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Habitat heterogeneity and diversity of bryophytes in *campos rupestres*

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ABSTRACT

Campos rupestres (rupestrian grasslands) are characterized by the presence of rock outcrops associated with an herbaceous-shrub physiognomy typically growing on quartzitic soils; they occur a wide variety of habitats. Bryophytes respond rapidly and efficiently to variation in microclimate. The present work aimed to study bryophyte species richness, diversity and composition, their life forms, and the substrates they colonize in exposed and shaded habitats in *campos rupestres* of Chapada Diamantina. Collections were made in 25 x 25 m sampling plots. One hundred and nine species were recorded and included a predominance of mosses (78 spp.) over liverworts (31 spp.). Most species (79 %) were restricted to one of the two types of habitat (exposed versus shaded). While the genera *Campylopus*, *Polytrichum*, *Schlotheimia*, *Macromitrium* and *Syrrhopodon* were prevalent in exposed habitats, *Sphagnum*, *Lepidozia*, *Micropterygium*, *Bazzania* and *Odontoschisma* prevailed in shaded habitats. The rupicolous community was more prominent than the other communities in both types of habitat. "Weft" was the most frequent life form in shaded areas, while "turf" predominated in exposed sites. The high number of rare, and exclusive, species illustrates the high degree of heterogeneity among bryophyte communities in *campos rupestres*, and demonstrates the importance of habitat heterogeneity for the high diversity.

Keywords: Chapada Diamantina, Bahia, Brazil, liverworts, mosses

Introduction

Bryophytes encompass three groups of plants - mosses, liverworts and hornworts - that share the absence of a vascular system, small size and water-dependent sexual reproduction. They usually have photosynthetic laminae (leaves) comprised of a single-cell layer and absorb nutrients and water throughout the surface of the gametophyte, and thus occur in humid and shady environments. They reach their greatest abundance and diversity in rainforests, but can be found in all types of environments from polar to arid regions including deserts; they even inhabit urban areas and industrial settings with high pollution levels (Glime 2007; Vanderpoorten & Goffinet 2009). Variation in bryophyte species richness, diversity and composition, and their life forms, are clearly linked to microclimatic conditions, but especially to light and water availability (Mägdefrau 1982). For this reason, bryophytes are considered efficient bioindicators of environmental quality (Frahm & Gradstein 1991).

Chapada Diamantina is a mountainous region located in the Caatinga of northeastern Brazil (IBGE 2004), and is one of the eight ecoregions recognized within this biome (Velloso *et al.* 2002). It exhibits a mosaic of plant formations mainly determined by topography, elevation, climate and hydrography,

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including *campos rupestres* (rupestrian grasslands), which is the most typical of these formations. According to Harley (1995a), *campos rupestres* are distributed in a manner analogous to an archipelago, with several elevated areas separated by lower areas with unique environmental characteristics.

Another striking feature of *campos rupestres* is the high degree of habitat heterogeneity as a result of substrate variation, proportion of exposed rock, and the presence of rock blocks and sandy sediments (Conceição 2000; 2008; Conceição & Giulietti 2002; Conceição & Pirani 2005; 2007). This heterogeneity facilitates high levels of diversity and endemism (Alves & Kolbek 1993; Harley 1995a; Giulietti *et al.* 1996; Conceição 2000; Conceição & Giulietti 2002; Conceição & Pirani 2005).

Studies have indicated that the composition of the phanerogamic flora of the *campos rupestres* of Chapada Diamantina varies considerably, even within small geographical distances and among equally rich areas (Conceição & Giulietti 2002; Zappi *et al.* 2003; Conceição & Pirani 2005; 2007; Conceição *et al.* 2005).

Knowledge of the bryophytes of the *campos rupestres* of Chapada Diamantina is limited to species lists for Pico das Almas, a municipality of Rio de Contas (Harley 1995b) and various other municipalities in this ecoregion (Bastos *et al.* 2000), and a survey of mosses carried out in the municipality of Miguel Calmon (Ballejos & Bastos 2009a; b).

Recent studies have revealed that the bryophyte flora of the Chapada Diamantina region is rich and diverse, and includes 80 % of the bryophyte taxa recorded in the state of Bahia (Valente *et al.* 2011), with 40 % of this richness being found in *campos rupestres* and 51 % in forests (Valente *et al.* 2013a; b). According to Bastos *et al.* (2000), the most represented families in the *campos rupestres* of Chapada Diamantina are Dicranaceae, Orthotrichaceae, Sphagnaceae and Leucobryaceae, among Bryophyta, and Lepidoziaceae, Plagiochilaceae, Herbertaceae and Trichocoleaceae, among Marchantiophyta. These authors also report that the most frequently encountered taxa are also restricted to Chapada Diamantina and have not been found elsewhere in the state. Bryophytes of *campos rupestres* have been surveyed in other regions of Brazil, including Serra do Cipó (Yano 1987) and Flora of Grão Mongol (Yano & Peralta 2009), both in the state of Minas Gerais.

This study aimed to survey the bryophyte communities of the *campos rupestres* of Chapada Diamantina and describe the species richness diversity and composition, the variety of life forms and the substrates colonized in different areas and habitats throughout this region.

Materials and methods

Study Area

Chapada Diamantina is located in the northern portion of the Cadeia do Espinhaço, the main mountain chain in eastern Brazil, and extends from Serra da Jacobina (10º00'S) in Bahia to Serra de Ouro Branco, near the city of Ouro Preto (21º25'S), in Minas Gerais (Harley 1995a). It encompasses an area of 50,000 km^2, and extends for 400 km north-south and 50 to 100 km east-west (10º00'-14º00'S; 40º10'-44º30'W), with elevations ranging from 400 to 2,033 m.a.s.l. (Harley 1995a; Rocha *et al.* 2005).

According to Nolasco *et al.* (2008), meteorological and rainfall stations in the Chapada Diamantina are few and insufficient for modeling local microclimates, and are generally used for describing regional trends based on data collected over multiple years. Based on rainfall data recorded by these stations over the past 20 years, a rainy season occurs between November and April, with maximum precipitation in December (139 mm), and a dry season occurs between May and October, with minimum precipitation in August (20 mm). Mean monthly rainfall exceeds 100 mm during the rainy season, while it averages only 35 mm during the dry season. Total annual precipitation varies between 600 and 1,100 mm (SEI 2003; Agritempo 2010).

Temperatures in Chapada Diamantina generally range 15-30 ºC, but can reach freezing (0 ºC) in the dry season between June and August, and 30 ºC in the rainy season between December and January. Fog is typically present until 09:00 h on ordinary days and 12:00 h on rainy days, and is common throughout the region (Nolasco *et al.* 2008).

Campos rupestres are mainly characterized by the presence of rock outcrops associated with herbaceous-shrub physiognomy typically growing on quartzitic soils. The main plant families present are Velloziaceae, Melastomataceae, Eriocaulaceae, Xyridaceae and Orchidaceae, usually at elevations above 900 m. Forest formations can occur in areas of *campos rupestres*, especially along watercourses, and numerous waterfalls and cliffs are present in these areas (Conceição *et al.* 2005).

Sampling and study material

Nine botanical sampling trips were made between the years 2007 and 2008. Material was collected within 25 x 25 m standard plots located in 15 different areas (Frahm 1994). The study areas were distributed from north to south with eight of them being within conservation units (Tab. 1).

The botanical material was identified using Fulford (1963; 1966; 1968), Crum (1984), Yano *et al.* (1985), Frahm (1991), Reese (1993), Sharp *et al.* (1994), Buck (1998), Gradstein *et al.* (2001), Allen (2002), Gradstein & Costa (2003) and Vaz-Imbassahy & Costa (2008), among other more specialized papers. Vouchers were deposited in HUEFS and UFP, according Thiers (2017). The classification system adopted for mosses was that of Goffinet *et al.* (2009), while for liverworts it was that of Crandall-Stotler *et al.* (2009).

The areas surveyed were classified, according to their physical features, into two habitat types, exposed and shaded. Exposed habitats possess a large proportion of exposed rock surface and herbaceous and shrub vegetation.

Table 1. Characterization of *campo rupestre* areas of Chapada Diamantina, Bahia, Brasil. PNCD - Parque Nacional da Chapada Diamantina; MCFD - Monumento Cachoeira do Ferro Doido; APA-SB - APA Serra do Barbado. E1 – E8 = habitat exposed areas; S1 – S7 = habitat shaded areas.

Areas	Municipality	Conservation unit	Altitude (m.a.s.l.)	Geographic coordinates
E1	Piatã	-	1,286	13°09'01.2"S – 41°45'38.7"W
E2	Piatã	-	1,479	13°08'57.8"S – 41°45'31.7"W
E3	Piatã	-	1,665	13°09'05.3"S – 41°45'07.4"W
E4	Abaíra	APA-SB	1,750	13°17'28.6"S – 41°54'12.1"W
E5	Abaíra	APA-SB	1,850	13°17'S – 41°54'W
E6	Abaíra	APA-SB	2,037	13°17'47.9"S – 41°54'26.8"W
E7	Palmeiras	APA-M	1,150	12°27'S – 41°28'W
E8	Palmeiras	APA-M	1,170	12°27'S – 41°28'W
S1	Morro do Chapéu	MCFD	1,000	11°37'30.0"S – 40°59'58.6"W
S2	Lençóis	-	722	12°27'42.6"S – 41°25'04.9"W
S3	Lençóis	-	720	12°27'42.8"S – 41°25'03.7"W
S4	Lençóis	PNCD	800	12°27'S – 41°28'W
S5	Piatã	-	1,289	13°05'10.2"S – 41°51'12.4"W
S6	Lençóis	PNCD	800	12°27'S – 41°28'W
S7	Morro do Chapéu	-	1,290	11°35'28.4"S – 41°12'27.9"W

They correspond to areas of *campos rupestres*, including primarily the habitats described by Conceição & Pirani (2005) as "rocky outcrops" and smaller proportions of "ditches" and "insets". Shaded areas possess rock cracks near waterfalls or rivers and large "ditch'" areas with a predominance of trees. They correspond to small caves in waterfalls and resemble the habitat described by Alves & Kolbek (1993) in *campos rupestres* of the southern portion of Cadeia do Espinhaço, except for its association with cascades and rivers.

The 15 study areas were coded according to the initial letter of the habitat type, that is, exposed (E1 to E8) and shaded (S1 to S7) habitats. Among shaded areas, S1 to S5 corresponded to cracks in rocks near waterfalls, while S6 and S7 correspond to large blocks of rock with trees and shrubs.

Classification of the life form of the bryophytes was based on Mägdefrau (1982), Richards (1984) and Bates (1998). This parameter refers to the manner in which individuals are assembled, which involves branching pattern, growth direction and modifications reflecting habitat conditions Thus, life forms are influenced by the environment.

The frequency of occurrence for each species was classified as: rare (up to three occurrences throughout the study areas), occasional (between four and 10 occurrences) and frequent (> 10 occurrences).

Data analysis

In order to verify sampling sufficiency, species richness was estimated with Chao's equation (1984) using EstimateS software (Cowell 2006). Species richness and diversity were calculated for each study area. The Shannon-Wiener (H ') index with natural logarithm (Napierian base) was used for calculating diversity. In this case, the frequency of each species (number of samples of the species collected in the area) instead of abundance (total number of individuals of each species collected in the area) was used in the calculations because the small size and fragmented nature of bryophytes prevent quantification of individuals (Bates 1982). Floristic composition of the study areas was compared based on the presence and absence of species using the Bray-Curtis method. Diversity and similarity were analyzed in PRIMER 5.1 software (Clarke & Warwick 1994).

Species richness of the study areas was compared using the T-test while normality was tested using the Kolmogorov-Smirnov test. The level of significance adopted was $p > 0.05$. Both tests were performed using BioEstat 2.0 software (Ayres *et al*. 2000).

Results

Richness, diversity and composition of study areas

One hundred and nine species (Tab. 2) were recorded in the study, representing 79 % of the total richness estimated for the *campos rupestres* of Chapada Diamantina according to Chao's estimator. The mean diversity for the areas was H'= 2.33 and the total diversity was H'= 4.13 (Tab. 3).

There was a predominance of mosses (72 spp.) over liverworts (37 spp.). The richest moss families were Leucobryaceae (15 spp.), Sematophyllaceae (12 spp.), Orthotrichaceae (nine spp.) and Sphagnaceae (seven spp.), while the richest liverwort families were Lepidoziaceae (nine spp.) and Lejeuneaceae (five spp.). Floristic composition differed considerably among areas, although there was one cluster of seven of the eight exposed areas, while four of the seven shaded areas formed a cluster (Fig. 1). However, similarities among areas were low, even among the exposed

Table 2. Bryophytes species found at *campo rupestre* areas studies in the Chapada Diamantina, Bahia, Brazil. Frequecy of species in the habitat E - Exposed, S - Shaded, T -Total frequency; C = community by substrate: Ru - Rupicolous, Te - Terricolous, Co - Corticicolous, Ex - Epixylous; L.F. = life forms: TF - turf, W - weft, TL - thallose, M - mat, P - pendant.

Taxa	E	S	T	C	L.F.	Voucher
Acroporium caespitosum (Hedw.) W.R. Buck	0	1	1	Ru	W	Valente, E.B. 473
Anastrophyllum piligerum (Reinw., Blume & Nees) Steph.	1	0	1	Ru	W	Valente, E.B. 795
Anoplolejeunea conferta (C.F.W. Meissn. ex Spreng.) A. Evans	9	0	9	Ru	W	Valente, E.B. 753
Aptychopsis pyrrhophylla (Müll. Hal.) Wijk & Margad.	0	2	2	Ru	W	Valente, E.B. 1535
Bazzania falcata (Lindenb.) Trevis.	2	0	2	Ru	W	Valente, E.B. 770
Bazzania heterostipa (Steph.) Fulford	4	0	4	Ru	W	Valente, E.B. 715
Bazzania nitida (F. Weber) Grolle	1	0	1	Ru	W	Valente, E.B. 750
Bryum argeteum Hedw.	3	0	3	Ru	Tf	Valente, E.B. 740
Callicostella merkelii (Hornsch.) A. Jaeger	0	4	4	Ru	W	Valente, E.B. 852
Callicostella pallida (Hornsch.) Ångstr.	0	2	2	Ru	W	Valente, E.B. 884
Calymperes palisotii Schwägr.	0	1	1	Ru	tf	Valente, E.B. 447
Calypogeia laxa Lindenb. & Gottsche	0	1	1	Ru	W	Valente, E.B. 638
Campylopus arctocarpus (Hornsch.) Mitt.	11	3	14	Ru, Te	Tf	Valente, E.B. 705
Campylopus heterostachys (Hampe) A. Jaeger	2	3	5	Ru	Tf	Valente, E.B. 942
Campylopus julaceus A. Jaeger	11	2	13	Ru, Te	Tf	Valente, E.B. 661
Campylopus filifolius var. *longifolius* (E.B. Bartram) E.B. Bartram	0	1	1	Ru	Tf	Valente, E.B. 518
Campylopus fragilis (Brid.) Bruch & Schimp.	1	0	1	Ru	Tf	Valente, E.B. 829
Campylopus occultus Mitt.	1	2	3	Ru	Tf	Valente, E.B. 717
Campylopus pilifer Brid.	45	4	49	Ru, Te	Tf	Valente, E.B. 656
Campylopus savannarum (Müll. Hal.) Mitt.	1	2	3	Ru, Te	Tf	Valente, E.B. 732
Campylopus subcuspidatus (Hampe) A. Jaeger	8	0	8	Ru	Tf	Valente, E.B. 1501
Campylopus uleanus (Müll. Hal.) Broth.	1	0	1	Ru	tf	Valente, E.B. 696
Campylopus widgrenii (Müll. Hal.) Mitt.	0	3	3	Ru	Tf	Valente, E.B. 937
Cheilolejeunea filiformis (Sw.) W. Ye, R.L. Zhu & Gradst.	0	1	1	Ru	W	Valente, E.B. 1247
Cheilolejeunea oncophylla (Ångstr.) Grolle & E. Reiner	4	0	4	Co	M	Valente, E.B. 756
Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe	1	0	1	Co	M	Valente, E.B. 690
Chiloscyphus martianus (Nees) J.J.Engel & R.M.Shust.	0	6	6	Ru	W	Valente, E.B. 609
Colobodontium vulpinum (Mont.) S.P. Churchill & W.R. Buck	0	1	1	Ru	Tf	Valente, E.B. 622
Dicranodontium pulchroalare subsp. *brasiliense* (Herzog) J.-P. Frahm	0	1	1	Ru	Tf	Valente, E.B. 642
Drepanolejeunea anoplantha (Spruce) Steph.	1	0	1	Co	W	Valente, E.B. 800
Entodontopsis leucostega (Brid.) W.R. Buck & Ireland	0	1	1	Ru	M	Valente, E.B. 950
Entodon cf. macropodus (Hedw.) Müll. Hal.	0	1	1	Ru	M	Valente, E.B. 530
Fabronia macroblepharis Schwägr.	1	0	1	Co	M	Valente, E.B. 815
Frullania atrata (Sw.) Dumort.	0	2	2	Ru	W	Valente, E.B. 1248
Frullania brasiliensis Raddi	7	0	7	Ru	W	Valente, E.B. 1504
Frullania kunzei Lehm. & Lindenb.	2	1	3	Ru	M	Valente, E.B. 735
Frullania riojaneirensis (Raddi) Spruce	0	1	1	Ru	M	Valente, E.B. 933
Frullania setigera Steph.	0	3	3	Co	W	Valente, E.B. 1262
Funaria hygrometrica Hedw.	6	0	6	Ru, Te, Co	Tf	Valente, E.B. 667
Gemmabryum radiculosum (Brid.) J.R. Spence & H.P. Ramsay	1	0	1	Ru	tf	Valente, E.B. 726
Holomitrium arboreum Mitt.	2	0	2	Ru	Tf	Valente, E.B. 1506
Holomitrium olfersianum Hornsch.	3	4	7	Ru	Tf	Valente, E.B. 1487
Isopterygium jamaicense (E.B. Bartram) W.R. Buck	0	3	2	Te	M	Valente, E.B. 626
Isopterygium tenerifolium Mitt.	0	2	2	Ru, Te	M	Valente, E.B. 629
Isopterygium tenerum (Sw.) Mitt.	0	1	1	Ru	M	Valente, E.B. 1204
Kurzia capillaris (Sw.) Grolle	2	6	8	Ru	W	Valente, E.B. 752
Lepidozia cupressina (Sw.) Lindenb.	8	1	9	Ru, Te	W	Valente, E.B. 750
Lepidozia inaequalis Lehm. & Lindenb.	2	0	2	Ru	W	Valente, E.B. 794
Leptoscyphus amphibolius (Nees) Grolle	1	0	1	Ru	W	Valente, E.B. 1471
Leucobryum albidum (Brid. ex P. Beauv.) Lindb.	2	0	2	Ru	Tf	Valente, E.B. 810
Leucobryum crispum Müll. Hal.	2	5	7	Ru	Tf	Valente, E.B. 1549
Leucobryum giganteum Müll. Hal.	0	5	5	Te	Tf	Valente, E.B. 1315
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.	0	8	9	Ru, Te, Co	Tf	Valente, E.B. 871
Lophocholea mandonii Steph.	0	2	2	Ex	W	Valente, E.B. 644

Table 2. Cont

Taxa	E	S	T	C	L.F.	Voucher
Macrocoma cf. *gastonyi* D.H. Norris & Vitt	0	1	1	Ru	Tf	Valente, E.B. 1291
Macromitrium cirrosum (Hedw.) Brid.	0	1	1	Co	Tf	Valente, E.B. 1300
Macromitrium cf. *longifolium* (Hook.) Brid.	0	1	1	Ru	tf	Valente, E.B. 1255
Macromitrium microstomum (Hook. & Grev.) Schwägr.	0	3	3	Co	Tf	Valente, E.B. 1319
Macromitrium punctatum (Hook. & Grev.) Brid.	1	0	1	Ru	Tf	Valente, E.B. 1466
Metzgeria decipiens (C. Massal.) Schiffn.	1	0	1	Ru	Tl	Valente, E.B. 706
Micropterygium campanense Spruce ex Reimers	0	2	2	Ru, Te	W	Valente, E.B. 862
Micropterygium reimersianum Herzog	5	2	7	Ru	W	Valente, E.B. 765
Neesioscyphus homophyllus (Nees) Grolle	0	1	1	Ru	W	Valente, E.B. 1394
Octoblepharum albidum Hedw.	3	9	12	Ru	Tf	Valente, E.B. 725
Octoblepharum cocuiense Mitt.	1	2	3	Ru	Tf	Valente, E.B. 773
Odontoschisma brasiliense Steph.	4	0	4	Ru	W	Valente, E.B. 671
Odontoschisma denudatum (Nees) Dumort.	5	1	6	Ru	W	Valente, E.B. 751
Odontoschisma falcifolium Steph.	1	2	2	Ru, Te	W	Valente, E.B. 470
Odontoschisma longiflorum Steph.	0	1	1	Ru	W	Valente, E.B. 456
Orthostichopsis praetermissa W.R.Buck	0	6	6	Co, Ru, Te	P	Valente, E.B. 1272
Pallavicinia lyellii (Hook.) Gray	0	1	1	Ru	Tl	Valente, E.B. 489
Philonotis cernua (Wilson) D.G. Griffin & W.R. Buck	0	1	1	Ru	Tf	Valente, E.B. 613
Philonotis hastata (Duby) Wijk & Margad.	0	2	2	Ru	Tf	Valente, E.B. 630
Plagiochila corrugata (Nees) Nees & Mont.	1	3	4	Co	W	Valente, E.B. 1283
Plagiochila fragilis Taylor	3	0	3	Ru	W	Valente, E.B. 780
Plagiochila simplex (Sw.) Lindenb.	1	1	2	Ru	W	Valente, E.B. 507
Polytrichum juniperinum Hedw.	15	0	15	Ru	W	Valente, E.B. 659
Pterogonidium cf. *pulchellum* (Hook.) Müll. Hal.	0	1	1	Ex	M	Valente, E.B. 1302
Pyrrhobryum spiniforme (Hedw.) Mitt.	0	3	3	Ru, Ex	tf	Valente, E.B. 1242
Rhacocarpus purpurascens (Brid.) Paris	6	0	6	Ru, Te	W	Valente, E.B. 1467
Rhacopilopsis trinitensis (Müll. Hal.) E. Britton & Dixon	0	1	1	Ru	M	Valente, E.B. 522
Riccardia sp.	0	1	1	Ru	Tl	Valente, E.B. 649
Schlotheimia jamesonii (Arn.) Brid.	0	3	3	Ru	Tf	Valente, E.B. 529
Schlotheimia rugifolia (Hook.) Schwägr.	10	15	25	Co, Ex, Ru	Tf	Valente, E.B. 698
Schlotheimia torquata (Sw. ex Hedw.) Brid.	0	1	1	Ru	Tf	Valente, E.B. 450
Schlotheimia trichomitria Schwägr.	0	4	4	Co, Ru	Tf	Valente, E.B. 1249
Sematophyllum adnatum (Michx.) E. Britton	1	4	5	Ru	W	Valente, E.B. 1304
Sematophyllum galipense (Müll. Hal.) Mitt.	0	2	2	Ru	W	Valente, E.B. 637
Sematophyllum subpinnatum (Brid.) E. Britton	0	2	2	Ru	W	Valente, E.B. 934
Sematophyllum subsimplex (Hedw.) Mitt.	0	5	5	Ru	W	Valente, E.B. 435
Sematophyllum sp.	1	4	5	Ru	W	Valente, E.B. 908
Sphagnum capillifolium var. capillifolium (Ehrh.) Hedw.	0	5	5	Ru, Te	Tf	Valente, E.B. 931
Sphagnum erythrocalyx Hampe	5	1	6	Ru, Te	Tf	Valente, E.B. 461
Sphagnum subsecundum var. rufescens (Nees & Hornsch.) Hueb.	0	4	4	Ru	tf	Valente, E.B. 854
Sphagnum longistolo Müll. Hal.	2	0	2	Ru	Tf	Valente, E.B. 1468
Sphagnum oxyphyllum Warnst.	1	1	2	Ru	Tf	Valente, E.B. 1572
Sphagnum palustre L.	2	7	9	Ru, Te	Tf	Valente, E.B. 1484
Sphagnum recurvum P. Beauv.	0	1	1	Ru	Tf	Valente, E.B. 615
Squamidium brasiliense (Hornsch.) Broth.	0	4	4	Co	P	Valente, E.B. 1280
Symphyogyna aspera Steph. ex MacCormick	0	1	1	Ru	Tl	Valente, E.B. 552
Symphyogyna brasiliensis Nees	0	3	3	Ru	Tl	Valente, E.B. 946
Syrrhopodon ligulatus Mont.	0	2	2	Ru	Tf	Valente, E.B. 443
Syrrhopodon prolifer var. *prolifer* Schwägr.	11	23	34	Ex, Ru	Tf	Valente, E.B. 722
Telaranea diacantha (Mont.) J.J. Engel & G.L. Merr.	0	1	1	Ru	W	Valente, E.B. 503
Thamniopsis undata (Hedw.) W.R. Buck	0	3	3	Ru	W	Valente, E.B. 907
Tortella humilis (Hedw.) Jenn.	3	0	3	Ru, Te	Tf	Valente, E.B. 694
Trichosteleum cf. *microstegium* (Besch.) A. Jaeger	0	1	1	Ru	M	Valente, E.B. 543
Trichosteleum subdemissum (Schimp. ex Besch.) A. Jaeger	0	1	1	Ru	M	Valente, E.B. 885
Wijkia flagellifera (Broth.) H.A. Crum	0	1	1	Ex	M	Valente, E.B. 1308

Table 3. Richness, sampling and diversity of bryophytes by *campo rupestre* area of Chapada Diamantina, Bahia, Brazil. E1 – E8 = habitat exposed areas; S1 – S7 = habitat shaded areas; S = specific richness; N = sample; H = diversity.

Áreas	E1	E2	E3	E4	E5	E6	E7	E8	S1	S2	S3	S4	S5	S6	S7	TOTAL
S	14	29	13	16	10	9	4	4	14	12	15	25	18	23	21	109
N	26	63	56	27	12	23	11	11	20	16	36	50	26	23	58	460
H'(loge)	2.15	3.2	2.1	2.6	2.3	1.9	1.2	0.9	2.5	2.3	2.3	2.9	2.7	3.2	2.7	4.11

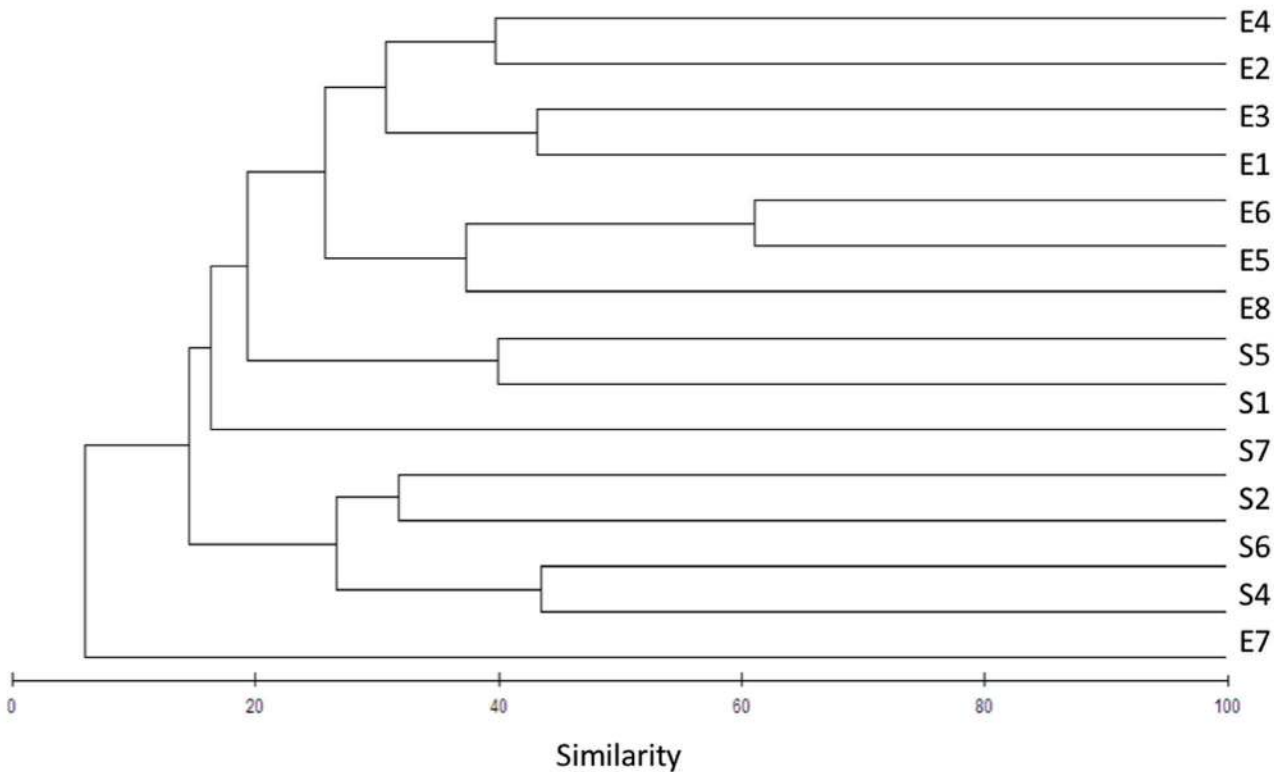

Figure 1. Dendrogram of similarity between the compositions of the bryophytes communities in the *campo rupestre* areas in the habitats exposed E1-E8 and shaded S1- S7, within Chapada Diamantina, Bahia, Brazil.

areas, most of which formed a cluster. Even geographically close areas exhibited low levels of similarity. Richness was significantly different among the studied areas (T-test = $p < 0.05$). Seventy-eight species occurred in shaded areas, with 57 being exclusive to this type of habitat, whereas 52 species occurred in exposed areas, with 29 being exclusive; twenty three species were common to both types of habitat.

Frequency of species

There was a predominance of rare species (70 %) followed by occasional species (23 %) and frequent species (7 %). Frequent species were well distributed among the study areas while other species were restricted to a small number of areas or even a single area. Among the frequent species, the following stood out: *Campylopus pilifer* (49 occurrences/9 areas), *Syrrhopodon prolifer* var. *prolifer* (34/9), *Schlotheimia rugifolia* (25/8), *Polytrichum juniperinum* (15/3), *Campylopus arctocarpus* (14/8), *Campylopus julaceus* (13/7) and *Octoblepharum albidum* (12/5). Among the occasional species were *Sphagnum palustre* (9/5), *Lepidozia cupressina* (9/3) and *Leucobryum martianum* (9/3), *Anoplolejeunea conferta* (9/2), *Kurzia capillaris* (8/5) and *Rhacocarpus purpurascens* (6/1). Among the rare species, the following stood out: *Anastrophyllum piligerum* (1/1), *Calymperes palisotii* (1/1), *Calypogeia laxa* (1/1), *Neesioscyphus homophyllus* (1/1), *Wijkia flagellifera* (1/1), *Lophocolea mandonii* (1/1), *Campylopus fragilis* (2/1), *Micropterygium campanense* (2/2), *Sphagnum oxyphyllum* (2/2), *Odontoschisma brasiliense* (4/2).

Substrate colonization

Four substrates were colonized within the study areas, and corresponded to the following communities: rupicolous, corticicolous, terricolous and epixilous. The rupicolous community predominated in the study (86 % of the total number of species), with 70 species being exclusive to this substrate (66 % of the total number of species). Nineteen species (18 %) were terricolous with only two exclusive species (1.8 %); fifteen species (14 %) were corticicolous, with nine being exclusive (8.4 %); and only six species (5.6 %) were epixilous, three of which were exclusive to this substrate (2.8 %). Shaded areas had a greater number of colonized substrates and more species colonizing more than one type of substrate than the exposed areas.

Life and growth forms

Five life forms were found among the bryophyte flora of Chapada Diamantina, with a predominance of turf (49 spp.), which was the life form of more than 50 % of the species occurred in 10 of the 15 study areas. The weft form (36 spp.) occurred in all areas, likewise the turf form, both corresponding to 78 % of the species. The thalloid form (five spp.) was less frequent. In relation to growth forms, we found 10.4 species on average of acrocarpous mosses and four of pleurocarpous mosses per area. Cladocarpous mosses were also well represented, although they were members of only two families, Orthotrichaceae and Rhizogoniaceae.

Discussion

The bryophyte flora found in the *campos rupestres* of Chapada Diamantina was represented mostly by mosses, particularly of the families Leucobryaceae, Sematophyllaceae, Orthotrichaceae and Sphagnaceae. Liverworts were represented by the family Lepidoziaceae. Bryophyte species richness and composition varied widely among the study areas, similar to what has been reported for vascular plants of *campos rupestres* (Conceição & Giulietti 2002; Zappi *et al*. 2003; Conceição & Pirani 2005; 2007; Conceição *et al*. 2005). The varied species composition is due to the variety of habitats, determined mainly by relief and proximity to a water source (Alves & Kolbek 1993; Conceição & Pirani 2005).

The heterogeneity of the selected habitats translated into distinct bryophyte communities in terms of both composition and life forms. Higher diversity and a greater number of rare species were observed in areas with at higher elevations and with less anthropic activity (areas that are difficult access and thus have low traffic), regardless of the type of habitat investigated.

Large patches of long and dense turfs of *Sphagnum* spp. were predominant in rock walls of shaded areas, located beneath or close to waterfalls where they are constantly splashed with water. Rock crack communities associated with waterfalls were represented mostly by pleurocarpous mosses of the genera *Callicostella*, *Thamniopsis* and *Sematophyllum* and by leafy liverworts of the genera *Micropterygium, Lophocholea* and *Odontoschisma*. Nevertheless, acrocarpous mosses, such as *Philonotis*, *Campylopus* and *Syrrhopodon*, were also present. In general, pleurocarpous mosses and liverworts are adapted to shaded conditions (Richards 1984; Gradstein & Pócs 1989; Glime 2007). The variety of desiccation tolerance adaptations exhibited by bryophytes is conditioned to the variety of habitats they colonize (Proctor *et al*. 2007).

The collective bryophyte community of the exposed habitats was represented mainly by acrocarpous mosses of the genera *Campylopus* and *Polytrichum*, which have morphological adaptations to withstand intense luminosity and desiccation. Representatives of these genera have lamellae, which possess cells containing chlorophyll aligned in a palisade arrangement on the ventral surface of leaves in such a manner that they are protected from damage caused by strong and prolonged incidence of UV radiation on the chlorophyll. Some species, such as *Polytrichum juniperinum*, also have extended leaf margins that prevent rapid desiccation, and some species of *Campylopus* have hyaline hair-point apexes, which give them a grayish appearance and contribute to the reflection of intense luminosity (Mägdefrau 1982; Glime 2007). Species of the genus *Polytrichum* possess a leaf movement mechanism that responds to environmental humidity by opening the leaves in the presence of water and closing them in dry conditions (Glime 2007). These species have well developed hydroids and are, therefore, endohydric (Schofield 1985; Glime 2007). This type of specialization is associated with humid substrates, and thus, reflects the presence of humidity, such as the misty conditions typical of high-elevation environments where air humidity is retained in the shallow soils of *campos rupestres*.

The high degree of variation in species composition among the study areas, and even over short geographic distances, corroborates the results found for vascular plants in *campos rupestres* (Conceição & Giulietti 2002; Zappi *et al*. 2003; Conceição & Pirani 2005; 2007; Conceição *et al*. 2005). However, unlike vascular plants, which exhibit similar species richness among different areas (Conceição & Pirani 2007), bryophyte richness and diversity differ significantly among the study areas. The low degree of similarity among study areas probably reflects differences in habitat related to the degree of steepness of the relief, quantity and size of rock blocks, presence and size of rock cracks, proportion of exposed rock and wind exposure.

The predominance of the rupicolous community over the others is obviously due to the great availability of rock surfaces. This contrasts with tropical forest environments, where corticicolous bryophytes predominate (Richards 1984; 1988; Gradstein & Pócs 1989). In the present study, the corticicolous community was generally associated with the stems of herbs and shrubs in exposed areas and with trees in the shaded areas (S6 and S7).

The appearance of bryophytes (life and growth form) as they are found in nature, is clearly influenced by abiotic factors, particularly water and light availability. The bryophyte flora of different vegetation communities and habitats develop diversified physiognomies in part due to these life forms, which are of major importance for several vital processes, but particularly water economy (Mägdefrau 1982; Proctor 1982; Bates 1998).

The predominance of turf over other life forms in exposed areas, where plants are subjected to stronger insolation, as well as bryophytes mainly occurring on rock and sandy soils, can be interpreted as evidence of the responses of the bryophytes to the environmental conditions in the studied habitats of the *campos rupestres* of Chapada Diamantina. This type of life form is known to be tolerant of these conditions, contributes to minimizing water loss of the assemblage of individuals (Mägdefrau 1982), and was exhibited by species of *Campylopus*, *Polytrichum*, *Schlotheimia*, *Macromitrium* and *Syrrhopodon*. Turf also occurred in shaded areas, as represented by the genus *Sphagnum*, which forms long turfs in humid environments (Mägdefrau 1982; Bates 1998). The weft form, typical of humid to more or less humid environments (Mägdefrau 1982; Bates 1998; Glime 2007), was found in larger proportions in shaded areas and was represented by species of *Lepidozia*, *Micropterygium*, *Bazzania* and *Odontoschisma*. The pendant form was recorded in only one shaded area. This form is typical of humid forests (Gradstein & Pócs 1989) and its occurrence in the present study is explained by the presence of an arboreal stratum and humidity from mist at the collection site, which was located on a hilltop at 1,290 m.a.s.l.

The high number of rare species, whether classified as restricted (occurring in one or a few areas) or of low frequency (few occurrences), and the high rate of exclusive species (79 % of the species were restricted to only one of the investigated habitats) provide evidence of the high degree of heterogeneity of bryophyte communities in the *campos rupestres* of Chapada Diamantina. Furthermore, these data show the importance of habitat heterogeneity for high diversity, a characteristic also reported for vascular plants (Giulietti & Pirani 1988; Alves & Kolbek 1993; Harley 1995a; Giulietti *et al*. 1996; Conceição & Giulietti 2002; Conceição *et al*. 2005; Conceição & Pirani 2005; 2007).

Some rare species, such as *Anastrophyllum piligerum, Lophocolea mandonii*, *Neesioscyphus homophyllus and Odontochisma brasiliense,* which were found inhabiting some study areas that were located within conservation units, have been considered endangered by red lists in the states of Minas Gerais and Rio de Janeiro (Costa *et al*. 2005; 2006; Costa & Santos 2009). This finding serves as a warning about the importance and need to preserve the flora of *campos rupestres* in Chapada Diamantina.

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