

BROMELIACEAE FROM CAPARAÓ NATIONAL PARK, MINAS GERAIS/ESPÍRITO SANTO STATES, BRAZIL, WITH NOTES ON DISTRIBUTION AND CONSERVATION

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ABSTRACT

High altitude grasslands occur at higher elevations of the Atlantic Forest and are rich in species and endemism. Bromeliaceae is one of the most diverse plant families of the Atlantic Forest, however its floristics and distribution is poorly investigated in this type of vegetation. In this study, we carry out an inventory of the family for the Caparaó National Park, an important protected area of southeastern Brazil, due to its high species richness and endemism, where a representative area of high altitude grassland is found. We also provide data on the species distribution in different habitats and at different elevations, species frequency and also implications for conservation. We recorded 12 genera and 46 species of Bromeliaceae, three of them new occurrences for Espírito Santo state: *Aechmea lilacanthia*, *Neoregelia brownii*, and *Vriesea paraibica*. Species richness of bromeliads was higher in the riparian forest and lower in the high altitude grassland. The highest richness was found between 900-1,300m where riparian forest is found. Only 9% of the species were considered common, whereas 32% were rare. Our results highlight the importance of associated habitats with high altitude grassland for the conservation of biological diversity, especially for rare species of bromeliads.

Keywords: Atlantic Forest; diversity; Neotropical mountain.

INTRODUCTION

Bromeliaceae, with around 3,500 Neotropical species and a single disjunct species occurring in west tropical Africa (Smith & Downs 1974, Butcher & Gouda 2016), has a marked diversity in Brazil, where 1,343 species are found most of them in the Atlantic Forest biome (Forzza *et al.* 2015). One of the most diverse plant families in the Atlantic Forest (Stehmann *et al.* 2009), Bromeliaceae also has the highest absolute number of endangered species (Martinelli *et al.* 2013). The distribution area of many species was severely affected by deforestation of the Atlantic Forest, currently reduced to 11% of its original extent, followed by habitat degradation due to the pressure of population expansion of large urban centers present along the coast (Ribeiro *et al.* 2009, Martinelli *et al.* 2013). Deforestation causes a decline in species richness, particularly of epiphytes, which make up much of the Bromeliaceae and require mature trees in order to get established (Gradstein 2008, Leão *et al.* 2014, Freitas *et al.* 2016). In secondary forests, canopy architecture, dry microclimate and

more solar radiation caused by open canopy and the lowest coverage by bryophytes can hinder the recolonization by epiphytes (Gradstein 2008).

The combination of characteristics such as highly specialized absorbing trichomes, water storage tanks, succulence and Crassulacean Acid Metabolism - CAM enabled Bromeliaceae to occupy an array of different environments (Benzing 2000). While many Bromeliads are rock-dwelling plants growing in crevices or in mats on rock outcrops, being exposed to either seasonal or daily water availability fluctuation, they can also occur as terrestrial and epiphytes in moist, humid and seasonal forests. Epiphytic bromeliads are able to resist periodic fluctuations of water availability in the canopy (Smith & Downs 1974, Benzing 2000). In southeastern Brazil, highlands with exposed rock outcrops and high altitude grasslands are of great importance for the diversity of Bromeliaceae as they harbor many endemic species (Versieux & Wendt 2007).

Within the Atlantic Forest, the high altitude grasslands are found both atop of the Serra do Mar and Serra da Mantiqueira Mountain ranges

(Martinelli & Orleans e Bragança 1996, Safford 1999, Vasconcelos 2011). These comprise vegetation mosaics with markedly different shifts in floristic composition as elevation increases (Safford 1999, Bertonecello *et al.* 2011). In more sheltered valleys, forest formations such as cloud or 'elfin' forests are found (Safford 1999). The upper limit for these forests is around 2,000 meters of altitude, featuring low canopies and undefined strata (Safford 1999) as well as a decrease in tree species number that is reversely accompanied by an increase in epiphyte richness (Gentry & Dodson 1987, Menini Neto *et al.* 2016), especially of orchids (Menini Neto *et al.* 2009). At higher altitudes, there is an increase of the areas of exposed rocks with less frequent, often isolated groups of trees and shrubs forming islands scattered on a grass matrix composed of perennials and xeromorphic herbs and subshrubs (Safford 1999).

Although Bromeliaceae is not one of the families with greater species richness in high altitude grasslands, it represents an important element of the vegetation, fulfilling an important ecological role such as the formation of vegetation mats (Safford 1999, Ribeiro *et al.* 2007) and providing shelter, water and food source for local wildlife (Martinelli & Oliveira e Bragança 1996). However, there are few studies that aim to describe the distribution and abundance of Bromeliaceae in microhabitats of high altitude grassland in order to understand the dynamic of this vegetation (*e.g.* Couto *et al.* 2013).

The Serra do Caparaó, an important mountain range in southeastern Brazil, has attracted botanical collectors since the nineteenth century (<http://inct.splink.org.br>; Accessed on 10 Oct 2014). In an attempt to carry out the flora of Caparaó National Park, some systematic studies have been conducted (*e.g.*, Ericaceae - Romão & Souza (2003), Eriocaulaceae - Trovó *et al.* (2006), Plantaginaceae - Souza & Souza (2002)) but the project has not been completed and many families are yet to be studied. The altitudinal gradient and the mosaic of vegetation, with a predominance of high altitude grasslands at higher elevations, provides great richness, with several species described and known only from this area, for example, *Achetaria caparoense* (Brade

V.C.Souza, *Chusquea caparaoensis* L.G.Clark, *Gaylussacia caparoensis* Sleumer, and *Xyris caparaoensis* Wand. (Sleumer 1967, Clark 1992, Wanderley 2003, Souza & Giuliatti 2009).

High altitude grassland habitats are considered important because they shelter high species richness as well as levels of endemism, even in a small area (Safford 1999). Therefore this study aims to survey the Bromeliaceae in the Caparaó National Park, describing species distribution patterns in the different habitats and elevations, and to analyze species rarity in connection with conservation implications.

MATERIAL AND METHODS

Study area

The Caparaó National Park (CNP) is located between 20°19'S and 20°37'S and 41°43'W and 41°53'W, on the state border between Minas Gerais and Espírito Santo, Brazil. The park was created in 1961 to offer protection for the Caparaó mountain range (Figure 1), covering an area of 31,853 ha that includes the highest peak in southeastern Brazil, the Pico da Bandeira, with 2,892 m of elevation (IBDF 1981, IBGE 2011). The geomorphological unit comprised by the CNP is known as the Caparaó massif, and belongs to the northern Mantiqueira region, marked by geological enclaves of igneous (granite/gneiss) precambrian rocks covered by tertiary and quaternary sediments (RADAMBRASIL 1983). The mean annual temperature is 11.1°C and the annual rainfall ranges from 1,000 mm to 1,500 mm, concentrated in November, December and January (IBDF 1981). The study area is inserted within the Atlantic Forest biome with a predominance of Dense Ombrophilous Forest and rupicolous vegetation typical of high altitude grasslands (Veloso *et al.* 1991, Oliveira Filho *et al.* 2006). The area is considered of special biological importance as it harbors great fauna and flora richness together with significant remnants of well preserved forest (Drummond *et al.* 2005).

Depending on the altitude and proximity of watercourses, we can identify four habitats (physiognomy) in the CNP area: 1) riparian forest between 900-1,300 m; 2) slope forests between

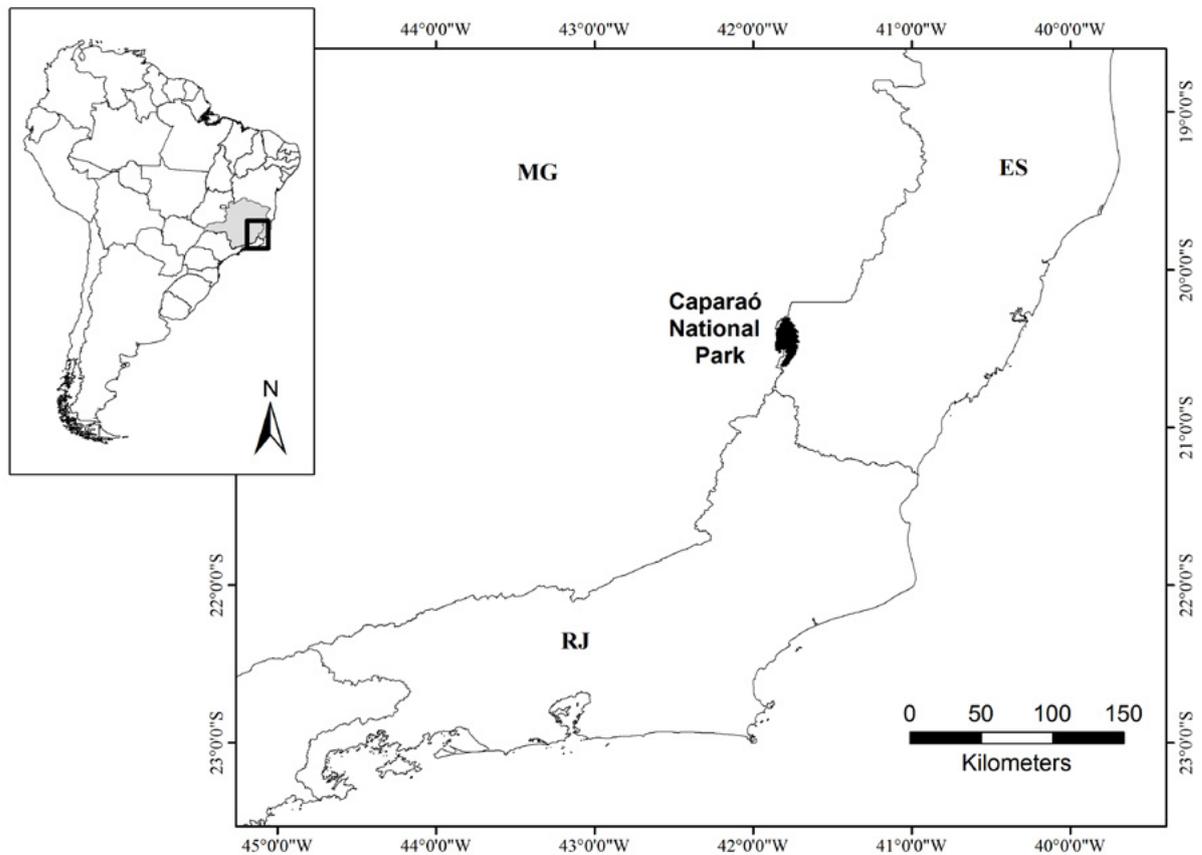


Figure 1. Location of the Caparaó National Park on the border between the states of Minas Gerais and Espírito Santo, Brazil.

1,301-1,500 m, covering steep valleys; 3) cloud forest between 1,501-1,900 m, at the transition with grassland formations; 4) high altitude grasslands, above 1,900 m (Figure 2).

Fieldwork and data analysis

From September 2010 to October 2011, collections were carried out in 23 sites representing the four habitats found in the study area (*e.g.* riparian forest, slope forests, cloud forest and high altitude grassland). Each habitat was represented by at least five sites. However, in some sites more than one habitat is found (*e.g.* close to riparian forest habitat is possible to find slope forest). In each site, walk methodology were performed along a transect following an altitudinal gradient (Figueiras *et al.* 1994). Selective walks were performed laterally to each side of the transect by at least 50 meters.

Once the identification of Bromeliaceae requires the presence of flowers, each site was visited at least three times throughout the year in different seasons, to ensure that all the species present on the site were sampled. In all sites each species had at least one sample collected. Fertile specimens were identified and deposited in the Herbarium of the Federal University of Minas Gerais (BHCB), and duplicates were sent to the Herbarium of the Botanical Gardens of Rio de Janeiro (RB). The collections of the herbaria BHCB, CESJ (Herbário Leopoldo Krieger – Federal University of Juiz de Fora), GFJP (Herbário Guido F. J. Pabst), MBML (Herbário do Museu de Biologia Mello Leitão) and RB (Herbário do Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro) (Thiers 2014) were consulted before the fieldwork, to list the species previously collected in the CNP and afterwards, to assist in their identification. To check whether

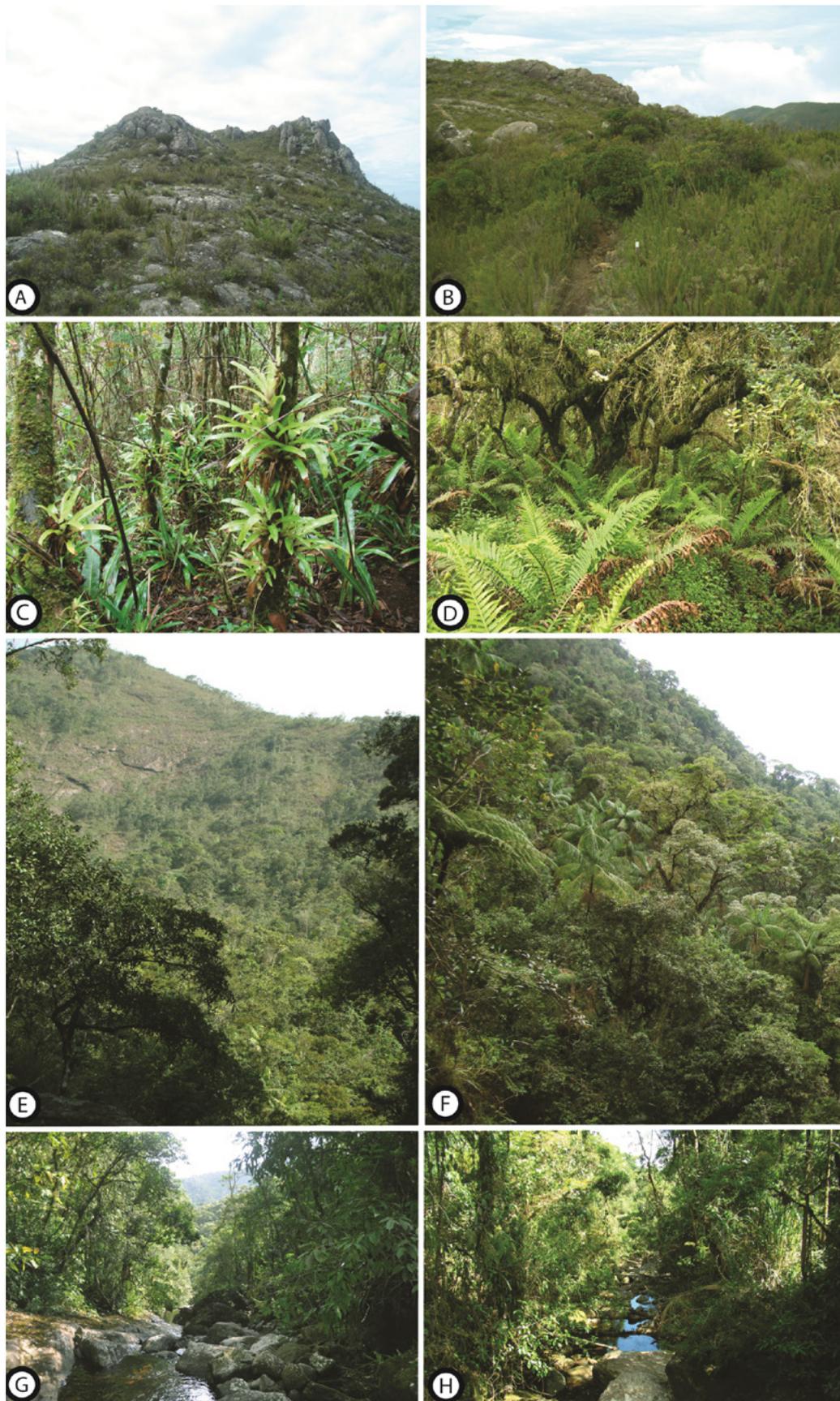


Figure 2. Physiognomy in Caparaó National Park, states of Minas Gerais and Espírito Santo, Brazil. A-B: High Altitude Grassland; C-D: Cloud Forest; E-F: Slope Forest; G-H: Riparian Forest.

species found are endangered, lists published by Forzza *et al.* (2013) were consulted.

Data such as habitat type, geographic coordinates, elevation, substrate preference and local population size were recorded for each species in each site. The population size was established by counting the genets of each species per site. Genets are all numerous attached ramets (clones) produced by the sympodial polycarpic type of bromeliads (Benzing 2000). Species with less than ten genets per site were considered as small local population size. To define habitat specificity a presence/absence matrix between species and habitats was used. Species that have been recorded in only one type of habitat was considered as “Habitat specificity restricted”, if they were recorded in two or more habitats were considered “Habitat specificity broad”.

The geographical distribution of each species was defined based on the literature, using Smith and Downs (1974, 1977, 1979), the Brazilian Species List (Forzza *et al.* 2015) and the Virtual Herbarium of Flora and Fungi database (INCT-<http://inct.splink.org.br/>). Species restricted to a region or recorded only in a few locations (less than five locations), or only in very close geographical locations (less than 30 km from each other in a straight line) were considered narrowly distributed. Further categorization of these species into the seven rarity forms defined by Rabinowitz *et al.* (1986) was made taking into account the information available: Rarity form 1: wide geographic distribution, broad habitat specificity, small local population size; Rarity form 2: wide geographic distribution, restricted habitat specificity, large local population size; Rarity form 3: wide geographic distribution, restricted habitat specificity, small local population size; Rarity form 4: narrow geographic distribution, broad habitat specificity, large local population size; Rarity form 5: narrow geographic distribution, broad habitat specificity, small local population size; Rarity form 6: narrow geographic distribution, restricted habitat specificity, large local population size; Rarity form 7: narrow geographic distribution, restricted habitat specificity, small local population size.

Specimens that were not fully identified, such as *Neoregelia* sp., *Neoregelia* aff. *simulans*

and *Portea* sp. were not considered for this analysis.

RESULTS

A total of 46 species of Bromeliaceae, distributed among 12 genera, were recorded in the CNP (Table 1; Figure 3). The most representative subfamily in the area was Bromelioideae, with seven genera and 22 species, followed by Tillandsioideae (three genera, 20 spp.) and Pitcairnioideae (two genera, 4 spp.). *Vriesea* was the richest genus with 16 species, followed by *Aechmea*, *Neoregelia* and *Nidularium* (five spp. each). The records of *Aechmea lilacinantha*, *Neoregelia brownii* and *Vriesea paraibica* were the first for the Espírito Santo state (Figure 4).

Species distribution varied along the elevation gradient, reaching greater richness between 900 m-1,300 m and decreasing with increasing altitude. Considering habitat types, species richness was higher in riparian (34 species) and slope forest (18 species) when compared to the cloud forest (10 species) and high altitude grassland (5 species) (Figure 5). Some species occurred in more than one habitat, this is the case of *Alcantarea extensa* that occurred at altitudes ranging from 900 m-1,700 m. This species was found on rocky cliffs, forming dense populations that dominated the outcrops or the edge of the riparian forest, and on isolated rocks in the middle of a watercourse, with less than 3 individuals per rock.

On the other hand, genera such as *Neoregelia*, *Billbergia* and some species of *Vriesea*, for example, were restricted to the humid forests up to 1,500 m. Some examples of species restricted to a single habitat were: *Dyckia bracteata*, restricted to the high altitude grassland above 1,900 m, and *Vriesea billbergioiodes*, found only in cloud forest. Other examples were *Pitcairnia decidua* and *P. carinata* which were found above 1,400 m, always growing as rupicolous plants, either dominating flooded areas in the high altitude grassland or cliffs near waterfalls. On the other hand, *Vriesea hoehneana* was sighted in the bushes in the transition vegetation between cloud forest and the high altitude grassland (1,900 m), near watercourses. *Vriesea crassa*, which occurs as either an epiphyte or a rupicolous plant, was always



Figure 3. Species of Bromeliaceae in Caparaó National Park, states of Minas Gerais and Espírito Santo, Brazil. A. *Vriesea hydrophora*; B. *Neoregelia lymaniana*; C. *Nidularium marigoii*; D. *Alcantarea extensa*; E-F. *Quesnelia kautskyi*; G. *Pitcairnia carinata*; H. *Billbergia vittata*; I. *Billbergia euphemiae*; J. *Aechmea vanhoutteana*; K. *Vriesea capixabae*; L. *Dyckia bracteata*. Rarity of the species classification according to the criteria of Rabinowitz *et al.* (1986): A. species with rarity form 7; B, C, G, L: species with rarity form 6; K. species with rarity form 5; D, H, I: species with rarity form 4; E, F, J: species with rarity form 4 and considered Vulnerable (VU) according Forzza *et al.* (2013).

Table 1. List of Bromeliaceae from Caparaó National Park (CNP), states of Minas Gerais and Espírito Santo, Brazil. Taxa are arranged alphabetically and followed by the collector name and number, all voucher were deposited in the Herbarium of the Federal University of Minas Gerais - BHCB. The distribution of species in the CNP was classified according to vegetation type and substrate preference. RF: Riparian Forest; SF: Slope Forest; CF: Cloud Forest; HAG: High Altitude Grassland; FE: Facultative Epiphyte; OE: Obligatory Epiphyte; T: Terrestrial and R: Rupicolous. *First record in the state of Espírito Santo. #This species was not collected by being on inaccessible height.

	Species	Physiognomy	Substratum	Elevation and geographic coordinated
1	<i>Aechmea lamarchei</i> Mez T. M. Machado 447	RF	T	900-1000; 20°20'57"S,41°45'19"W
2	<i>Aechmea lilacinantha</i> Leme* T. M. Machado 178	RF	R	1000-1200; 20°26'50"S,41°44'08"W
3	<i>Aechmea nudicaulis</i> (L.) Griseb. T. M. Machado 431	RF	FE	1000-1200; 20°23'39"S,41°44'06"W
4	<i>Aechmea organensis</i> Wawra T. M. Machado 380	RF,SF	FE	1100-1300; 20°26'42"S,41°44'18"W
5	<i>Aechmea vanhoutteana</i> (Van Houtte) Mez T. M. Machado 207	RF,SF	FE	1200-1400; 20°25'09"S,41°50'46"W
6	<i>Alcantarea extensa</i> (L.B.Sm.) J.R.Grant. T. M. Machado 320	RF, SF, CF, HAG	R	900-1800; 20°26'47"S,41°44'14"W
7	<i>Billbergia amoena</i> (Lodd.) Lindl. T. M. Machado 293	RF, SF	OE	1100-1200; 20°28'05"S,41°44'00"W
8	<i>Billbergia euphemiae</i> E.Morren T. M. Machado 182	RF, SF	FE	1100-1400; 20°23'37"S,41°44'09"W
9	<i>Billbergia lymanii</i> E.Pereira & Leme T. M. Machado 406	RF, SF	FE	1100-1400; 20°25'54"S,41°50'44"W
10	<i>Billbergia vittata</i> Brong. ex Morel T. M. Machado 391	RF, SF	FE	1100-1700; 20°35'40"S,41°48'39"W
11	<i>Dyckia bracteata</i> (Wittm.) Mez T. M. Machado 215	HAG	R	2000-2500; 20°27'25"S,41°48'02"W
12	<i>Neoregelia brownii</i> Leme* T. M. Machado 322	RF	FE	1100-1200; 20°26'44"S,41°44'09"W
13	<i>Neoregelia farinosa</i> (Ule) L.B.Sm. T. M. Machado 342	RF	FE	1000-1200; 20°33'16"S,41°45'46"W
14	<i>Neoregelia lymaniana</i> R.Braga & Sucre T. M. Machado 325	RF	FE	1100-1200; 20°26'42"S,41°44'10"W
15	<i>Neoregelia</i> aff. <i>simulans</i> L.B.Sm. T. M. Machado 321	RF	FE	1000-1200; 20°26'44"S,41°44'09"W
16	<i>Neoregelia</i> sp. T. M. Machado 433	RF	FE	1100-1200; 20°20'58"S,41°48'42"W
17	<i>Nidularium alegrense</i> Leme & Kollmann T. M. Machado 388	RF	T	1000-1200; 20°32'59"S,41°45'49"W
18	<i>Nidularium bicolor</i> (E.Pereira) Leme T. M. Machado 222	CF	T	1800-1900; 20°24'21"S,41°50'16"W
19	<i>Nidularium espiritosantense</i> Leme T. M. Machado 432	RF	FE	1100-1200; 20°23'40"S,41°44'10"W
20	<i>Nidularium longiflorum</i> Ule T. M. Machado 349	RF, SF	FE	1000-1300; 20°33'16"S,41°45'46"W
21	<i>Nidularium marigoii</i> Leme T. M. Machado 194	CF	T	1800-2000; 20°24'21"S,41°50'16"W

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Species	Physiognomy	Substratum	Elevation and geographic coordinated
22 <i>Pitcairnia carinata</i> Mez T. M. Machado 279	HAG	R	1400-2300; 20°27'59"S,41°48'50"W
23 <i>Pitcairnia decida</i> L.B.Sm. T. M. Machado 339	HAG	R	1400-2000; 20°21'18"S,41°48'39"W
24 <i>Pitcairnia flammea</i> Lindl. T. M. Machado 246	RF	R	1000-1200; 20°23'47"S,41°44'11"W
25 <i>Portea</i> sp. [#] only photo			
26 <i>Quesnelia kautskyi</i> C.M.Vieira T. M. Machado 225	RF, SF, CF	T, R	1100-1900; 20°26'47"S,41°44'13"W
27 <i>Tillandsia geminiflora</i> Brongn. T. M. Machado 175	RF, SF	OE	1000-1500; 20°23'38"S,41°44'08"W
28 <i>Tillandsia stricta</i> Sol. T. M. Machado 201	RF, SF	OE	1100-1500; 20°23'37"S,41°44'09"W
29 <i>Tillandsia usneoides</i> (L.) L. A. K. L. Venda 26	RF	OE	1100-1200; 20°26'42"S,41°44'10"W
30 <i>Vriesea billbergioides</i> E.Morren ex Mez. T. M. Machado 223	CF	OE	1800-2000; 20°24'23"S,41°50'20"W
31 <i>Vriesea bituminosa</i> Wawra T. M. Machado 365	RF, SF	FE	1000-1300; 20°27'57"S,41°44'25"W
32 <i>Vriesea capixabae</i> Leme T. M. Machado 409	RF, CF	OE	1100-1600; 20°36'04"S,41°48'56"W
33 <i>Vriesea carinata</i> Wawra T. M. Machado 354	RF, SF	OE	1100-1500; 20°27'58"S,41°44'29"W
34 <i>Vriesea crassa</i> Mez T. M. Machado 318	CF, HAG	FE	1800-2300; 20°27'57"S,41°48'45"W
35 <i>Vriesea flammea</i> L.B.Sm. T. M. Machado 427	RF	OE	1000-1300; 20°26'51"S,41°44'46"W
36 <i>Vriesea gigantea</i> Gaudich. T. M. Machado 345	RF	R	900-1000; 20°29'43"S,41°44'01"W
37 <i>Vriesea guttata</i> Linden & Arruda T. M. Machado 183	RF	FE	1100-1300; 20°25'12"S,41°50'43"W
38 <i>Vriesea heterostachys</i> (Baker) L.B.Sm. T. M. Machado 181	RF, SF	OE	1000-1300; 20°29'39"S,41°44'04"W
39 <i>Vriesea hoehneana</i> L.B.Sm. T. M. Machado 204	HAG	T, R	1900-2000; 20°24'43"S,41°49'50"
40 <i>Vriesea hydrophora</i> Ule T. M. Machado 348	RF	FE	1100-1200; 20°33'04"S,41°45'45"W
41 <i>Vriesea longicaulis</i> (Baker) Mez T. M. Machado 224	RF, SF	FE	1300-1900; 20°24'18"S,41°50'19"W
42 <i>Vriesea pabstii</i> McWill. & L.B.Sm. T. M. Machado 414	RF	OE	1000-1200; 20°29'36"S,41°44'09"W
43 <i>Vriesea paraibica</i> Wawra* T. M. Machado 405	RF, SF	FE	1000-1400; 20°26'44"S,41°44'09"W
44 <i>Vriesea ruschii</i> L.B.Sm. T. M. Machado 217	RF, SF	FE	1000-1400; 20°25'12"S,41°50'55"W
45 <i>Vriesea vagans</i> (L.B.Sm.) L.B.Sm. T. M. Machado 382	RF	OE	1000-1100; 20°33'24"S,41°45'44"W
46 <i>Wittrockia gigantea</i> (Baker) Leme T. M. Machado 408	RF, SF, CF	FE	1000-1600; 20°20'58"S,41°48'42"W

found at the water edge in the transition between cloud forest and high altitude grassland.

Most species (58%) have only one type of substrate preference, being 28% obligatory epiphytes, 21% rupicolous and 9% terrestrial. The other 42% are considered facultative epiphytes, because they occur both as epiphytic, rupicolous and/or terrestrial plants. In the riparian forest habitat, rupicolous and terrestrial bromeliads were well represented (14% and 5%), but the more common were the obligatory (29%) and facultative epiphytes (55%), which were also the most represented in the slope forests (27% and 55%). It was observed a decrease of epiphytes richness and an increase of terrestrial and rupicolous bromeliads with increasing altitude and in the transition to the high altitude grassland (Figure 4).

The species categorization according to the criteria of Rabinowitz *et al.* (1986) showed that

91% (39 spp.) of the species fit within one of the rarity forms and only 9% (4 spp.) were considered common due to their broad geographic distribution, varied habitat and large local populations (Table 2). Among the rarity types, the one encompassing the largest number of taxa was rarity type 4, with 28% (12 spp.) of the species combining restricted geographical distribution, varied habitats and a large local population. Combining the highest forms of rarity, forms 6 and 7, we find even more species (32%/14 spp.) with restricted local geographic distribution, specific habitat and differing only according to their local population size (Table 2).

Four species recorded in the CNP are endangered: *Aechmea vanhoutteana* and *Quesnelia kautskyi* are considered Vulnerable (VU), *Pitcairnia decidua* is considered Endangered (EN) and *Neoregelia brownii* is considered Critically Endangered (CR).



Figure 4. First records of bromeliads for Espírito Santo state, Brazil. A-B. *Aechmea lilacinantha*; C-D. *Neoregelia brownii*, considered Critically Endangered (CR) according Forzza *et al.* (2013); E-F: *Vriesea paraibica*. Rarity of the species classification according to the criteria of Rabinowitz *et al.* (1986): A,B,C,D: species with rarity type 7; E, F: species with rarity type 4.

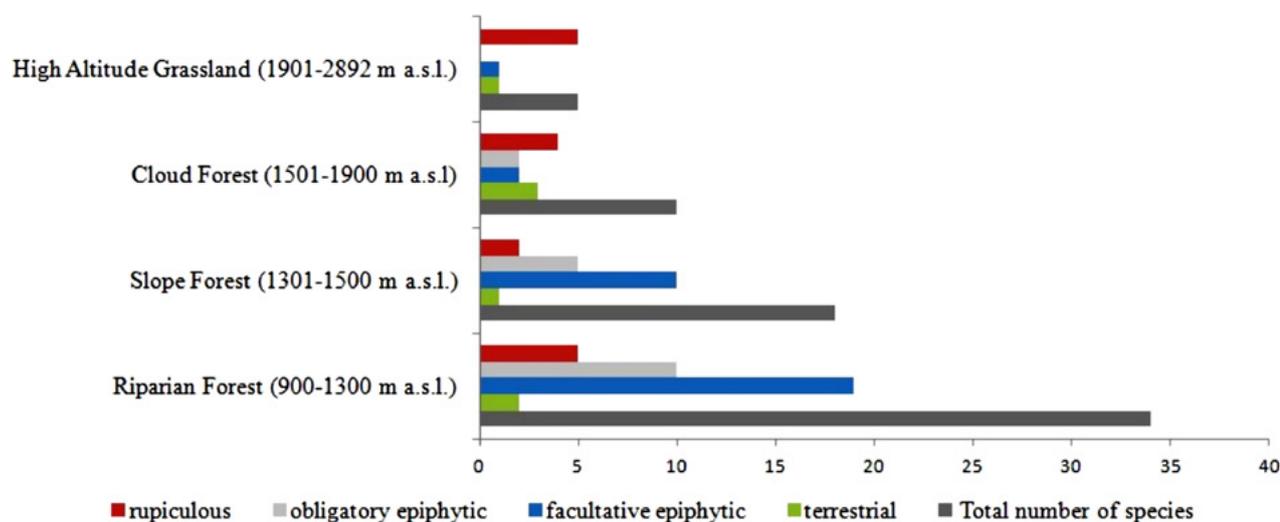


Figure 5. Distribution of Bromeliaceae species in Caparaó National Park, states of Minas Gerais and Espírito Santo, Brazil, according elevation, physiognomy and substrate. The bars represent number of species.

Table 2. Classification of Bromeliaceae species from Caparaó National Park into seven forms (F) of rarity following the criteria of Rabinowitz *et al.* (1986), with the percentage of distribution of species in each form. The parameters for classification of the variables “Geographical distribution”, “Habitat specificity” and “local population size” are found in the “Material and Methods” section.

Geographic distribution	Wide		Narrow	
	Broad	Restrict	Broad	Restrict
Small local population size	F1(0%)	F3 (7%) <i>V. flammea</i> , <i>V. gigantea</i> , <i>V. hoehneana</i>	F5 (12%) <i>A. lamarchei</i> , <i>B. lymanii</i> , <i>V. bituminosa</i> , <i>V. capixabae</i> , <i>V. crassa</i>	F7 (16%) <i>A. lilacinantha</i> , <i>N. brownii</i> , <i>N. farinosa</i> , <i>N. bicolor</i> , <i>N. alegrense</i> , <i>V. hydrophora</i> , <i>V. pabstii</i>
		Common (9%) <i>B. amoena</i> , <i>T. geminiflora</i> , <i>T. stricta</i> , <i>V. carinata</i>	F2 (12%) <i>A. nudicaulis</i> , <i>P. flammea</i> , <i>T. usneoides</i> , <i>V. guttata</i> , <i>V. vagans</i>	F4(28%) <i>A. organensis</i> , <i>A. vanhoutteana</i> , <i>A. extensa</i> , <i>B. euphemiae</i> , <i>B. vittata</i> , <i>N. longiflorum</i> , <i>Q. kautskyi</i> , <i>V. heterostachys</i> , <i>V. longicaulis</i> , <i>V. paraibica</i> , <i>V. ruschii</i> , <i>W. gigantea</i>

DISCUSSION

The high species richness recorded at the CNP was expected, because the southeastern Brazil is considered the center of diversity of bromeliads, especially of the subfamily Bromelioideae and the genus *Vriesea* (Smith & Downs 1974, Givnish *et al.* 2004, Forzza *et al.* 2015). A variety of climatic, topographic and environmental conditions found in southeastern Brazil, especially in the Atlantic Forest and adjacent dry areas were important in driving the diversification of Bromeliaceae lineages (Benzing 2000, Givnish *et al.* 2011). The genera of Bromeliaceae best represented in the CNP were *Vriesea*, *Aechmea*, *Neoregelia* and *Nidularium*, which also correspond with the richest genera in the Atlantic Forest as a whole (Martinelli *et al.* 2008).

Three species were recorded for the first time in the state of Espírito Santo. *Aechmea lilacinantha* was described less than five years and was previously known only from the type locality in mountainous areas between Paty do Alferes and Petrópolis in the state of Rio de Janeiro (Leme 2009). In the original work (Leme 2009), the author who described the species comments that returned to the place where the type specimen was collected, but it was found modified by anthropogenic disturbances which could affect the development of the population. The new distribution record of *A. lilacinantha* is important because it is located in a conservation unit that protects the habitat where the species is inserted ensuring its preservation. *Neoregelia brownii* was known only in the State Park of Serra do Brigadeiro, eastern of the Minas Gerais state, distant 80 Kilometers straight from the PNC (Leme 2000). Finding new areas of occurrence for this species is important because it is in the Brazilian list of endangered species and is considered a rare species (form 7). *Vriesea paraibica* was previously restricted to Minas Gerais and Rio de Janeiro states (Forzza *et al.* 2015).

According to Sanchez *et al.* (2013), altitude influences the floristic composition and structure of the arboreal community in the Atlantic Forest. In the Andes, the greatest wealth of Bromeliads can be found between 1,000-1,500 m (mid elevation pattern) (Kessler 2000, Kessler 2002a). However

this distribution seems to be strongly related to the environmental parameters as frost frequency or ecophysiological properties of each group (Kessler 2000, Kessler 2002a). Particularly in the high altitude grassland, the vegetation distribution is controlled by the local topography, drainage network and soil type distribution (Safford 1999).

At the CNP, the altitudinal gradient between 900 m and 2,892 m causes the establishment of different habitats that provide varied conditions for bromeliads to thrive. The greatest richness was concentrated around the moist riparian forest (between 900-1,300 m), while it decreased with increasing altitude and variation of vegetation, with fewer species in the high altitude grassland where the harshest environment is found. In this last habitat, there was a larger area covered by rocky substrate rather than forest thus facultative epiphytes were found as rupicolous in the high altitude grassland or as epiphytes at the edge of watercourses.

The Bromeliaceae species composition can be influenced by environmental variables, with high humidity being related to higher richness of epiphytic species of the genera *Tillandsia* and *Vriesea* (Fontoura *et al.* 2012). Although dealing with lower elevation areas, Fischer & Araújo (1995) also found greater richness of bromeliads in riparian forest, this being attributed to the higher humidity available and intrinsic spatial complexity of this formation, noticeably the diversity of substrates. On the other hand, high altitude grassland presents shallow soils, low water and nutrient retention, ample temperature variation including occasional frost and very intense UV-B radiation during the day (Safford 1999, Scarano *et al.* 2001). This range of extreme conditions limits the occupation of these habitats to plants with morphologic and physiological adaptations (*e.g.* congested, highly reflective foliage often covered by dense indumentum and/or accumulation of antocyanins) (Benzing 2000).

Some species of Bromeliaceae were generalists or specialists in terms of their distribution within the CNP habitats. This may be related to seed germination requirements which, as shown by Marques *et al.* (2014), respond to the environmental factors of microenvironments, such as substrate humidity and light availability. Thus,

the species distributed in specific environments have a reduced germination niche, while species with more general distribution have wider germination niches. Therefore, even if the species have the ability to disperse over long distances, their actual distribution in the environment relates to the availability of germination niches (Marques *et al.* 2014).

Depending on the variables analyzed, the concept of rarity can be considered rather broad and controversial, therefore the use of Rabinowitz *et al.* (1986) seven rarity forms is an objective tool to distinguish priority areas for conservation by taking into account the particularities of environmental requirements for the species distribution (Caiafa & Martins 2010, Fontana *et al.* 2014). In the CNP, a large percentage of species were categorized amongst the rarest forms (6 and 7), reflecting the restricted distribution usually found among Bromeliaceae (Versieux & Wendt 2007). Small ranges in Andean bromeliads can be related to terricolous and rupicolous habit, wind-dispersed seeds without appendages and fragmented topography while there is a tendency towards larger distribution ranges among epiphytic bromeliads (Kessler 2002b). Indeed, at the CNP we observed that, among the rarest species, there is a predominance of terrestrial and rupicolous taxa whereas the most common species are epiphytes.

In general terms consistency was found between the categories of threat (Forzza *et al.* 2013) and the rarity forms. Species such as *Aechmea vanhoutteana* and *Quesnelia kautskyi*, categorized as Vulnerable, were classified as rarity form 4. Moreover, *Pitcairnia decidua* was categorized as Endangered and considered form 6, while *Neoregelia brownii*, in the category Critically Endangered, was the rarest (form 7). In our analysis, it is noticeable that the rarest species are also under more threat. However, data such local population size or habitat preferences are often not available in the literature, making it difficult to categorize the species either as rare or as threatened (Leão *et al.* 2014).

In summary, the data provided in this work on environmental occupation and geographic distribution of species can assist works in ecology and conservation. The expansion of the species distribution for taxa previously considered

endemic, such as *Neoregelia brownii* and *Aechmea lilacinantha*, increment the knowledge of the flora of the state of Espírito Santo and can also offer subsidies for biogeographic studies showing floristic connections between nearby mountains (*e.g.* Serra do Caparaó and Serra do Brigadeiro). In terms of the habitats, high altitude grassland did not harbour the highest species richness, but had exclusive species to this type of environment, including some of the endangered species that were categorized as rare (form 6). It was confirmed that species are not equally distributed along the altitudinal gradient, some being restricted to certain niches, suggesting the importance of carrying out detailed studies on bromeliad community structure in Brazilian mountains. The majority of species found at the CNP were considered rare and restricted to certain niches. This example from the Bromeliaceae reinforces the importance of protecting and preserving the environments associated to the high altitude grassland, as those provide heterogeneous environment for plant species occupation.

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