 2017), abundance (Conceição 2003; Conceição & Pirani 2007), diversity (Kluge & Brulfert 2000) and phenology (Conceição 2003).

Concerning the life-form spectrum, phanerophytes were the most commonly represented, as in other studies (Safford & Martinelli 2000; Caiafa & Silva 2005; Ribeiro *et al*. 2007; Gomes & Alves 2010; de Paula *et al*. 2017). However, other studies have recorded chamaephytes (Conceição & Giulietti 2002; Conceição *et al*. 2007) and therophytes (Biedinger *et al*. 2000; Gomes & Sobral-Leite 2013) to be predominant. The lack of a clear pattern between different geographic regions for inselberg life-form spectrum is still unknown (Safford & Martinelli 2000), *e.g.*, therophytes are predominant on inselbergs in tropical Africa (Biedinger *et al*. 2000), whereas in neotropical inselbergs phanerophytes, chamaephytes, and hemicryptophytes are more representative. Here, we assume that our results are related to microtopography variability, which can promote the accumulation of sediments in depressions, contributing to a greater establishment of phanerophytes and consequently their plant habits (mat-form and shrubs). Finally, life-form patterns will be better understood with a greater number of basic researches (Ribeiro *et al*. 2007) associated with researches about ecological competition, biogeography (Safford & Martinelli 2000) and changes in Pleistocene climate cycles (Yates *et al*. 2019).

A contrasting edaphoclimatic pattern was observed in the inselbergs studied, which topographic differences (altitude) and, especially, the geomorphological and microclimatic conditions (Gröger 2000; Porembski 2007) of these outcrops can have a strong impact on plant community composition and structure. A recent study comparing Neotropical inselbergs demonstrated that altitude influence significantly the community composition and species richness and explain more variance than climate models (Pinto-Junior *et al*. 2020). Plant coverage can be more sensitive than species diversity along an environmental gradient (He 2014; Qin *et al*. 2018). Since plant coverage is the proportion of the community's physical space occupied by plants (Ji *et al*. 2009), it is plausible that communities of plants with high coverage are more likely to use environmental resources efficiently than those with low coverage and thereby exhibit increased diversity (Ji *et al*. 2009; Sanaei *et al*. 2018a; b).

Our results showed that plant coverage was higher in sites with higher altitude and precipitation. Thus, the decrease in plant coverage might affect the sensitivity of dryland plant communities to environmental changes within the same vegetation type or within a given region (Vicente-Serrano *et al*. 2012). For example, a dominant trend toward decreased vegetation coverage is evident, mainly in summer and in areas affected by the most severe water stress conditions (*i.e.* low precipitation, higher evapotranspiration rates, and sun-exposed slopes), and sites with low plant coverage (< 30 %) are more sensitive to environmental changes than those with higher coverage (Vicente-Serrano *et al*. 2012).

We presume that, besides climate, fine-scale factors could also be determinant in plant coverage (*i.e.* soil depth and inclination) and consequently affect plant community composition and species richness. A previous study showed how patches size (which may be related to plant coverage) on a tropical inselberg has a strong influence on species composition, richness, and species abundance distribution (Villa *et al*. 2018a). Thus, one of challenges for future research is to assess the relationship between habitat types and plant coverage, and how these affect diversity patterns in Neotropical inselbergs.

We observed changes in species richness and composition, as well as contrasting differences in species shared between regions, probably due to factors acting on communities at a local and fine-scale (environmental filters), which may explain the high floristic dissimilarity between them. Perhaps, another important factor is the dispersal limitation of geographical distance, which can change markedly over relatively short distances (Schut *et al*., 2014). Island ecosystems such as inselbergs combine isolation with historical and environmental filtering and stochastic factors (Parmentier *et al*. 2005; Parmentier & Hardy 2009). Therefore, different degrees of antiquity, occurrence in both tropical and temperate regions, overlaying a broad spectrum of sizes, can compensate the lower degree of geographical isolation and improving the effects of isolation (Porembski *et al*. 2000b). Thereby, as islands, inselbergs have an important phytogeographic contribution to regional diversity, due to their acting as a shelter for xeric vegetation of other domains, such as the Cerrado (Ratter *et al*. 1997). In addition, our results showed a marked contrast in species shared with other phytogeographic domains, demonstrating a high degree of isolation, endemism, and species unique to Atlantic Forest inselbergs.

The high proportion of threatened species (12.5 %) and species exclusive to rocky outcrops (14.2 %) is surprising, due to the constant threats to this ecosystem, such as quarrying, plant overharvesting, weed invasion, fires, climate change, farming and tourism/sports/cultural activities (Porembski *et al*. 2016). Another threat to inselbergs, and very common in the Espírito Santo State, is the so-called high altitude agriculture (Martinelli 2007), as coffee and *Eucalyptus* plantations, which act as a gateway to invasive species. We observed high plant coverage of *M. minutiflora* (exotic and invasive) and *P. arachnoideum* (invasive) in the two most diverse communities of this study (Forno Grande and Pedra de Pontões). The presence of exotic and invasive species in inselberg communities is worrying because can lead to exclusion of native, endemic, and/or threatened species, resulting in loss of global biodiversity hotspot.

Our study indicated that communities have specific flora on each inselberg, giving an insular character to each community, as well as similar diversity patterns. Since floristic dissimilarity between these outcrops is so high (high β-diversity between outcrops), to protect the flora on inselbergs is a real challenge (de Paula *et al*. 2019). Effective conservation strategies will need to focus on protecting multiple inselbergs across the entire climate gradient of the region (Yates *et al*. 2019), rather than a few inselbergs or those with higher species richness. In addition to ecological factors, the low genetic connectivity between isolated populations (*e.g. Encholirium horridum*) in Espírito Santo is already a strong indicator of the strategy of conserving multiple inselbergs (Hmeljevski *et al*. 2015; 2017).

In this context, attention should be drawn to the "Monumento Natural dos Pontões Capixabas", conservation unit with the highest number of inselbergs in the Atlantic Forest. More investments from the federal government are needed and most probably other conservation units in Espírito Santo State are highly recommended, as well as promoting the solution to several issues between local farmers and environmental agencies. We also propose other urgent conservation practices for inselbergs landscape, such as conservation initiatives "off-reserve" (Yates *et al*. 2019); local educational programs in conservation of biodiversity and water (Porembski *et al*. 2016); to encourage sustainable tourism practices; creation of *ex situ* conservation programs for endangered species and the ones affected by mining (Porembski *et al*. 2016); to guarantee the execution of mitigation actions by environmental agencies, and implementation of effective restoration strategies (Porembski *et al*. 2016).

Conclusions

Our study demonstrated marked differences in plant community structure and diversity among local and regions scale, in addition to a specific flora on each inselberg, giving an insular character to each community. We believe this study and conservation strategies can contribute to the development of international legislation for the conservation of inselbergs at different scales. We highlight that the protection of many inselbergs is the most appropriate strategy for the conservation of this global biodiversity hotspot.

Acknowledgements

We thank the CAPES and CNPq for the scholarships of the first and second authors, respectively. This study is part of the master's thesis of the first author. We are grateful to PPGBT/UFES and IEMA for structure and research license. We thank IF Ribeiro, C Covre and WJ Souza for help with fieldwork. We are also grateful to DR Couto, RC Forzza, CN Fraga, LJC Kollmann and I Cordeiro for helped with plant identification.

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