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Floristics, structure and soil of insular vegetation in four quartzite-sandstone outcrops of "Chapada Diamantina", Northeast Brazil

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ABSTRACT – (Floristics, structure and soil of insular vegetation in four quartzite-sandstone outcrops of "Chapada Diamantina", Northeast Brazil). Soil islands on rocky surfaces often harbor aggregated vegetation that consists of insular plant communities. These islands are typical of the rocky outcrops and in various parts of Brazil form the so-called "campos rupestres" vegetation. Four of such sites have been selected in the state of Bahia, Northeast Brazil, for this comparative study on floristics and vegetation structure: three areas situated inside the "Parque Nacional da Chapada Diamantina" (Guiné, Fumaça and "Gerais da Fumaça") and one is at the border of the Environmental Protection Area of "Marimbus-Iraquara" ("Mãe Inácia"). All occurring vegetation islands were studied in four random plots of 10 × 10 m per site. Soil was often shallow, sandy and acidic. Vascular plant species were determined, with respective life forms and canopy coverage areas. The total number of species when all four sites were added was 135, and the number of species per island varied from 2 to 32. The areas of the 214 soil islands varied from 0.015 to 91.9 m^2, totaling 568 m^2 in the four sites. Monocotyledon families were dominant, essentially Velloziaceae, as well as Orchidaceae, Bromeliaceae, Amaryllidaceae and Cyperaceae. Among the eudicotyledons, dominant families were mainly Clusiaceae, Asteraceae and Melastomataceae. The biological spectra revealed that phanerophytes and hemicryptophytes predominated among the life forms, while chamaephytes had the largest coverage area. Epilithic and desiccant chamaephytes composed the most conspicuous interspecific associations, and were probably related to early successional processes. Sites closest to one another were not the most similar in structure, indicating that other factors more relevant than distance might be involved in the abundance of species in space.

Key words - floristics, rocky outcrops, soil islands on rocks, vegetation islands, vegetation structure

RESUMO – (Florística, estrutura e solo da vegetação insular em quatro afloramentos de quartzito-arenito na Chapada Diamantina, nordeste do Brasil). Ilhas de solo abrigam comunidades vegetais agregadas no espaço e delimitadas pela superfície rochosa. Tais ilhas são típicas dos afloramentos rochosos de várias regiões brasileiras e, por vezes, integram parte da vegetação chamada de campo rupestre. Quatro sítios caracterizados por elevadas proporções de superfície rochosa foram selecionados para este estudo de florística e estrutura vegetacional: três situados dentro do Parque Nacional da Chapada Diamantina (Guiné, Fumaça e Gerais da Fumaça) e um no limite com a APA Marimbus-Iraquara (Mãe Inácia). Sortearam-se quatro parcelas de 10 × 10 m por sítio, onde todas as ilhas de solo ocorrentes tiveram suas áreas estimadas. O solo foi em geral raso, arenoso e ácido. Foram determinadas as espécies de plantas vasculares, com respectivas formas de vida e áreas de cobertura vegetal. O número de espécies nos quatro sítios foi 135, variando de 2 a 32 espécies por ilha. As áreas das 214 ilhas de solo variaram de 0,015 a 91,9 m^2, somando 568 m^2 nos quatro sítios. Famílias de monocotiledôneas foram as dominantes, especialmente Velloziaceae, além das Orchidaceae, Bromeliaceae, Amaryllidaceae e Cyperaceae. Dentre as eudicotiledôneas ressaltam-se as Clusiaceae, Asteraceae e Melastomataceae. Os espectros biológicos revelaram as formas de vida fanerófita e hemicriptófita como predominantes, apesar da caméfita possuir maior área de cobertura. Espécies camefíticas epilíticas e camefíticas dessecantes formaram as associações mais conspícuas, provavelmente relacionadas com os processos iniciais de sucessão da vegetação na rocha. Os sítios mais próximos entre si não foram os mais similares na estrutura, indicando outro(s) fator(es) mais relevante(s) do que a distância, envolvidos na abundância das espécies no espaço.

Palavras-chave - afloramentos rochosos, estrutura vegetacional, florística, ilhas de solo sobre rocha, ilhas de vegetação

Introduction

Rocky outcrop vegetation is often aggregated on soil islands surrounded by the exposed rock (McCormick *et al*. 1974, Wiser *et al*. 1996). Severe environmental conditions, such as soil scarcity and nutrient deficiency, high daily temperature oscillations and intense irradiation restrict the occupation of the exposed rock by plants (Shure & Ragsdale 1977, Burrows 1990, Ware 1990), although these unfavorable conditions are somewhat ameliorated when the vegetation is denser (Daubenmire 1968). These plant aggregations surrounded by rock surfaces are called "soil mat communities" (Hambler 1964), "island communities" (Burbanck & Platt 1964, McCormick *et al.* 1974, Shure & Ragsdale 1977),

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"vegetation islands" (Medina *et al.* 2006) or "soil islands" (Conceição & Pirani 2005). In this paper we adopt the latter terminology.

Studies on soil islands on rocks are more abundant in granitic-gneiss outcrops in Africa and in the United States. In South America, Ibisch *et al.* (1995) referred to families such as Bromeliaceae, Cactaceae, Cyperaceae, Orchidaceae, Poaceae, and Velloziaceae as typical of local inselbergs, while Velloziaceae is typical also of African inselbergs (Sarthou & Villiers 1998, Michelangeli 2000). In Brazil, some of the earliest studies on plant communities in rock outcrops were those of Segadas-Vianna (1965), Oliveira *et al.* (1975) and Carauta & Oliveira (1982). Again, Bromeliaceae, Velloziaceae and Orchidaceae appeared as important components in rocky slopes and/or high altitude zones of Rio de Janeiro, organized in "plant clumps that were similar to islands", as described by Carauta & Oliveira (1982).

In Brazil, there appears to be a very restricted number of taxa that are common on rocky outcrop vegetation (França *et al.* 1997, Meirelles *et al.* 1999, Ribeiro & Medina 2002, Conceição & Pirani 2005, 2007, Medina *et al.* 2006, Conceição *et al.* 2007). The "Chapada Diamantina" region, inserted in the semi-arid "caatinga" biome of the Brazilian northeast (Giulietti & Pirani 1988), has been chosen for this study for its high biodiversity, high level of endemisms and the presence of quartzite-sandstone rock outcrops (Harley & Simmons 1986, Giulietti *et al.* 1987, 1996, 1997, Giulietti & Pirani 1988, Alves & Kolbek 1994, Harley 1995, Stannard 1995, Conceição 2000, Conceição & Pirani 2005, 2007). According to Harley & Simmons (1986), "campo rupestre" is the expression that defines the vegetation that grows on quartzite-sandstone substrate, although this terminology is used to refer to Brazilian vegetation on other types of rocky substrate such as granitic-gneiss (*e.g.*, Queiroz *et al.* 1996) or ferruginous (*i.e.*, the locally called "canga", *e.g.*, Viana & Lombardi 2007). Still according to Harley & Simmons (1986), "campos rupestres" occur in altitudes higher than 900 m in the Brazilian states of Goiás, and some isolated areas in São Paulo and Rio de Janeiro, and along the Espinhaço mountain chain in Minas Gerais and Bahia States.

"Morro do Pai Inácio", an inselberg with elevations between 1,100 and 1,170 m, is the single location at "Chapada Diamantina" that has been studied in respect to the vegetation ecology on soil islands (Conceição *et al.* 2007). This "campo rupestre" vegetation is composed essentially of shrubs and herbs (Conceição & Giulietti 2002). The present study adds four other locations to the list of study sites of "Chapada Diamantina" as regards the ecology of vegetation on soil islands. To each of them, we aimed to describe and discuss the relationships between edaphic conditions, floristics and vegetation structure.

Material and methods

Study sites – This study was carried out at four "campo rupestre" sites with a great proportion of exposed rock on hilltops and ridge tops at "Serra do Sincorá" ("Sincorá" Range), "Chapada Diamantina", state of Bahia, Northeast Brazil (figure 1). "Mãe Inácia" site (12°27' S and 41°28' W) is located in the municipality of Palmeiras, and is the only site outside the "Parque Nacional da Chapada Diamantina", with elevations between 1,100 and 1,140 m a.s.l. It is the most isolated hill of our four study sites and has four small summits (1 to 3 ha) isolated from each other by three cleefs of 5 to 10 m of width. "Cachoeira da Fumaça" (12°35' S and 41°27' W) and "Gerais da Fumaça" (12°36' S and 41°28' W) outcrops are located at "Serra da Larguinha", in the municipality of Palmeiras, between 1,310 and 1,360 m of altitude. "Gerais da Fumaça" is the less isolated site from the surrounding vegetation. Guiné outcrops are found on the western border of "Serra do Sincorá" and "Parque Nacional da Chapada Diamantina", at "Serra do Esbarrancado", municipality of Mucugê (12°45' S and 41°30' W). They are the highest outcrops (*ca.* 1,400 m a.s.l.) among our study sites.

The climate at the study sites is Central Brazil Tropical, sub-hot, semi-humid, with a humid summer and four to five dry months concentrated during spring. From June to August, months are cooler and the first morning hours are often cloudy. Mean annual temperatures at locations with elevations between 1,000 and 1,100 m are lower than 20 °C, and minimum daily temperatures lower than 4 °C may occur (Nimer 1989). Predominant winds come from the southeast and orographic rains occur in the eastern sector, where our study sites are found (Jesus *et al.* 1985).

Sandstones and quartzites formed in the Pre-Cambrian make up the rugged topography of the "Chapada Diamantina", resulting from differential erosion (Moreira & Camelier 1977). The rocky outcrops studied are included in the "Chapada Diamantina" Group, which starts near Mucugê, extending through "Santo Inácio", and is part of the Tombador Formation (Torquato & Fogaça 1981). The soil sediments upon which the vegetation stands are shallow, sandy, and acidic, concentrating high organic matter and clay contents in relation to locations with more continuous vegetation (Conceição & Giulietti 2002, Conceição & Pirani 2005).

Soil islands – The soil islands were taken as sample units defined as combinations of two or more individuals of vascular plants sharing the same patch of soil that is surrounded by a bare rock surface devoid of any vascular plants (Conceição & Pirani 2005). In each of the four sites, four random 10 × 10 m plots were drawn, and within these limits all soil islands were labeled and numbered. Islands only partly included

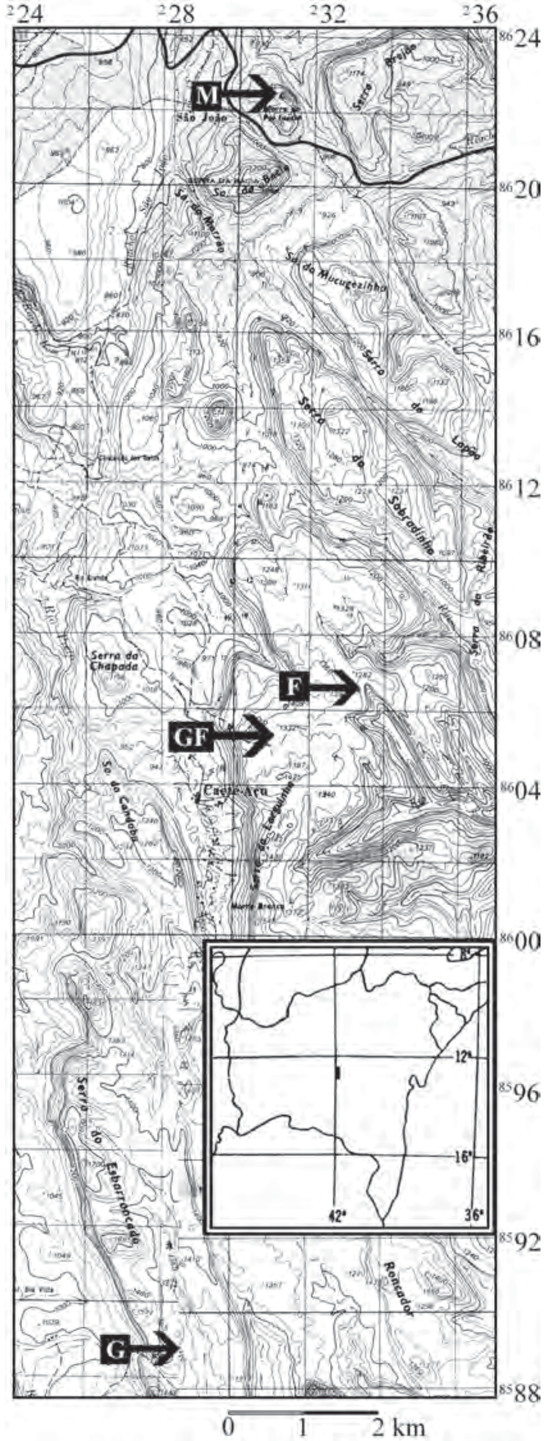

Figure 1. Location of the study sites: "Morro da Mãe Inácia" (M), Fumaça (F), "Gerais da Fumaça" (GF) and Guiné (G) at "Chapada Diamantina", Bahia, Brazil. Adapted from Conceição & Pirani (2007) [pages Lençóis, Palmeiras, Seabra and Utinga of map SUDENE (1977) 1:100000].

within the plots were also sampled entirely. Thus, establishing plots was a strategy only to standardize the islands sampled.

Soil sampling – The collection of soil samples was hindered by the small quantity of sediments in the soil islands, both at surface and in depth. Shallow sediments appeared associated to fractures and other unevenness on the rock surfaces. The sediments were composed mainly by organic and inorganic material and root mass, while ant and termite nests were often found.

For each site, two out of the four 10 × 10 m plots were randomly chosen for the extraction of two sediment samples at 10 cm of depth in each of them, totaling four soil samples per site. These collections were made in the central portions of the largest and the smallest island that had at least 10 cm of depth. In one of the plots at "Morro da Mãe Inácia", only one island had 10 cm of depth, which meant a smaller number of samples for this site (15 soil samples rather than 16).

Soil samples were analyzed at the Department of Soils and Plant Nutrition at the "Escola Superior de Agricultura Luiz de Queiroz", Piracicaba, state of São Paulo, following the methods described by Ruggiero *et al.* (2002). Between-site comparison of edaphic parameters were done by one-way ANOVA (Callegari-Jacques 2003), calculated by the software *Statistica* 6.0. Initially, variables were tested for normality (Kolmogorov-Smirnov, $P > 0.05$) and homocedasticity (Levene, $P > 0.05$). The hypothesis tested by ANOVA was that means were equal in each site (H_0: $\mu_M = \mu_F = \mu_{GF} = \mu_G$, $\alpha = 0.05$; where sites are M = "Mãe Inácia", F = Fumaça, GF = "Gerais da Fumaça" e G = Guiné). Rejection of H_0 meant between-site difference, and Tukey test (a = 0.05) was applied to test such differences (Callegari-Jacques 2003).

Surface area of vegetation islands and cover area of individual species – The surface areas of the islands were estimated by measuring their longest axis (l) and greatest width (w). Then, based on the general form of the island, either the area of an ellipse ($\frac{1}{4}\,l.w.\pi$) or a rectangle ($l.w$) was calculated. The percent area covered by the different plant species composing each island was visually estimated based on the vertical projection of all aerial plants parts (Westhoff & Maarel 1978).

Species composition and life forms – Fertile specimens of all species on the soil islands were collected and oven-dried. Voucher specimens were deposited at the herbarium SPF ("Universidade de São Paulo"). Family names followed Cronquist (1981), except for Amaryllidaceae and Fabaceae *s.l.* (= Leguminosae). The abbreviations of the names of the botanical authorities followed Brummitt & Powell (1992). Raunkiaer's life-forms were determined according to Ellenberg & Müeller-Dombois (1967) and further details are provided in Conceição & Pirani (2005).

Data analyses – Community structure was explored applying the multivariate statistical techniques of classification and ordination on the patterns of species distribution and abundance in soil islands of the different sites.

A cluster procedure was used for representation of species co-occurring in soil islands on all sites. The procedure was applied on a Jaccard similarity coefficient matrix calculated from the species presence-absence data on soil islands. Only species that occurred in more than 9% of the soil islands were included in the analysis. The construction of the similarity dendrogram was based on the unweighed pair-group mean clustering algorithm (UPGMA).

For exploring the patterns arising from species abundance by site, an ordination procedure by correspondence analysis (CA) of the detrended variant (DCA) was applied as a strategy for unbiased indirect gradient detection (Ter Braak 1997). This ordination procedure was applied on a matrix of sites and species abundance values in soil islands occurring on 100 m^2 plots. Detrending was done by segments. The ordination of sites on the two first axes was examined by interpolation of DCA scores resulting from the DCA.

Detrended correspondence analysis ordinations and the r-mode UPGMA cluster analyses were performed using MVSP version 3.12 software (Kovach Computing Service, Anglesey, UK) (Kovach 1999).

Results

Soil – Soil analyses showed marked variations in regard to the edaphic features of our four study sites (table 1). Calcium concentration was higher at Fumaça, as compared to "Mãe Inácia" and "Gerais da Fumaça" ($F_{\mathrm{Ca}\ (3,\ 11)} = 5.9066$, $P = 0.0118$). The percentage of silt was higher also at Fumaça as compared to "Gerais da Fumaça" ($F_{\mathrm{silt}\ (3,\ 11)} = 5.5784$, $P = 0.0142$). Aluminum concentration was higher at "Mãe Inácia" than at Fumaça and Guiné ($F_{(3,\ 11)} = 9.8631$, $P = 0.0019$). At Fumaça, pH was more acidic than at "Mãe Inácia" ($F_{(3,\ 11)} = 6.7698$, $P = 0.0075$). However, three out of seven edaphic variables that satisfied the assumptions of ANOVA were statistically similar between the study sites ($P > 0.05$): organic matter ($F_{(3,\ 11)} = 1.0783$), cation exchange capacity ($F_{(3,\ 11)} = 0.8456$) and sodium ($F_{(3,11)} = 0.2444$).

Vegetation – Table 2 lists the 135 species of angiosperms (distributed in 43 families) found in the 214 soil islands of four rocky outcrops of "Chapada Diamantina". There were nine species included in seven families of vascular cryptogams. Eudycotyledons were represented by 58 species included in 24 families. The family Piperaceae was represented by one species and monocots were 67 species of 11 families. The surface area of the soil islands varied from 0.015 to 91.9 m^2, and 2 to 32 plant species were found per island. The total surface area of soil islands when all 214 islands of our four sites were added was 568 m^2, while the total coverage of vascular plant species in these islands was 675 m^2. The difference between the two values is due to overlaps between branches of different species in given soil islands. Thus, there was an average of 0.23 plant species m^{-2} of soil islands. The site Fumaça had the highest number of species (85) on 216 m^2 of soil islands (0.39 species m^{-2}), while "Gerais da Fumaça" had the lowest (39 species m^{-2}) on 213 m^2 of soil islands (0.18 species m^{-2}). Guiné had 57 species on 74 m^2 (0.76 species m^{-2}) and "Morro da Mãe Inácia" had 42 on 63 m^2 (0.66 species m^{-2}) of soil islands.

Orchidaceae was the most species-rich family (26), followed by Poaceae (12), Asteraceae (10), Velloziaceae

Table 1. Mean values of chemical and granulometric soil parameters, from soils collected in 15 soil islands. Study sites, located at "Chapada Diamantina", Bahia, Brazil, are: M = "Morro da Mãe Inácia", F = Fumaça, GF = "Gerais da Fumaça", and G = Guiné. Parameters analysed: OM = organic matter; BS = base sum; CEC = cation exchange capacity; PBS = percent base saturation; AlS = aluminum saturation.

	M	F	GF	G	M + F + GF + G
OM (g dm^{-3})	159.6 ± 18.4	148.8 ± 17.3	129.8 ± 11.7	146.8 ± 26.6	145.33 ± 21.95
pH (H_2O)	3.5 ± 0.1	3.9 ± 0.2	3.7 ± 0.1	3.9 ± 0.1	3.7 ± 0.2
P (mg kg^{-1})	7.7 ± 4.5	21.8 ± 12.7	8.0 ± 3.5	14.3 ± 7.8	13.3 ± 10.0
Na (mmolc kg^{-1})	1.2 ± 0.4	1.2 ± 0.3	1.1 ± 0.1	1.0 ± 0.2	1.1 ± 0.3
K (mmolc kg^{-1})	2.1 ± 0.2	5.3 ± 0.6	1.8 ± 0.5	5.8 ± 3.5	3.8 ± 2.6
Ca (mmolc kg^{-1})	1.7 ± 0.9	23.3 ± 6.6	3.0 ± 2.9	13.3 ± 11.1	10.9 ± 11.1
Mg (mmolc kg^{-1})	3.7 ± 1.2	19.0 ± 4.5	4.5 ± 2.1	19.3 ± 16.5	12.1 ± 11.6
Al (mmolc kg^{-1})	37.0 ± 4.1	16.8 ± 1.9	26.5 ± 2.3	21.5 ± 7.0	24.7 ± 8.3
H+Al (mmolc kg^{-1})	268.0 ± 32.9	180.8 ± 24.9	194.5 ± 33.2	190.3 ± 62.5	204.4 ± 52.5
BS (mmolc kg^{-1})	8.6 ± 2.0	48.7 ± 9.4	10.4 ± 5.4	39.3 ± 28.7	27.9 ± 23.6
CEC(mmolc kg^{-1})	276.6 ± 34.5	229.5 ± 30.6	204.9 ± 33.2	229.5 ± 82.4	232.3 ± 56.5
PBS	3.3 ± 0.5	21.3 ± 3.3	5.3 ± 2.8	16.8 ± 9.5	12.2 ± 9.2
AlS (%)	81.3 ± 1.7	26.0 ± 3.7	73.0 ± 11.0	42.5 ± 20.9	54.0 ± 25.4
Sand (%)	78.7 ± 2.1	68.3 ± 3.8	84.3 ± 2.5	79.8 ± 12.8	77.7 ± 9.3
Silt (%)	11.3 ± 1.2	21.3 ± 3.3	8.0 ± 1.4	11.3 ± 7.1	13.1 ± 6.6
Clay (%)	10.0 ± 1.4	10.5 ± 0.9	7.8 ± 1.1	9.0 ± 5.7	9.3 ± 3.3

Table 2. Species or morphospecies of vascular plants sampled in 214 soil islands at "Morro da Mãe Inácia", Fumaça, "Gerais da Fumaça" and Guiné study sites, "Chapada Diamantina", Bahia, Brazil. Life forms (LF): microphanerophyte (mF), nanophanerophyte (nF), epilithic chamaephyte (eC), desiccation tolerant chamaephyte (dC), chamaephyte not epilithic and not desiccation-tolerant (Ch), hemicryptophyte (H), cryptophyte (Cr), therophyte (T), epiphyte (E), succulent (S) and liana (L).

Family Species	LF	Voucher material
AMARYLLIDACEAE		
Hippeastrum puniceum (Lam.) Kuntze	Cr	*V.C.Souza 5226*
Hippeastrum solandriflorum (Lindl.) Herb.	Cr	*Conceição 616*
APOCYNACEAE		
Mandevilla bahiensis (Woodson) M. F. Sales	Cr	*Conceição 219*
Mandevilla tenuifolia (Mikan) Woodson	Cr	*Conceição 208*
AQUIFOLIACEAE		
Ilex amara (Vell.) Loes.	nF	*Conceição 735*
ARACEAE		
Philodendron pachyphyllum Krause	nF	*Conceição 402*
ASCLEPIADACEAE		
Metastelma harleyi Fontella	L	*Conceição 432*
Metastelma myrtifolium Decne.	Cr	*Conceição 300*
ASTERACEAE		
Acritopappus hagei R. M. King & H. Rob.	nF	*Grillo 70*
Baccharis cf. *salzmannii* DC.	nF	*Conceição 964, 1077*
Bahianthus viscosus (Spreng.) R. M. King & H. Rob.	nF	*Conceição 56*
Lasiolaena duartei R. M. King & H. Rob.	nF	*Conceição 133*
Lychnophora triflora (Mattf.) H. Rob.	nF	*Conceição 55*
Mikania glandulosissima W. C. Holmes	L	*Conceição 780*
Paralychnophora bicolor (Mart. ex DC.) MacLeish	nF	*Conceição 34*
Stylotrichium rotundifolium Mattf.	nF	*Conceição 884*
Verbesina baccharifolia Mattf.	nF	*Conceição 607*
Vernonia cotoneaster (Willd. ex Spreng.) Less.	T	*Conceição 841*
BEGONIACEAE		
Begonia grisea A.DC.	nF	*Conceição 205*
BROMELIACEAE		
Hohenbergia cf. *catingae* Ule	H	*Conceição 407*
Neoregelia bahiana (Ule) L. B. Sm.	H	*Conceição 640*
Orthophytum albopictum Philcox	H	*Conceição 1097*
Orthophytum burle-marxii L. B. Sm. & Read	H	*Conceição 75*
Tillandsia stricta Sol.	E	*PCD 507*
Vriesea atra Mez	H	*Conceição 408*
Vriesea friburguensis Mez	H	*Conceição 602*
CACTACEAE		
Arrojadoa bahiensis (P. J. Braun & Esteves) N. P. Taylor & Eggli	S	*Harley 24522*
Micranthocereus purpureus (Gürke) F. Ritter	S	*Zappi 141*
Pilosocereus pachycladus F. Ritter	S	*Harley 25562*
CLUSIACEAE		
Clusia obdeltifolia Bittrich	nF/mF	*Conceição 287*
Clusia melchiorii Gleason	nF	*Conceição 830*
CONVOLVULACEAE		
Evolvulus jacobinus Moric.	Ch	*Conceição 303*
Jacquemontia sp. nov.	nF	*Conceição 823, 942*

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Family Species	LF	Voucher material
CYPERACEAE		
Abildgaardia scirpoides Nees	T	*Conceição 877*
Abildgaardia sp.	T	*Conceição 560*
Bulbostylis aff. *jacobinae (*Steud.) Lindm.	T	*Conceição 984*
Lagenocarpus rigidus (Kunth) Nees	H	*Conceição 422*
Trilepis lhotzkiana Nees	dC	*Conceição 308, 448*
DIOSCORIACEAE		
Dioscorea sincorensis R. Knuth	Cr	*Conceição 293, 435*
DRYOPTERIDACEAE		
Rumohra adiantiformis (Forst.) Ching	H	*Conceição 779*
ERICACEAE		
Gaylussacia brasiliensis (Spreng.) Meisn.	nF	*Conceição 605, 838*
Gaylussacia incana Cham. & Schltdl.	nF	*Conceição 873*
ERIOCAULACEAE		
Leiothrix angustifolia (Koern.) Ruhland	T	*Conceição 635*
Paepalanthus pulchellus Herzog	T	*Conceição 606*
Paepalanthus sp. nov.	H	*Conceiçao 612*
EUPHORBIACEAE		
Croton timandroides Müll. Arg.	nF	*Conceição 667*
Phyllanthus klotzschianus Müll. Arg.	nF	*Conceição 706*
Stillingia saxatilis Müll. Arg.	nF	*Conceição 766, 848*
FABACEAE *s.l.*		
Calliandra asplenioides (Nees) Renvoize	nF	*Conceição 749, 1016*
Calliandra cf. *viscidula* Benth.	nF	*Conceição 1021*
Calliandra sp.	nF	*Conceição 776,993*
Chamaecrista cytisoides (Collad.) Irwin & Barneby	nF	*Conceição 778*
Zornia flemmingioides Moric.	Cr	*Conceição 216*
GENTIANACEAE		
Curtia verticilaris (Spreng.) Knobl.	T	*Conceição 879*
Schultesia pachyphylla Griseb.	T	*Conceição 795, 818*
GESNERIACEAE		
Paliavana tenuiflora Mansf.	nF	*Conceição 115*
Sinningia elatior (Kunth) Chautems	nF	*Conceição 228*
GRAMMITIDACEAE		
Cochlidium punctatum (Raddi) L. E. Bishop	E	*Conceição 854*
HYMENOPHYLLACEAE		
Hymenophyllum polyanthos (Sw.) Sw.	H	*Conceição 564*
LAMIACEAE		
Eriope exaltata Harley	nF/mF	*Conceição 36*
Hyptis hagei Harley	nF	*Conceição 48*
LOGANIACEAE		
Spigelia cremnophila Zappi & E. Lucas	Ch	*Conceição 64*
LYCOPODIACEAE		
Huperzia mooreana (Baker) Holub.	Ch	*Conceição 447*
LYTHRACEAE		
Cuphea sp.	nF	*Conceição 673*
Cuphea ericoides Cham. & Schltdl.	nF	*Conceição 672*

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Family Species	LF	Voucher material
MELASTOMATACEAE		
Marcetia vellutina Markgr.	nF	*Conceição 142*
Microlicia sp.	nF	*Conceição 57, 688*
Tibouchina oreophila Wurdack	nF	*Conceição 825*
Tibouchina pereirae Brade & Markgr.	H/nF/mF	*Grillo 32*
MYRTACEAE		
Myrcia myrtifolia DC.	nF	*Conceição 295, 730*
ORCHIDACEAE		
Acianthera hamosa (Barb.Rodr.) Pridgeon & M. W. Chase	E/Ch	*Conceição 126*
Acianthera ochreata (Lindl.) Pridgeon & M. W. Chase	eC	*Conceição 70*
Bifrenaria magnicalcarata (Hoehne) Pabst	Ch	*Conceição 979*
Cattleya elongata Barb. Rodr.	eC	*PCD 1741*
Cyrtopodium aliciae Lindau	Ch	*PCD 1136*
Epidendrum saxatile Lindl.	eC	*Conceição 721*
Epidendrum secundum Jacq.	eC	*Conceição 394*
Habenaria pseudohamata Toscano	Cr	*Conceição 788*
Oncidium blanchetii Rchb.f	Ch	*Conceição 129*
Oncidium sp.	Ch	*Conceição 762*
Pelexia viridis (Cogn.) Schltr.	Cr	*Conceição 689, 1009*
Prescottia plantaginea Lindl.	Cr	*Conceição 894*
Sacoila lanceolata (Aubl.) Garay	Cr	*Conceição 755, 977*
Skeptrostachys congestiflora (Cogn.) Garay	Cr	*Conceição 214*
Sophronitis bahiensis (Schltr.) Van den Berg & M. W. Chase	eC	*Conceição 600*
Sophronitis sincorana (Schltr.) Van den Berg & M. W. Chase	eC	*Conceição 719*
Veyretia sincorensis (Schltr.) Szlach.	Cr	*Conceição 717, 897*
Zygopetalum mackayi Hook.	H	*Conceição 519, 793*
Zygopetalum selowii Rchb.f	H	*Conceição 1103*
Orchidaceae sp. 1	Cr	–
Orchidaceae sp. 2	Cr	–
Orchidaceae sp. 3	H	–
Orchidaceae sp. 4	H	–
Orchidaceae sp. 5	Cr	–
Orchidaceae sp. 6	Cr	–
Orchidaceae sp. 7	Ch	–
PIPERACEAE		
Peperomia galioides Kunth	eC	*Conceição 442*
POACEAE		
Andropogon sp.	H	*Conceição 786*
Axonopus aureus P. Beauv.	H	*Conceição 304*
Panicum belmontae Renvoize	H	*Conceição 1089*
Panicum cumbucana Renvoize	H	*Conceição 1054*
Ichnanthus inconstans (Trin. ex Nees) Doell	H	*Conceição 1055*
Panicum animarum Renvoize	H	*Conceição 882*
Panicum trinii Kunth	H	*PCD 690; Grillo 30*
Panicum sp.	H	*Conceição*
Paspalum minarum Hack.	H	*Conceição 311, 847*
Schizachyrium sanguineum (Retz.) Alst.	H	*Conceição 576*
Trachypogon macroglossus Trin.	H	*Conceição 915*
Trachypogon spicatus (L. f.) Kuntze	H	*Conceição 839*

continue

continuation

Family Species	LF	Voucher material
POLYGALACEAE		
Polygala guedesiana Marques	T	*Conceição 857*
Polygala tuberculata Chodat	nF	*Conceição 771*
Polygala sincorensis Chodat	H	*Conceição 773*
POLYPODIACEAE		
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	H	*Conceição 1111*
Polypodium catharinae Langsd. & Fish	H	*Conceição 818*
Polypodium triseriale Sw.	H	*Conceição 874*
PTERIDACEAE		
Doryopteris ornithopus (Mett. ex Hook. & Baker) J. Sm.	H	*Conceição 782*
RUBIACEAE		
Borreria capitata (Ruiz & Pav.) DC.	T	*Conceição 468*
Declieuxia aspalathoides Müll. Arg.	nF	*Grillo 25*
Hillia parasitica Jacq.	nF	*Conceição 358*
SCROPHULARIACEAE		
Esterhazya splendida J. C. Mikan	nF	*Conceição 935, 948*
SELAGINELLACEAE		
Selaginella marginata (Humb. & Bonpl.) Spring	dC	*Conceição 565*
SMILACACEAE		
Smilax elastica Griseb.	L	*Conceição 539*
VELLOZIACEAE		
Barbacenia blanchetii Goethart & Henrard	dC	*Conceição 49*
Barbacenia sp. nov.	dC	*Conceição 511*
Vellozia dasypus Seub.	dC	*Conceição 909*
Vellozia hemisphaerica Seub.	dC	*Conceição 113*
Vellozia punctulata Seub.	dC	*Conceição 210*
Vellozia sincorana L. B. Sm.	dC	*Conceição 912*
Vellozia jolyi L. B. Sm.	dC	*Conceição 956, 968*
VERBENACEAE		
Lantana caatingensis Moldenke	Ch	*Conceição 35*
Lippia alnifolia Schauer	nF	*Conceição 273*
Stachytarpheta crassifolia Schrad.	nF	*Conceição 31*
Stachytarpheta froesii Moldenke	nF	*Conceição 1050*
XYRIDACEAE		
Xyris mello-barretoi L. B. Sm.	T	*Conceição 1034*
Xyris cf. *obcordata* Kral & Wand.	T	*Conceição 1029*

and Bromeliaceae (seven each), Cyperaceae and Fabaceae (five each), and Verbenaceae and Melastomataceae (four each). Most families (27; 63%) had only one or two species. Out of the ten most frequent families, seven were monocots (figure 2A). The surface area covered by species belonging to the Velloziaceae family amounted to 43% of the 675 m^2 of total coverage area when all vascular species belonging to the 214 soil islands are added (figure 2B).

Figure 3 shows percentage occurrence (A) and percent cover (B) of the seven most representative botanical families per site. From all families in the two legends, six were the same throughout (Velloziaceae, Asteraceae, Cyperaceae, Bromeliaceae, Orchidaceae, and Melastomataceae), while Amaryllidaceae was representative for occurrence and Clusiaceae for aerial plant coverage. “Gerais da Fumaça” had the highest proportion (47%) of occurrence of species belonging to

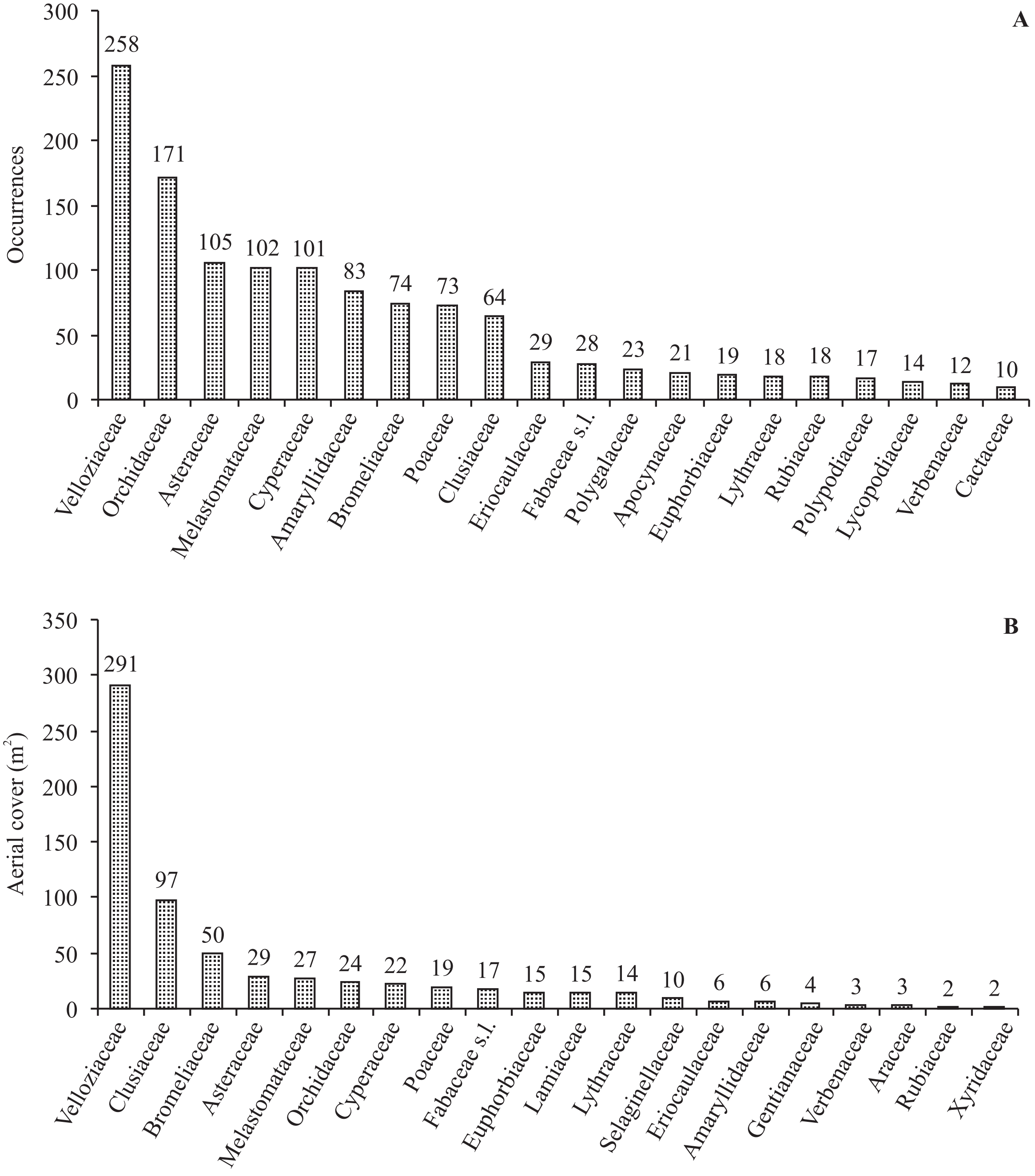

Figure 2. Plant families with more than 9 occurrences (A) or more than 2 m^2 of aerial cover (B), on 214 soil islands with 135 species, at “Morro da Mãe Inácia”, Fumaça, “Gerais da Fumaça” and Guiné study sites, “Chapada Diamantina”, Bahia, Brazil.

“other families”, *i.e.*, those that do not belong to the seven plant families in the legend of figure 3A, whereas in “Morro da Mãe Inácia” these families were the most representative (80%). In terms of aerial coverage, the seven families were again more strongly represented in the latter site (figure 3B).

Phanerophyte and hemicryptophyte life forms were predominant, while therophytes were numerous in site “Gerais da Fumaça” (figure 4A). Percent cover was expressive for desiccation-tolerant chamaephyte, phanerophyte and thallo-chamaephyte (lichens), while hemicryptophytes covered high proportions of sites “Gerais da Fumaça” and Guiné, and epilithic chamaephyte did so at “Mãe Inácia” (figure 4B).

Classification and ordination analysis – The classification of the 22 species according to their occurrence in 214 soil islands revealed distinct patterns of floristic composition among the soil islands. The dendrogram in figure 5 shows that there are four distinct groups of co-occurring species

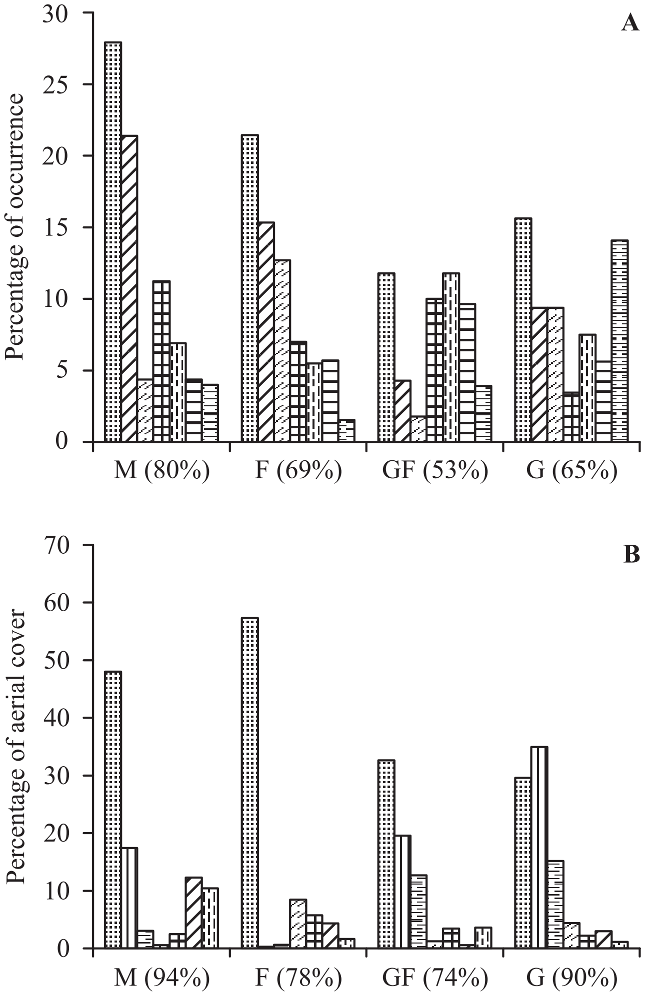

Figure 3. Percentage of occurrence (A) and aerial cover (B) of plant families per study site at "Chapada Diamantina", Bahia, Brazil: "Morro da Mãe Inácia" (M), Fumaça (F), "Gerais da Fumaça" (GF) and Guiné (G). Numbers in parenthesis are the sum of the percentages of the families with higher local percentage at each site. (⊟ = Amaryllidaceae; ▨ = Asteraceae; ▤ = Bromeliaceae; ◫ = Clusiaceae; ▣ = Cyperaceae; ⊞ = Melastomataceae; ⧄ = Orchidaceae; ▦ = Velloziaceae).

in soil islands. These groups are related to specific sites, which was evidenced by the presence of exclusive species for "Mãe Inácia" (*Barbacenia blanchetii* and *Vellozia hemisphaerica*), Fumaça (*Vellozia punctulata* and *Vellozia dasypus*), Guiné (*Orthophytum albopictum*) and "Gerais da Fumaça" and Guiné (*Vellozia jolyi*). In addition to the exclusive species, there were exclusive combinations of species for the soil islands, such as the pair *Trilepis lhotzkiana* and *Cattleya elongata* in the "Mãe Inácia" site. The islands characterized by the combination of *Orthophytum albopictum* and *Mandevilla bahiensis* occurred at Guiné, and included *Lasiolaena duartei* and *Vriesea atra*. Islands containing the combination of *Hippeastrum solandriflorum, Abildgaardia* sp., *Schizachyrium sanguineum* and *Tibouchina pereirae* were typical for "Gerais da Fumaça" and Guiné, but are common species in soil islands of all sites.

The two first axes resulting from DCA analysis of the abundance matrix represented together 31.64% of the total variation in the matrix with 23.22% and 8.42% in the first and the second axis respectively. A gradient can be depicted through the interpolation of the site scores on the first two axes. The arrangement of site scores is polarized by the "Mãe Inácia" plots in opposition to Fumaça, while Gerais and "Gerais da Fumaça" are in intermediate positions. The second axis discriminates the Gerais and "Gerais da Fumaça" plots. All the plots appear in very distinct groups in the interpolation of the two first axes scores. The "Mãe Inácia" plots occur in a small gradient on the first axis, which suggests a higher heterogeneity in this site.

Discussion

Soil type and site isolation – The soil type of the vegetation islands and the degree of isolation of the study sites were often two of the main factors related to between-site variation in diversity and species composition for the four sites studied at "Chapada Diamantina". This pattern probably results in a high beta-diversity, as already described for inselbergs in the state of Rio de Janeiro (Meirelles *et al.* 1999).

The shallow, sandy and acidic soil of the vegetation islands of "Chapada Diamantina" resembled those of other "campos rupestres" (Duarte 1967, Joly 1970, Harley 1995, Vitta 1995, Conceição & Giulietti 2002, Conceição & Pirani 2005). Since community structure is influenced by resource availability (Huggett 1995), soil type is likely to be related to the differences in diversity between sites found here. For instance, the high percentages of silt and base saturation, plus the high concentration of phosphorus and low aluminum saturation, might help explain the highest species richness found at the Fumaça site. The higher humidity in this site is due to a neighboring waterfall that might benefit decomposers (Huggett 1995), as well as the plants directly. Moreover, the finest soil particles (clay) are related to a higher capacity of nutrient retention (Raven *et al.* 2001). Conversely, the "Gerais da Fumaça" site that had the lowest species richness also had low percentages of silt, clay, organic matter, low capacity for cation exchange, soil acidity, and a relatively high concentration of aluminum. The "Morro da Mãe Inácia" site had similarly low species richness, and despite

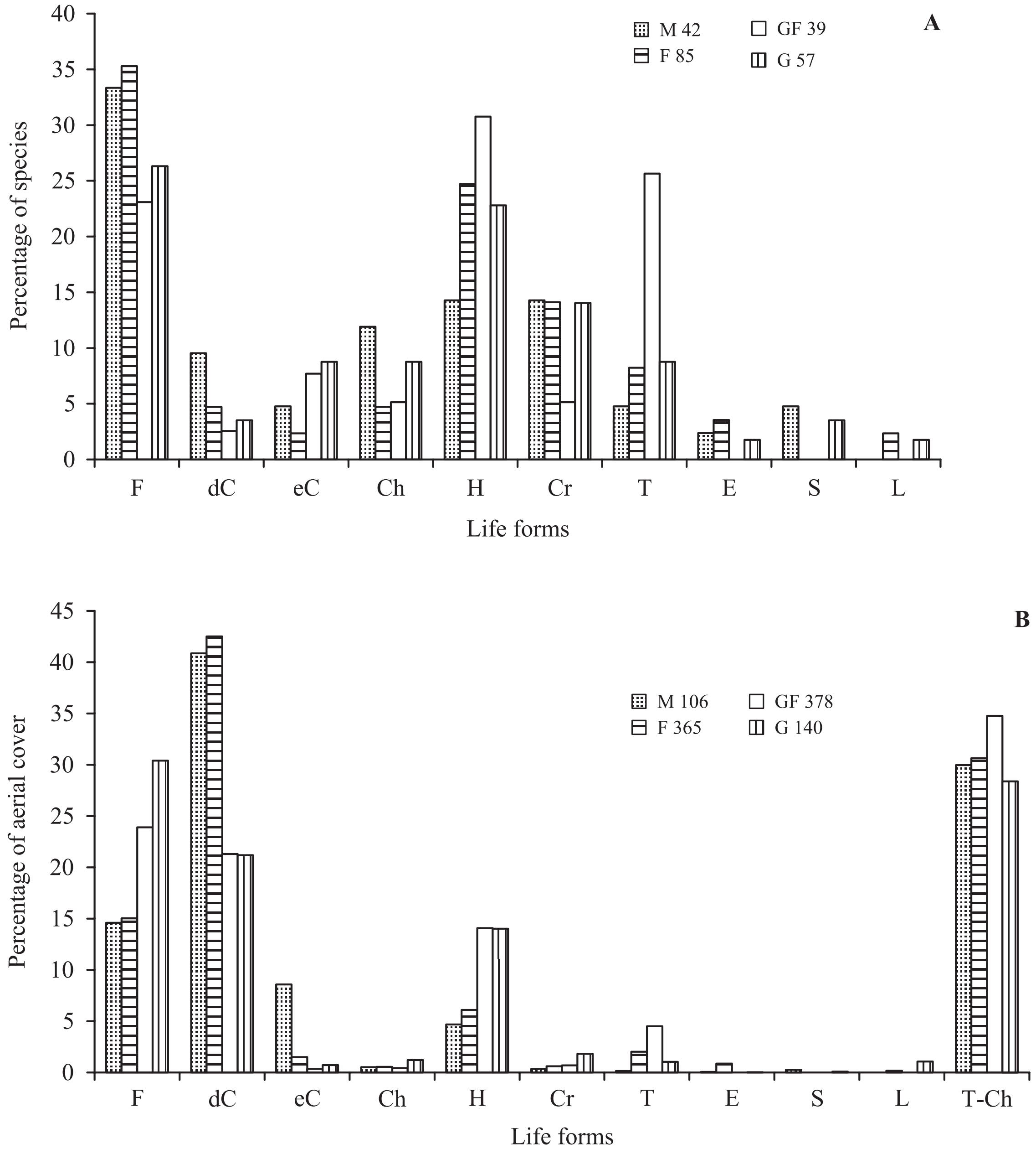

Figure 4. Percentage of species (A) and cover (B) of life forms on the 214 soil islands at "Morro da Mãe Inácia" (M), Fumaça (F), "Gerais da Fumaça" (GF) and Guiné (G) study sites at "Chapada Diamantina", Bahia, Brazil. Numbers following letters are the total of species (A) or areas in m^2 (B). Life forms: F = phanerophyte, dC = desiccation tolerant chamaephyte, eC = epilithic chamaephyte, Ch = chamaephyte not epilithic and not desiccation-tolerant, H = hemicryptophyte, Cr = cryptophyte, T = therophyte, E = epiphyte, S = succulent, L = liana, T-Ch = thallo-chamaephyte.

a high concentration of organic matter, all other parameters resembled "Gerais da Fumaça". Guiné, which was the site with intermediate species richness, also had intermediate values for soil parameters, particularly for organic matter, base saturation and aluminum.

Species composition of "Morro da Mãe Inácia", the most isolated site, revealed a number of microendemisms, not found on the other sites less isolated from the surrounding vegetation. However, although this is an indication that isolation should affect species composition and local endemisms, proximity between sites did not grant species composition similarity. For instance, "Gerais da Fumaça" and Fumaça were not the most similar to each other. This was surprising since these sites were closest to each other and were both adjacent to extensive fields, which might have favored in both cases the entrance of grassland

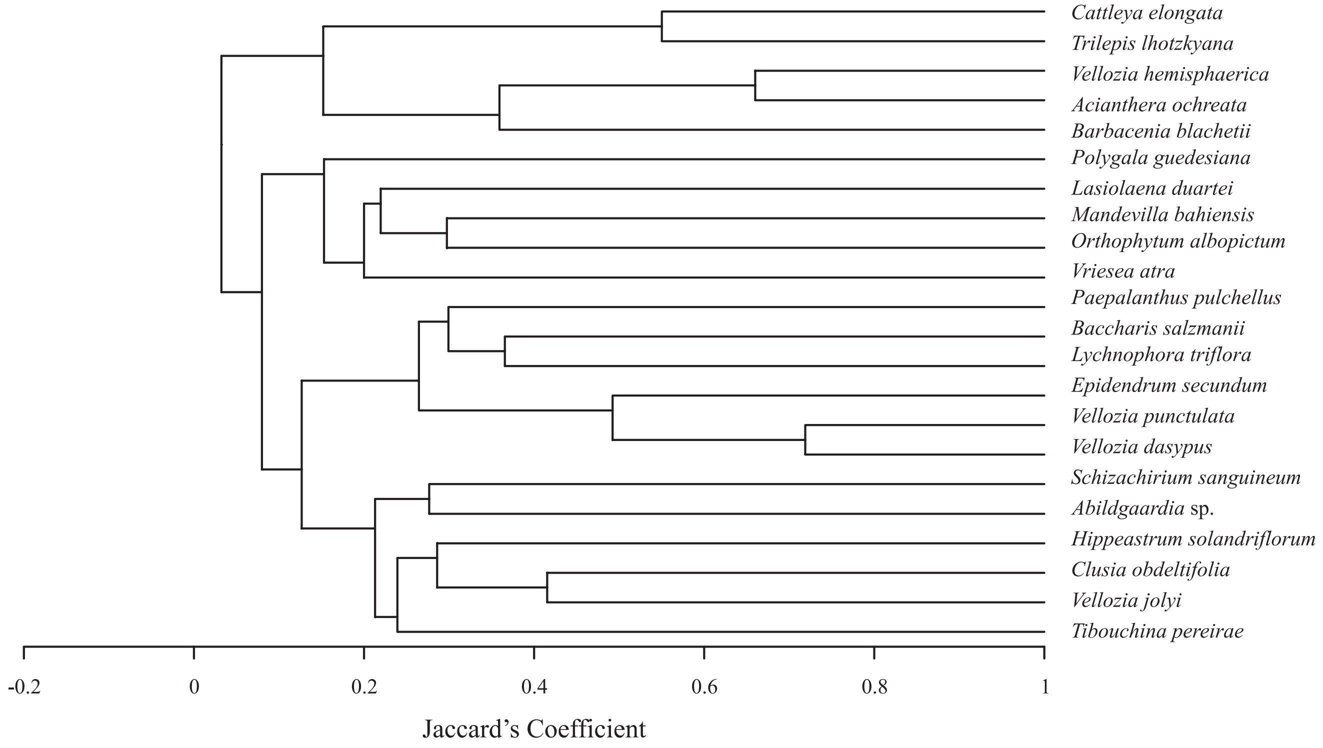

Figure 5. Dendrogram using UPGMA on the matrix of Jaccard similarity values calculated for the presence/absence matrix that included species with more than 20 occurrences on the 214 soil islands at "Morro da Mãe Inácia", Fumaça, "Gerais da Fumaça" and Guiné study sites, "Chapada Diamantina", Bahia, Brazil.

species. This is an indication that factors other than distance alone might be more relevant to determine spatial patterns of species occurrence, such as soil discussed above.

Floristic patterns – Despite the regional variation between sites and the overall diversity found, the taxonomic entities of the studied flora largely resemble those of other rock outcrops in Brazil. For instance, the predominance of monocots confirms a well-known pattern for neotropical rock outcrops (Ibisch *et al.* 1995, Meirelles 1996, Porembski *et al.* 1998, Meirelles *et al.* 1999, Gröger 2000, Safford & Martinelli 2000, and Ribeiro *et al*. 2007, in this issue). The main families of vascular plants found here were also found elsewhere in "Chapada Diamantina" (Conceição *et al.* 2007) and even in south-east Brazil (*e.g.*, Velloziaceae, Bromeliaceae, Orchidaceae, Cyperaceae, Asteraceae, Amaryllidaceae, Poaceae, Melastomataceae, Clusiaceae). Interestingly, there are some species co-occurrences with nepheline-syenite outcrops at high altitude in Itatiaia, Rio de Janeiro State (*Ilex amara*, *Peperomia galioides* and *Polypodium catharinae*; Ribeiro & Medina 2002) and in granitic outcrops in Atibaia, São Paulo State (four vascular cryptogams, *Tillandsia stricta*, *Trilepis lhotzkiana*, *Hillia parasitica* and *Epidendrum secundum* [syn. *Epidendrum elongatum* Lindl.]; Meirelles 1996, Meirelles *et al.* 1999).

Similarly, genera such as *Abildgaardia*, *Acianthera* (*Pleurothallis*), *Barbacenia*, *Clusia*, *Epidendrum*, *Hippeastrum*, *Lychnophora*, *Orthophytum*, *Polypodium, Tibouchina*, *Trilepis*, *Vellozia* and *Vriesea* are commonly found in our study site and in other rock outcrops in Brazil (Oliveira *et al.* 1975, Carauta & Oliveira 1982, Ibisch *et al.* 1995, Meirelles 1996, França *et al.* 1997, Porembski *et al.* 1998, Waldemar 1998, Meirelles *et al.* 1999, Safford & Martinelli 2000, Conceição *et al.* 2007). Although some of these genera are broadly distributed, many species are endemic to "Chapada Diamantina" – including new species found that belong to the genera *Barbacenia* (Velloziaceae), *Paepalanthus* (Eriocaulaceae) and *Jacquemontia* (Convolvulaceae) – which confers a regional floristic peculiarity.

Life-forms – Life-form abundance and distribution patterns also resemble that found elsewhere in Brazil: 1) the predominance of phanerophytes and hemicryptophytes (such as in Meirelles 1996, Meirelles *et al.* 1999, Ribeiro & Medina 2002); 2) the high cover area of desiccation-tolerant chamaephytes in locations with a high proportion of exposed rocks (see also Meirelles *et al*. 1997, 1999, Conceição & Giulietti 2002, Conceição & Pirani 2005, Conceição *et al.* 2007); 3) the relatively high proportion of cryptophytes (*e.g.*, *Mandevilla bahiensis*, *Hippeastrum* spp., and several orchids) suggest an adaptive value for underground structures capable of tolerance to fire, drought (see also Conceição 2003) and trampling by cattle; 4) the commonness of thallo-chamaephytes demonstrates the importance of lichens in such vegetation type (see also Burrows 1990). However, the high proportion of therophytes found at "Gerais da Fumaça" is less commonly described in other neotropical rock outcrops and might result from the proximity with surrounding grassland fields, as already mentioned, which harbor many such species prone to temporary waterlogging.

"Morro do Pai Inácio" (surveyed by Conceição *et al.* 2007) had a higher number of species per area than the sites studied here (table 3). Interestingly, this site had the lowest mean island size (total island size/number of islands). This seems to suggest that, considering two cases where total island areas are the same, the one with a high number of small islands is likely to harbor more species than that with a low number of larger islands. This pattern points to the environmental heterogeneity and competition as probable sources of species richness in these rock outcrops. Similar patterns have been described elsewhere (Virolainen *et al.* 1998).

The well defined groups obtained from the classification analysis of soil islands can be related to the occurrence of defined island "types", similar in composition and structure. These island types can be represented by species combinations more or less related to the site of occurrence. The cluster analysis presented some of these "island types" in groups. Some examples were the *Trilepis lhotzkiana* – *Cattleya elongata* and *Vellozia hemisphaerica* – *Acianthera ochreata* islands. These islands types are dominated by plants with desiccation tolerant behavior (*T. lhotzkiana* and *V. hemisphaerica*) being probably related to primary succession patterns on "Mãe Inácia" site. Similar compositions were found on Fumaça with combinations of *Vellozia punctulata* – *V. dasypus* and *Epidendrum secundum*. Clues on the cause of the clear segregation of plot scores resulting from DCA (figure 6), can be found on the difference in surface roughness (crested on "Mãe Inácia" and smooth on Fumaça.) and site specific features such as available humidity on Fumaça site, due to the proximity of a waterfall.

One of the most remarkable features of rock outcrop vegetation is the tendency to harbor microendemisms that can be produced even on a scale in which is unlike to occur segregation. This pattern is possibly related to the combination of the rock outcrop extreme conditions and species competitive advantages and requirements in the limited space of the soil islands. Soil, as well as minor local microclimate variations, can be responsible for a higher competitive advantage of a given species on a particular island. Thus, the observed effect is the arrangement of typical species assemblages on soil islands on rock outcrops situated nearby as well as microendemisms. Such features emphasize the extreme sensitivity of rock outcrop plant populations as the microendemics can become extinct with minor environmental changes produced by human interference or natural dynamics of the substrate and microclimate.

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Table 3. Number of soil islands and species, island area and species per area (Species m^{-2}) on studies performed in Bahia (BA), Rio de Janeiro (RJ) and São Paulo (SP), Brazil.

Site	Study	Islands	Species	Area (m^2)	Species m^{-2}
Four sites (BA)	present	214	135	568	0.23
Pai Inácio (BA)	Conceição *et al.* 2007	78	63	74.8	0.84
Itatiaia (RJ)	Ribeiro & Medina 2002	197	114	336.6	0.34
Rio de Janeiro (RJ)	Meirelles *et al.* 1999	347	85	1264	0.07
Atibaia (SP)	Meirelles 1996	88	105	609	0.17

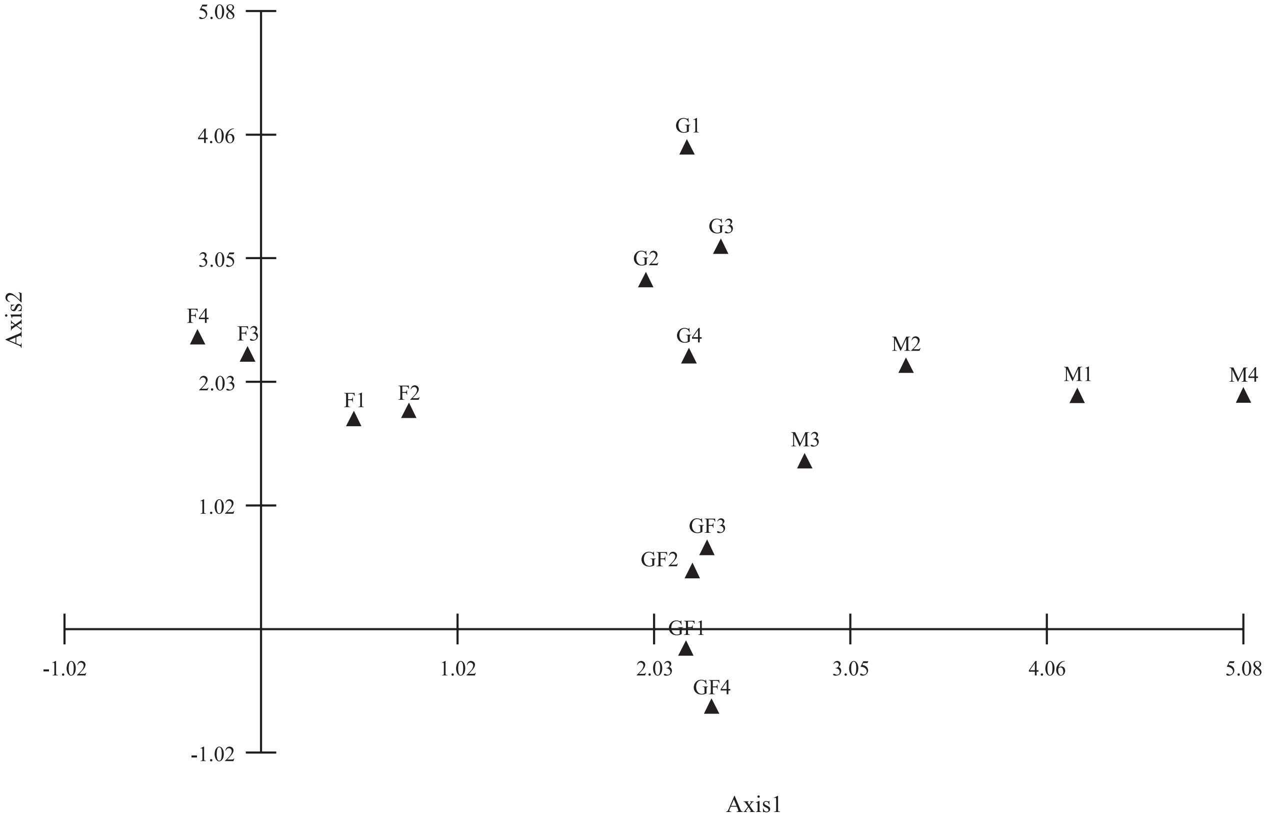

Figure 6. Interpolation of scores obtained by the DCA procedure applied on the matrix of species occurring in plots of 10 × 10 m, in the sites Guiné (G), "Gerais da Fumaça" (GF), Fumaça (F) and "Morro da Mãe Inácia", (M) at "Chapada Diamantina", Bahia, Brazil.

(Asteraceae), P. Labiak (criptógamas vasculares), P. Sano (Eriocaulaceae), R. Forzza (Bromeliaceae), R. Harley (Lamiaceae), R. Mello-Silva (Velloziaceae), R. Simão-Bianchini (Convolvulaceae), S. Atkins (Verbenaceae), T. Silva (Verbenaceae) and W. W. Thomas (Cyperaceae).

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