

cryptogamie

Bryologie

2019 • 40 • 17

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bottom-to-top bryophyte richness in
a seasonally dry forest in Brazil

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Photo de / by Dr. Joan Bruno Silva, Catimbau National Park overview in a rainy season.

Cryptogamie, Bryologie est indexé dans / *Cryptogamie, Bryologie is indexed in:*

- Biological Abstracts
- Current Contents
- Science Citation Index
- Publications bibliographiques du CNRS (Pascal).

Cryptogamie, Bryologie est distribué en version électronique par / *Cryptogamie, Bryologie is distributed electronically by:*

- BioOne® (<http://www.bioone.org>)

Cryptogamie, Bryologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Bryologie is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonia, Geodiversitas, Zoosystema, Anthropolzoologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections Algologie, Mycologie.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

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Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / print): 1290-0796 / ISSN (électronique / electronic): 1776-0992

A small elevational gradient shows negative bottom-to-top bryophyte richness in a seasonally dry forest in Brazil

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Submitted on 6 November 2018 | Accepted on 9 April 2019 | Published on 5 November 2019

Silva J. B., Germano S. R., Maciel-Silva A. S. & dos Santos N. D. 2019. — A small elevational gradient shows negative bottom-to-top bryophyte richness in a seasonally dry forest in Brazil. *Cryptogamie, Bryologie* 40 (17): 219-231. <https://doi.org/10.5252/cryptogamie-bryologie2019v40a17>. <http://cryptogamie.com/bryologie/40/17>

ABSTRACT

Elevational gradients can serve as powerful tools for testing ecological relationships between species richness versus environmental variables. Although the patterns be usually from positive to humped-shaped, elevational gradients may run in a negative way with the species richness decreasing in relation to the altitude. The floristic gradient may vary according species biology, site and, scale for analyses. Therefore, elevational gradient can be useful for detecting points for biological conservation and may be analyzed by using sensitive species as approach for others species including banner-species. Along an elevational gradient in a harsh semiarid environment we are showing a negative relationship between bryophyte species richness and increasing elevation. The observed floristic gradient reflects environmental constraints related to light requirements and low humidity as environmental conditions become more severe at higher altitudes, where anthropogenic activities such as farming dramatically alter the vegetation covering. The diversity of bryophytes in terms of their light requirements makes them excellent bioindicators of environmental quality. We provide data that will be useful for conservation planning and management, and report species with rare distributions in Brazil and others not yet recorded as occurring in dry forests.

KEY WORDS

Plant distribution,
elevation,
functional traits,
gradient,
Caatinga.

RÉSUMÉ

Un petit gradient d'altitude montre une richesse négative en bryophytes de bas en haut dans une forêt asséchée de façon saisonnière au Brésil.

Les gradients d'élévation peuvent constituer de puissants outils pour tester les relations écologiques entre la richesse en espèces et les variables environnementales. Bien que les schémas soient généralement de positifs à en forme de bosses, les gradients d'altitude peuvent être négatifs, la richesse en espèces diminuant par rapport à l'altitude. Le gradient floristique peut varier selon la biologie de l'espèce, le site et l'échelle à des fins d'analyse. Par conséquent, le gradient d'élévation peut être utile pour détecter des points de conservation biologique et peut être analysé en utilisant des espèces sensibles comme approche pour d'autres espèces, y compris les espèces bannières. Le long d'un gradient d'altitude dans un environnement semi-aride sévère, nous montrons une relation négative entre la richesse en espèces de bryophytes et l'altitude croissante. Le gradient floristique observé reflète les contraintes environnementales liées aux besoins en lumière et à une faible humidité, alors que les conditions environnementales deviennent plus rigoureuses à des altitudes plus élevées, où des activités anthropiques telles que l'agriculture modifient considérablement le couvert végétal. La diversité des bryophytes en termes de besoins en lumière en fait d'excellents bioindicateurs de la qualité de l'environnement. Nous fournissons des données qui seront utiles pour la planification et la gestion de la conservation, et nous rapportons les espèces ayant des répartitions rares au Brésil et d'autres non encore enregistrées comme étant présentes dans les forêts sèches.

MOTS CLÉS

Distribution des plantes, élévation, traits fonctionnels, gradient, Caatinga.

INTRODUCTION

Elevational gradients can be powerful tools for examining the ecological requirements of species since environmental conditions change along elevational transects (Körner 2007; Kessler 2009), reflecting the adaptive traits or life strategies of species found at different altitudes. Even small elevational gradients can provide good descriptions of assemblage compositions and species distributions in tropical environments (Austrheim *et al.* 2005; Körner 2007; Silva *et al.* 2014a) and those belts can be used as proxies for environmental changes.

Several studies using bryophytes have investigated how elevational gradients are related to the structures, compositions, and reproductive behaviors of tropical rainforest communities (e.g. Gradstein & Salazar-Allen 1992; Frahm 2002; Maciel-Silva & Valio 2011; Maciel-Silva *et al.* 2012; Silva & Pôrto 2013; Santos *et al.* 2014, 2017). However, no studies have focused on bryophyte richness along elevational gradients in the Caatinga (classified as a seasonally dry tropical forest – Bullock *et al.* 1995). Caatinga is composed of a mosaic of dry forests and shrub vegetation (savannah-steppe), with enclaves of humid montane and closed forests (Tabarelli & Silva 2002). This heterogeneity contributes to high biodiversity and considerable number of endemic species (see Meyer *et al.* 2000; Giuliatti *et al.* 2002). Caatinga occupies 10% of the land area of Brazil (IBGE 2004), and has been experiencing the impacts of desertification due to extensive clearing for agriculture and pasture (Leal *et al.* 2005), specially by goats, which thrive at higher altitudes (Joshi *et al.* 2004).

Few studies have been done focusing on an altitude gradient in Brazilian dry forests. This includes a study focusing on a short gradient (400-600 m a.s.l) for vascular plants (Silva *et al.* 2014a) that found a positive relationship between

plant richness and increased altitude. For bryophytes, two recent studies focused on shift in diversity along a horizontal gradient of regional rainfall (Silva *et al.* 2014c; Germano *et al.* 2016). There is thus an urgent need for studies of plant richness in semiarid regions, especially to identify biodiversity hotspots (Silva *et al.* 2014a), and indicator species (Magurran 2004) that can be used to monitor ecosystem integrity (Chao *et al.* 2005). Bryophytes are sensitive to local environmental conditions and substratum availability (Reese 1993; Smith & Stark 2014) and can serve as excellent environmental bioindicators (Delgadillo & Cárdenas 1990; Glime 2015) along elevational gradients (Frahm & Gradstein 1991; Austrheim *et al.* 2005; Santos *et al.* 2014, 2017). Elucidating drivers of distribution can be the first step to understand what drives species distribution (Anderson *et al.* 2011) and for protecting bryophyte diversity and their habitats (Smith & Stark 2014).

We hypothesized that there will be an inverted gradient of bryophyte species richness along a short altitudinal gradient in the Caatinga (650-980 m a.s.l), with higher diversity at lower altitudes, and that the differences between elevational belts should reflect different life history traits of the resident species and different substrates colonized. The reason is that land use intensifies with increasing altitude. The main animals used for subsistence in harsh environments are goats, generalist animals well suited for harsh environments at high altitudes (Chynoweth *et al.* 2013). We examined the relationships between elevation and richness, species composition, substratum influence and life history traits to address three issues: 1) is the bryophyte composition in a disturbed dry seasonal forest area unique inside the Caatinga?; 2) do bryophytes show a distinctive response to the short elevational gradient in the Caatinga? And if there is such a response 3) how do bryophyte assemblages behave along the gradient?

MATERIAL AND METHODS

CATIMBAU NATIONAL PARK

The Catimbau National Park (Catimbau NP) was created in 2002 (Decree n° 4.340/2002) in the Caatinga domain of Pernambuco State, Brazil. The park (8°24'–8°36'S, 37°09'–37°14'W) (Melo 2012) is situated in an ancient geological region underlain by weathered Paleozoic sedimentary deposits (Ferreira 2010), and covers 62 000 ha at elevations varying from 600 to 1000 m.

The climate is semiarid, rainfall varies from 0 to 256 mm/mo, with a mean annual temperature of 23°C (ICMBio 2013). The phytophysiognomies found in the region include dense arboreal Caatinga, shrubby spineless vegetation on sandy soils, and rupestrian fields that are mostly characterized by cactus and bromeliad species (Andrade *et al.* 2005). The region is of extreme biological importance (MMA 2002) due to its many endemic species (Forzza *et al.* 2010) and other species with rare distributions in Brazil (Ellis *et al.* 2016a, b).

SAMPLING DESIGN

Three elevational belts were considered: 650–750 m (B1); 760–860 m (B2); 870–980 m (B3). Each belt shows important changes in vegetation cover landscape and levels of anthropic disturbance. The precipitation gradient in Catimbau NP is horizontal rather than vertical (Rito *et al.* 2016). However, the vegetative modification along the gradient (i.e., the vegetation cover decreases with increasing altitude) is due to anthropic actions such as land use for goat farming and planting. The predominant vegetation is Steppical-Savannah that occurs in the lowest elevations (600–800 m a.s.l.); at higher elevations predominates the pioneer vegetation of fluvial influence. Animal agricultural activities occur predominantly in high elevations (above 800 m a.s.l.). Particularly for the park, this implies soil dependent effects (i.e., exposed soil increase) and causes biotic homogenization towards the higher end of the gradient disturbance (Ribeiro *et al.* 2015; Ribeiro-Neto *et al.* 2016).

Samples of bryophyte were collected in 10 subplots (2 × 5 m) randomly distributed within each belt. Random plots were established in each belt, at least 20 m apart to ensure statistical independence (see Silva *et al.* 2018a, b), which were surveyed for three years starting in 2014. Floristic collections were made within the randomly established plots, collecting bryophytes samples of standard of 5 × 5 cm (Frahm 2003) from all available substrates by plot: 31 samples on tree trunks, 18 on soil, and 12 on rocks in B1; 17, 18, and 11 in B2; 3, 34, and 14 in B3.

It is important to note that an El Niño event affecting the entire region in 2012 resulted in an almost continuous dry period in the Catimbau NP, eliminating seasonal effects between 2012 and 2016. El Niño events generate significant impacts on the climate of the Atlantic and South American regions because produce large-scale anomalous circulations in the atmosphere (Grimm *et al.* 2000; Grimm 2004). Among the variations, the decrease in rainfall is one of the most pronounced (Marengo 2006).

We considered the frequencies of the bryophyte species at both local and regional scales in the statistical analyses. The local scale was considered here to be represented by each elevational belt; the regional scale was considered as composing all the elevational belts together. We used the last scale in order to evaluate the floristic uniqueness of the Catimbau NP. We used the checklists of Pôrto *et al.* (1994) and Pôrto & Bezerra (1996) and data from Silva *et al.* (2014b), and Germano *et al.* (2016), all of them from Caatinga areas. We included areas with rock outcrops as they are of difficult access and may function as species refuges (Silva & Germano 2013) or protected sites (Salvatierra *et al.* 2017).

LIFE HISTORY TRAITS

We selected life history (functional) traits likely related to xeric conditions as the explanatory variables. To that end, we surveyed the life history data of those bryophytes in the scientific literature (Sharp *et al.* 1994; Gradstein *et al.* 2001; Frahm 2002) concerning their sexual system, their frequencies of sexual reproduction, frequencies of asexual reproduction, mean spore sizes, light requirements, and life forms (Appendix 1). Those functional traits should influence plant colonization success and the richness of bryophyte species – and therefore act as proxies for estimating the environmental filtering intensity at each elevational belt.

We categorized each of the attributes selected, with the exception of mean spore size – which was obtained from the literature. When only the minimum and maximum values of spore sizes were available, we calculated the means from those values. We adopted three categories for the attribute sexual system (monoecious [1], dioecious [2] and polyoecious [3]); two categories for the frequency of sexual reproduction, i.e., the frequencies of sporophytes encountered in the field, and the frequency of asexual reproduction (rare (1) and frequent (2)); three standard categories for the light requirement (shade tolerant [1], light demanding [2] and generalist [3]). The life-forms were assigned with importance values for xeric environments, in increasing order, following Glime (2015): 1, Thalloid mats; 2, Mat; 3, Weft; 4, Fan; 5, Cushion; 6, Tuft.

DATA ANALYSIS

Regional and local flora compositions

The Sørensen similarity index (gives lower weights to rare species – Valentin 2012) was used to evaluate the floristic similarities of the bryophyte flora in the Catimbau NP with other Caatinga areas and rock outcrop sites using incidence data (presence vs absence). We used the Weighted Pair Group Method with Averaging (WPGMA) using checklists of the Caatinga, including rocky outcrop areas. That analysis was chosen to ensure that noise due to differences in collection efforts did not influence the final result by assuming all distances contributed equally to each computed average (Valentin 2012).

Richness along the elevational gradient

We performed the generalized linear model (GLM), to a 5% confidence level and Poisson distribution with the log con-

nection method. Then, we tested the influence of the gradient using a 95% bootstrap confidence interval, i.e., $n = 1999$ (Zar 2010). We evaluate how the species richness of bryophytes were related to elevation and whether the elevation gradient imposed a dispersion limit for the bryophytes. We argue that spore size should influence the structure of assemblages along the gradient by restricting the reach of large spore producing species to low altitudes. This should characterize dispersion limit. Thereby we used the species richness and mean spore size as descriptors and the 30 subplots as samples.

We analyzed that life history trait, i.e., spore size, because it is central and independent trait of others (Bonte & Dahirrel 2016). We ordered the richness of each family by elevational belt, using Comunidata 1.5 software (Dias 2006) to evaluate their elevational distributions.

Substratum influence

We used Principal Component Analysis (PCA) to evaluate substrate influences on species compositions along the elevation gradient by evaluating the significance of the first two ordination axes (Zar 2010). We considered all the substrates encountered in the different subplots inventoried for that purpose. Because of the difference in the number of samples per substrate in each belt, we performed a Student's *t*-test of a sample (Ayres *et al.* 2007) proving the non-significant difference between them.

Life history traits as descriptors of elevational belts

We performed Spearman's correlation in order to evaluate the independence of the explanatory variables: sexuality (monoecious, dioecious, polyoicous); frequency of sexual and asexual reproduction; light-demands; life-forms (Zar 2010).

RESULTS

BRYOPHYTE COMPOSITION IN THE CATIMBAU NATIONAL PARK

We recorded 28 species of bryophytes (20 mosses and eight liverworts). In terms of the liverworts, *Targionia hyophylla* L. was a new record for Pernambuco State, *Marchantia polymorpha* L. and *Noteroclada confluens* Taylor ex Hook. & Wilson were new records for northeastern Brazil; in terms of mosses, *Brachymerium fabronoides* (Müll.Hall.) Paris constituted a new record for Pernambuco (Table 1).

The most frequent regional species were the mosses *Fabronia ciliaris* var. *wrightii* (Sull. ex Sull. & Lesq.) W.R.Buck, *Campylopus pilifer* Brid., *Octoblepharum albidum* Hedw., and *Brachymerium exile* (Dozy & Molk.) Bosch & Sande Lac.; the most frequent liverwort species was *Fuscocephaloziopsis crassifolia* (Lindenb. & Gottsche) Vána & L. Söderstr. In terms of the mosses, only *O. albidum* and *C. pilifer* occurred in all the elevational belts, with the latter being the most frequent in the upper two belts. Although *F. ciliaris* var. *wrightii* was recorded at both the base and the top of the elevational gradient, it was more frequent at lower altitudes. In terms of the

liverworts, *F. crassifolia* was the most frequent and the only species that occurred in all belts.

At a regional scale, the bryophyte flora in Catimbau NP is unique within the Caatinga (Fig. 1). Analysis of the representativity of bryophyte families in the elevational belts indicated the presence of some exclusive families within each belt, although other families are represented throughout the gradient. The richest taxa in terms of species were Bryaceae and Fissidentaceae (mosses), with their representativity being greater in the first elevational belt (Fig. 2); Frullaniaceae (liverworts) was recorded at all elevations, although with greater representativity in the intermediate belt.

BRYOPHYTES ARE GOOD INDICATORS OF ELEVATIONAL BELTS IN THE CAATINGA

The richness of the local pool of species decreased with increasing elevation (GLM-L = 13.57, $P = 0.0002$; Fig. 3) for the model generated about 42% (intercept value) failure rate. The floristic similarity and the quantities of species shared between belts decreased with altitude (Fig. 4). In relation to substrate influences along the elevational gradient, the first PCA axis explained 33.74% of the data variation, and the second axis 29.12% (totalling 62.86%; Fig. 5). Tree trunks and rocks were related to axis 1 (−0.82 and 0.80 respectively); while the soil substrate was negatively related to axis 2 (−0.93). There was no correlation, however, between elevational belts and the types of substrates colonized (Table 2).

LIFE HISTORY TRAITS OF BRYOPHYTES DIFFER ACCORDING TO ELEVATION IN THE CAATINGA

We found a positive correlation between light demands and asexual reproduction ($R_s = 0.10$; $p = 0.02$). Since light demands are more important to the establishment of bryophytes and their individual maintenance, we excluded asexual reproduction from the analysis. Our findings show that the species richness is related to light-requirements at the base of the elevational gradient (Table 3; Figure 6A) and life-forms at the top (Table 3; Figure 6B). However, no variations in the mean sizes of the spores were observed according to elevation (Table 4).

DISCUSSION

BRYOPHYTE COMPOSITION IN THE CATIMBAU NATIONAL PARK

The bryophyte families found at all elevation levels were those typically associated with xeric conditions (Bryaceae, Calymperaceae, Dicranaceae among the mosses, and Frullaniaceae and Cephaloziaceae among liverworts) (Frahm 2000; Silva & Germano 2013; Silva *et al.* 2014c). Costa & Peralta (2015) stated that the Cephaloziaceae occur in environments such as evergreen and gallery forests in Brazil, but never within the Caatinga, although Cephaloziaceae species have, in fact, been recorded in the latter domain (Silva & Germano 2013). *Fuscocephaloziopsis crassifolia* was encountered in the present

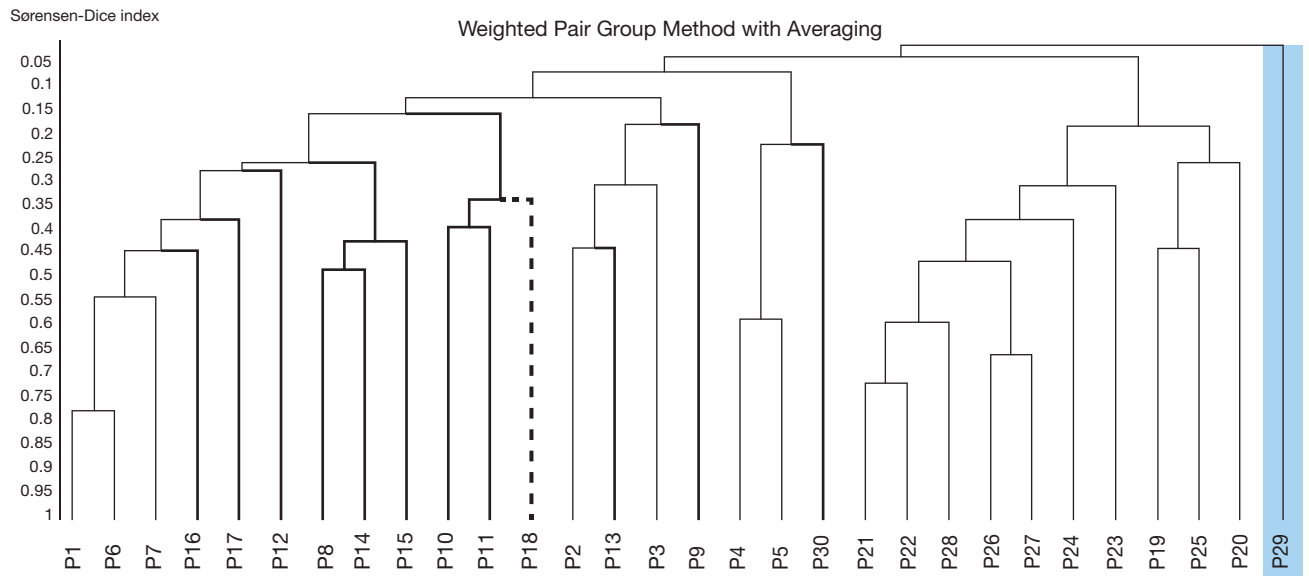


Fig. 1. — Results of the clustering with weighted average between Caatinga areas (including rocky outcrops) based on the Sørensen similarity index showing that the bryophyte flora of Catimbau NP is singular: **dotted arm** indicates Rocky outcrop in Bahia state; **brackets in light gray** indicates areas in Paraíba state and the **bold arms** indicate the areas in Pernambuco state; site P29, highlighted in **blue** shows the isolation of Catimbau NP. Bahia state is approximately 370 km from Pernambuco state and 930 km from Paraíba, in a straight line. Coefficient of Cofenetic Correlation (CCC) = 0.80. Own illustration: *Fabronia ciliaris* (Brid.) Brid.

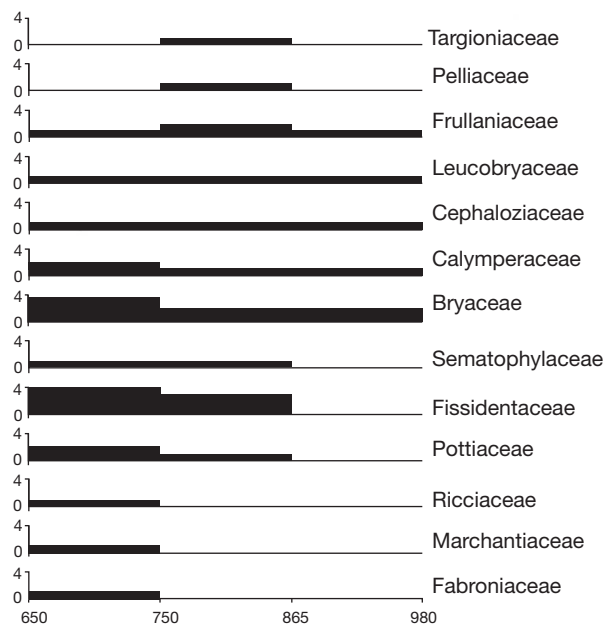


Fig. 2. — Elevational distribution and representativeness of bryophyte families in the Catimbau National Park. The width of the bars denotes the number of species per family. The elevation is measured in meters.

study, and had previously been noted for Pernambuco State (Silva *et al.* 2014c); it has been recorded in the Caatinga among other species of robust mosses (e.g. Bryaceae spp.), probably benefiting from the more humid conditions associated with their host phorophytes.

Fabronia ciliaris var. *wrightii* is a generalist species that occurs on shaded tree trunks in xeric environments (Delgadillo & Cárdenas 2011). It was the most frequent taxon

throughout the elevational gradient, and was encountered at higher frequencies at lower elevations. We found that *F. ciliaris* var. *wrightii* occurred extensively on shaded *Syagrus coronata* (Mart.) Becc. trunks. Since epiphytic bryophytes require high humidity levels (Delgadillo & Cárdenas 1990), the presence of that species indicated more favorable environmental conditions at lower elevations in the Caatinga as opposed to higher elevations – confirming the existence of an elevational gradient and decreasing species richness with increasing elevation.

The bryophyte flora of the Catimbau NP includes species with rare distributions in Brazil (Ellis *et al.* 2016a, b). The park is located in a transition zone between the Caatinga domain and Atlantic Forest fragments, which helps explain its atypical flora. Moreover, protected areas of Caatinga are unique in relation to other dry forest sites because of their more amenable climatic conditions that are unaffected by deforestation (Melillo *et al.* 2016). On the other hand, Catimbau NP experiences chronic disturbance, which causes drastic decreases in forest cover with emphasis on habitat loss and fragmentation as the main threats to tropical biodiversity and services (Laurance *et al.* 2014). Although the entire Caatinga, including rock outcrops, is affected by trails, camping areas, overgrazing and sites for religious rituals that provoke alterations in their floras (Leal *et al.* 2005), in the park, the disturbance intensity increases with the altitude and which turns the lower altitudes in a refuge for a number of species.

Species richness is a measure of diversity that is widely used for selecting conservation areas (Mazaris *et al.* 2008), but the lack of complete datasets containing information on species distributions represents a challenge to conservation planning (Mandelik *et al.* 2007). Our results therefore bring new insights into the dynamics of plant communities along elevational gradients in harsh environments and provide data

TABLE 1. — Checklist to bryophytes species and families registered to Catimbau NP with data of vegetation type and cover, disturbance degree and species frequency by elevational belt: * = new record for Pernambuco state; ♦ = new record for Brazilian Northern Region; + = presence of animal agriculture (double plus indicates higher intensity).

	Elevation		
	B1	B2	B3
Vegetation type	Wooded Steppical-Savanna	Forested Steppical-Savanna+	Pioneer Formation of Fluvial Influence++
Vegetation cover	High	Intermediate	Low
Disturbance degree	Low	Intermediate	High
Division/Family/Specie	–	–	–
BRYOPHYTA			
Bartramiaceae (1/2)	–	–	–
<i>Philonotis hastata</i> (Duby) Wijk & Margad.	0	1	0
<i>Philonotis uncinata</i> (Schwägr.) Brid.	0	0	1
Bryaceae (3/4)	–	–	–
<i>Bryum argenteum</i> Hedw.	1	2	0
<i>Bryum chryseum</i> Sull.	0	1	2
<i>Brachymerium exile</i> (Dozy & Molk.) Bosch & Sande Lac.	7	1	5
<i>Brachymerium fabronoides</i> (Müll.Hall.) Paris	1	0	0
<i>Rosulabryum billardieri</i> (Schwägr.) J.R. Spence	0	0	1
Calymperaceae (2/2)	–	–	–
<i>Octoblepharum albidum</i> Hedw.	8	2	2
<i>Syrrhopodon prolifer</i> Schwägr.	1	–	–
Fabroniaceae (1/1)	–	–	–
<i>Fabronia ciliaris</i> var. <i>wrightii</i> (Sull. ex Sull. & Lesq.) W.R.Buck	20	0	3
Fissidentaceae (1/5)	–	–	–
<i>Fissidens lagenarius</i> Mitt. var. <i>lagenarius</i>	1	0	0
<i>Fissidens radicans</i> Mont.	1	2	0
<i>Fissidens serratus</i> Müll.	1	2	0
<i>Fissidens submarginatus</i> Bruch.	1	2	1
<i>Fissidens zollingeri</i> Mont.	0	1	0
Helicophyllaceae (1/1)	–	–	–
<i>Helicophyllum torquatum</i> (Hook.) Brid.	0	0	1
Leucobryaceae (1/1)	–	–	–
<i>Campylopus pilifer</i> Brid.	7	6	5
Pottiaceae (2/2)	–	–	–
<i>Archidium ohioense</i> Schimp. ex Müll. Hal.	1	0	0
<i>Tortella humilis</i> (Brid.) Jenn.	5	2	1
Sematophyllaceae (1/1)	–	–	–
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.	1	2	0
MARCHANTIOPHYTA			
Cephaloziaceae (1/1)	–	–	–
<i>Fuscocephaloziopsis crassifolia</i> (Lindenb. & Gottsche) Váňa & L. Söderstr	4	5	2
Frullaniaceae (1/3)	–	–	–
<i>Frullania duseii</i> Steph.	0	0	1
<i>Frullania gibbosa</i> Nees	1	1	0
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	0	1	0
Marchantiaceae (1/1)	–	–	–
♦ <i>Marchantia polymorpha</i> L.	1	0	0
Pelliaceae (1/1)	–	–	–
♦ <i>Notoecloclada confluens</i> Taylor ex Hook. & Wilson	0	1	0
Ricciaceae (1/1)	–	–	–
<i>Riccia vitalii</i> Jovet-Ast	1	0	1
Targioniaceae (1/1)	–	–	–
* <i>Targionia hypophylla</i> L.	0	1	0

TABLE 2. — Correlation among substrates with their respective axes chosen (Axis 1 and 672 Axis 2) for Principal Component Analysis (PCA) showing no correlation with elevational belts.

Substrates and elevational variable	Axis 1	Axis 2
Trunk	-0.8249	0.3875
Rock	0.8044	0.3676
Soil	-0.0257	-0.9378
Altitude	0.1466	-0.0016

that can be used for conservation planning and management. Bryophytes provide important non-redundant ecosystem services such as stabilizing soils, capturing and distributing nutrients, regulate seed germination, and colonizing disturbed areas (Belnap & Lange 2001). Nevertheless, Alves *et al.* (2016) noted that “bryophytes usually go unnoticed in conservation planning because of their small size, difficulty of identification and unrecognized levels of local diversity.”

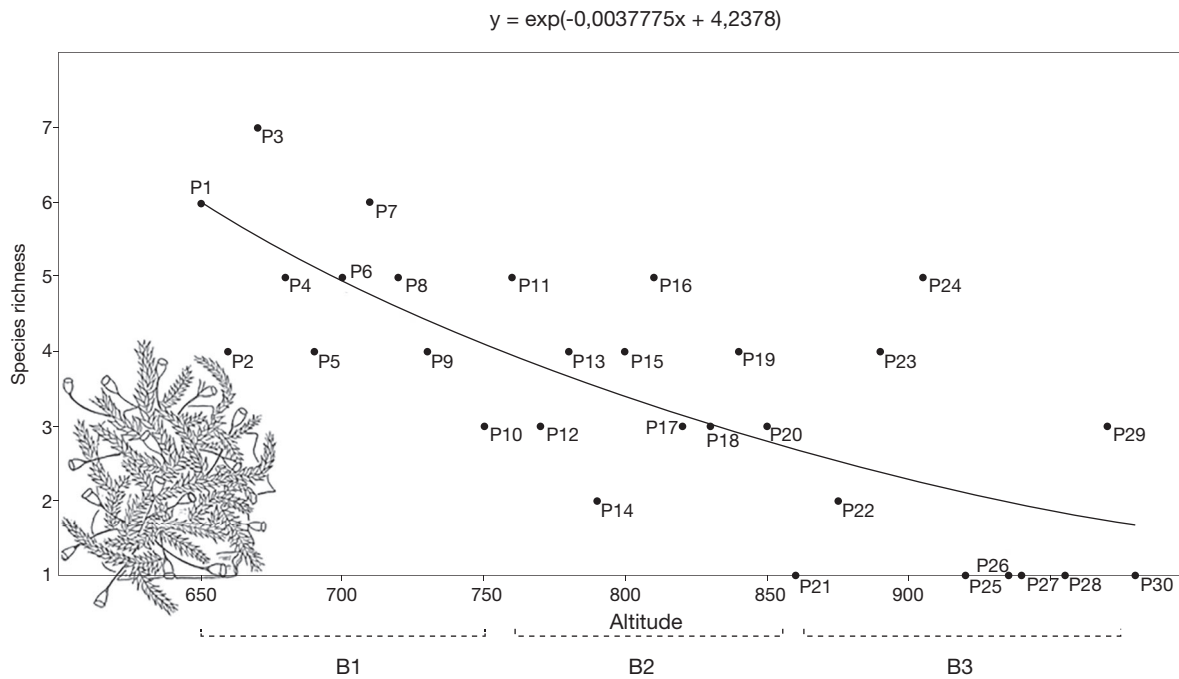


FIG. 3. — The effects of altitude decomposed into three elevational belts on bryophyte richness. Model based on the Poisson distribution and log connection method for unprocessed data. Own illustration: *Fabronia ciliaris* (Brid.) Brid.

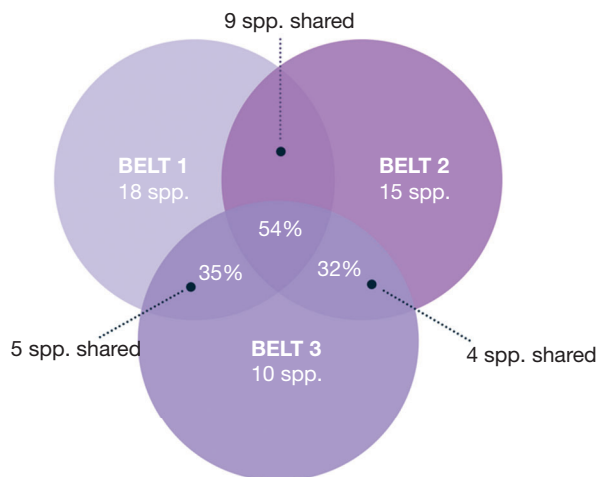


FIG. 4. — Venn diagram showing the low percentage of similarity between the belts levels based on the Sørensen-Dice index, total number of species per belt, and the amount of species shared between each belt.

THE ELEVATIONAL GRADIENT IN THE CAATINGA AFFECTS BRYOPHYTE COMMUNITIES

Studies undertaken in forest environments with vascular (Grytnes & Veetas 2002; Grytnes 2003; Silva *et al.* 2008; Pescador *et al.* 2015) and non-vascular plants (Frahm & Gradstein 1991; Austrheim *et al.* 2005; Stehn *et al.* 2010; Sun *et al.* 2013; Santos *et al.* 2014, 2017) have reported that species richness increases along a base-to-top elevational gradient. Those types of studies have been rare in harsh environments, although showing same results (e.g. Austrheim *et al.* 2005; Mazimpaka *et al.* 2009).

A negative relationship between the species richness and increasing elevation has been found to be more common (Stevens 1992; Rahbek 1995), with a peak at intermediate elevations (Grytnes & McCain 2007). The elevational gradient studied here (650-980 m a.s.l.) showing higher species richness at lower elevations and decreasing to the top. This pattern appears because as altitude increases, factors such as habitat availability become more restricted and local climatic conditions can change within just a few hundred meters (Rahbek 1995; Grytnes & Vetaas 2002).

For bryophytes, the gradient is largely influenced by the relationships between environmental conditions and plant adaptive strategies that limit dispersal (Smith & Stark 2014) or substrate (microhabitat) influences (e.g. Santos *et al.* 2017). The Catimbau NP is affected by agricultural activities with intensification at altitudes above 800 m a.s.l. The main animal agricultural activity is the rearing of goats, animals with a fundamental niche at higher altitudes (Joshi *et al.* 2004). These activities lead to a vegetative cover gradient that influences the higher exposure of the plants to insolation and low humidity.

The Catimbau NP experiencing a horizontal water gradient instead vertical one (Rito *et al.* 2016). Therefore, water available is not a filter for bryophytes along the elevational gradient. Thereby, the type and plant cover should be the main factors acting on the composition of bryophytes along the gradient. Above 800 m the vegetation changes from the Steppical-Savanna to a Pioneer Formation influenced by fluvial processes. Pioneer Formation is in constant succession and is typical of unstable environments (Leite 1994). We observed along the gradient a marked decrease of the substrates available for colonization of bryophytes.

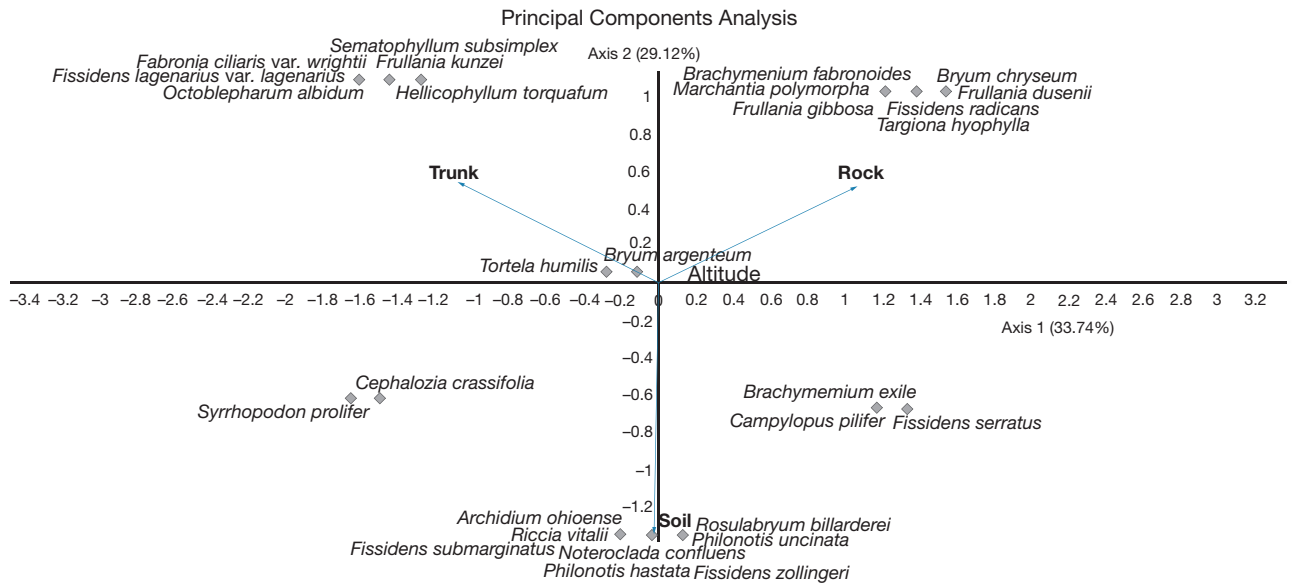


Fig. 5. — Principal Component Analysis (PCA) based on the substrates colonized along elevational gradient in Catimbau National Park.

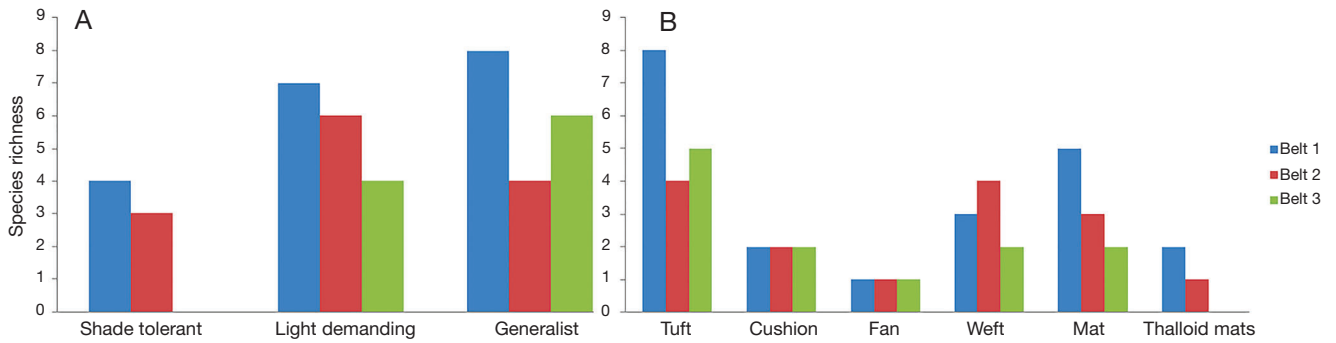


Fig. 6. — Bryophytes species distributions along an elevational gradient in Catimbau National Park according to life history traits: **A**, light requirements; **B**, life-forms.

TABLE 3. — Spearman (Rs) correlation table between life history traits showing that light demanding and life-forms are correlated with the species richness in base and top of elevational gradient, respectively. **Italic font** indicates Spearman value and **normal font** indicates Spearman coefficient (Rs). P-value in **bold** are significant ($p < 0.05$).

	Common sexual reproduction	Sexuality	Light requirement	Life-forms	B1	B2	B3
Common sexual reproduction	–	0.29095	0.6777	0.16056	0.12953	0.72681	0.24378
Sexuality	<i>–0.20684</i>	–	0.85852	0.2107	0.99435	0.74949	0.11929
Light requirement	<i>–0.082154</i>	<i>0.035285</i>	–	0.094813	0.00061095	0.74859	0.18566
Life-forms	<i>–0.27255</i>	<i>0.24407</i>	<i>0.32191</i>	–	0.63361	0.98418	0.026055
B1	<i>–0.29352</i>	<i>–0.001403</i>	<i>0.60725</i>	<i>0.094172</i>	–	0.22876	0.18654
B2	<i>–0.069096</i>	<i>–0.063163</i>	<i>–0.063397</i>	<i>0.0039257</i>	<i>0.23496</i>	–	0.87387
B3	<i>–0.22775</i>	<i>0.30124</i>	<i>0.25762</i>	<i>0.42004</i>	<i>0.25713</i>	<i>–0.03143</i>	–

Spitale (2016) and Santos *et al.* (2017) demonstrated substrate effects on bryophyte responses to elevational gradients in montane forests. The importance and strength of substrate-specificity is still being debated, with some studies providing considerable evidence for substrate-related effects (Söderstrom 1988), while others have not (Frego & Carleton 1995). We noted no preferences or substrate influences on bryophyte

community compositions along the elevational gradient in the Catimbau NP. Although the species encountered mainly colonized soil and rock, that colonization was related only to substrate availability. Those results are in agreement with other studies conducted in Brazilian dry forests – suggesting that bryophytes colonize most any available substrate in harsh environments (Silva *et al.* 2018a, b) and that microen-

TABLE 4. — Generalized Linear Models (GLM) testing variance along elevational gradient for spore size mean. For this model the spore size, dependent variable, occur homogeneously along the elevational belts, the explanatory variable.

	d.f.	SQ (Adj.)	QM (Adj.)	F-value	p-value
B1	1	287.5	287.5	0.1	0.757
B2	1	570.4	570.4	0.19	0.664
B3	1	2877.6	2877.6	0.98	0.332
Error	24	70569	2940.4	—	—
Shortage adjustment	3	9494.5	3164.8	1.09	0.376
Pure error	21	61074.5	2908.3	—	—
Total	27	73593.1	—	—	—

vironments are more variable in arid regions and influence community compositions more than substrate types. *Syagrus coronata* sheaths and rock cracks, for example, appeared to provide equivalent conditions for epiphytic species – with greater shading and higher concentrations of moisture than found in the surrounding matrix environment. That palm tree species is largely concentrated in belt 1 and accompanies the decrease of epiphytic species with increasing elevation.

BRYOPHYTE LIFE HISTORY TRAITS AND THE SPECIES COMPOSITION ALONG THE ELEVATION

We examined whether there was a dispersal limitations, and our outcomes do not indicate dispersal limitations. In line with the results of Patiño *et al.* (2014), bryophyte geographic reaches has no relationship to dispersive structures size.

Life-forms are closely related to environmental conditions (Mägdefrau 1982) and changes in light, temperature, and moisture conditions will alter life-form compositions (Stehn *et al.* 2010). Additionally, physiographic characteristics (such as topography) are usually associated with particular life-forms as they create specific climatic conditions (Matorell & Ezcurra 2002). Life-form diversity was found to be reduced along the elevational gradient, with drought-tolerant forms being mainly found at extreme elevations (e.g. tuft; Glime 2015). The local predominance of only drought-tolerant life forms will restrict the numbers of species in certain gradient belts, as drought-tolerant bryophytes species are considerably fewer in numbers than those occurring, for example, in evergreen tropical forests. On the other hand, bryophyte assemblages in low-altitude Caatinga sites containing both shade and full-sunlight specialists indicates that are better preserved and demonstrate humidity and temperature conditions adequate for the establishment of ecologically demanding species such as epiphytes.

Caatinga vegetation covers nearly 10% of the Brazilian territory (IBGE 2004), but its species diversity and richness have only been poorly studied – and certainly underestimated (Leal *et al.* 2005; Santos *et al.* 2011). Our results show that environmental conditions become more restrictive at higher elevations in harsh environments (above 750 m a.s.l.), decreasing species richness and concentrating drought-tolerant species. Life history traits related to the tolerance of species to stress conditions in dry forests represent excellent bioindicators of species richness and the environmental conditions along an

elevational gradient, as the differences in the compositions of assemblies along that gradient are not related to dispersal limitations of those species.

Acknowledgements

This research was funded by the Fundação de Amparo a Ciência e Tecnologia do Estado de Pernambuco (FACEPE). The authors thank the valuable contributions of anonymous reviewers.

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*Submitted on 6 November 2018;
accepted on 9 April 2019;
published on 5 November 2019.*

APPENDIX 1. — Life history traits values for the Catimbau National Park (Catimbau NP) bryophytes species. For the spore size we obtained the mean value in literature, however, for the species in which the literature only indicates the minimum and maximum values for their respective spores, we calculated the average from these values. For the sexuality attribute we have adopted three categories: monoicous (1), dioicous (2) and polyoicous (3); for the frequency of sexual reproduction, i.e., frequency of recording of the sporophyte in the field, and frequency of asexual reproduction, we adopt two categories: rare (1) and frequent (2); for the light requirement, we adopted the three usual categories: shade tolerant (1), light demanding (2) and generalist (3). Life-forms are signed by a representative number in increasing way according its importance by Glime (2015): 1 – Thalloid mats; 2 – Mat; 3 – Weft; 4 – Fan; 5 – Cushion; 6 – Tuft.

Life history traits						
Species	Common sexual reproduction	Sexuality	Spore size mean (μm)	Assexual reproduction	Light requeriment	Life-forms
<i>Archidium ohioense</i>	1	0	227	0	1	6
<i>Brachymenium fabronoides</i>	0	1	12	0	2	6
<i>Bryum argenteum</i>	1	1	12.5	1	2	5
<i>Bryum chryseum</i>	1	1	11.5	0	1	6
<i>Brachymenium exile</i>	0	1	9	1	2	6
<i>Campylopus pilifer</i>	0	1	13	1	2	6
<i>Fabronia ciliaris</i> var. <i>wrightii</i>	1	1	14.75	0	2	3
<i>Fissidens lagenarius</i> var. <i>lagenarius</i>	1	0	19	0	1	2
<i>Fissidens radicans</i>	1	0	18.5	0	1	2
<i>Fissidens serratus</i>	1	0	15	0	1	2
<i>Fissidens submarginatus</i>	1	0	17	0	1	2
<i>Fissidens zollingeri</i>	1	0	11.25	0	1	2
<i>Frullania duseii</i>	1	2	30	0	1	3
<i>Frullania gibbosa</i>	1	2	28	0	1	3
<i>Frullania kunzei</i>	1	2	29	0	1	3
<i>Fuscocephaloziopsis crassifolia</i>	0	1	121	0	0	4
<i>Helicophyllum torquatum</i>	1	0	31	0	1	4
<i>Marchantia polymorfa</i>	0	1	22.5	1	1	1
<i>Noteroclada confluens</i>	1	0	100	0	0	3
<i>Rosulabryum billarderei</i>	1	1	11.5	1	1	6
<i>Philonotis hastata</i>	0	2	22.5	0	0	6
<i>Philonotis uncinata</i>	1	2	24.5	0	0	6
<i>Octoblepharum albidum</i>	1	2	19.5	1	2	5
<i>Riccia vitalii</i>	1	2	122	1	1	1
<i>Sematophyllum subsimplex</i>	1	1	21.2	0	0	3
<i>Syrrophodon prolifer</i>	1	1	18	0	2	6
<i>Targiona hyophylla</i>	1	0	140	0	0	1
<i>Tortela humilis</i>	1	0	11.5	0	2	6