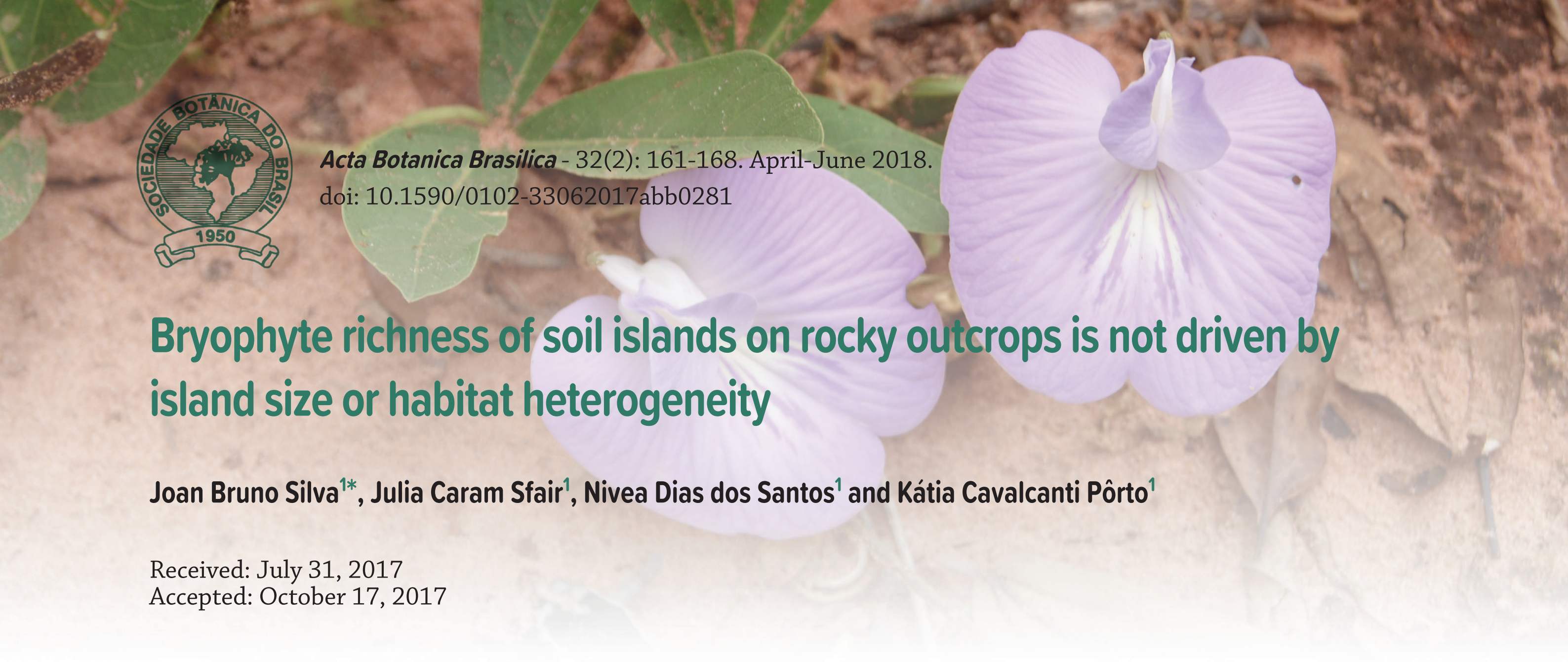

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Bryophyte richness of soil islands on rocky outcrops is not driven by island size or habitat heterogeneity

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ABSTRACT

The species-area relationship (SAR) is one of the oldest and most studied ecological models, having even served as the foundation of the Theory of Island Biogeography. Nevertheless, the relative importance of habitat heterogeneity to SAR remains poorly understood. Our aim was to test the relative importance of habitat heterogeneity to the SAR of bryophyte assemblages of soil islands of rocky outcrops in the semi-arid region of Brazil. We randomly selected 15 to 20 soil islands on each of four outcrops for a total of 59 soil islands, and calculated the area, mean depth, and number of substrates for each. We used Generalized Linear Models (GLM) to test the SAR with two models, one using species richness and another using life-form richness as the dependent variables. We found no positive relationship between area and habitat heterogeneity, nor any evidence of a SAR, such as a positive relationship between area and species or life-form richness neither between habitat heterogeneity and species richness. However, our findings did show that life-form richness is related to bryophyte species richness on the soil islands. We conclude by suggesting that not only can microclimate influence bryophyte richness, but opportunistic colonization by bryophytes is also important.

Keywords: Caatinga, inselbergs, Island Biogeography, microhabitat, species area relationship

Introduction

The species-area relationship (SAR) is one of the oldest (Arrhenius 1921; Gleason 1922) and most studied patterns in ecology (Lomolino 2000; Losos & Schluter 2000; Peay *et al*. 2007; Dengler 2009), and has served to provide foundations to ecological theories such as the Theory of Islands Biogeography (MacArthur & Wilson 1967) and the Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001). SAR predicts that larger areas have more species based on two non-exclusive processes: (1) larger areas have more structural complexity or environmental heterogeneity, which support more habitat-specialist species (MacArthur & Wilson 1967; Connor & McCoy 2001); and (2) larger areas have more resources, which permits greater population densities and, consequently, lower extinction rates (Connor & McCoy 2001; Lomolino 2004). Additionally, the larger target area of larger islands means they are more likely to intercept colonizers (Lomolino 1990). However, these processes imply that the environment is important for the stability and maintenance of populations and communities (Rosindell *et al*. 2012).

Although SAR was first developed for oceanic islands and continents (Lomolino 2000; Losos & Schluter 2000; Dengler 2009), it has also been applied to other ecosystems, such as trees (Löbel *et al*. 2006; Flores-Palacios & García-Franco 2006; Magalhães & Lopes 2015) and soil islands on

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rocky outcrops. Soil islands on rocky outcrops can harbor considerable plant diversity (Conceição *et al*. 2007; Silva *et al*. 2014). Each rocky outcrop can harbor hundreds of soil islands (Conceição *et al*. 2007) in which the number of colonizing plant species depends on many factors, such as island size and the depth of its soil. For instance, deeper soil islands can maintain more robust vascular plant species than shallower soil islands (Scarano 2002) due to greater moisture and space for root growth.

Among all the habitats of a rocky outcrop (e.g. crevices, depressions, soil islands), soil islands are the richest in bryophyte species. Bryophytes (liverworts, mosses and hornworts) are small plants without the ability to regulate water content, and thus are very sensitive to slight variations in environmental conditions (Delgadillo & Cárdenas 1990). In spite of this, bryophytes have broad geographical distributions that encompass conditions ranging from wet to dry (Frahm 1996). Their life-forms (i.e., functional groups associated with humidity and light conditions; Glime 2007; Bates 1982) are important for studies of ecology and conservation since they can reflect habitat heterogeneity in the availability of moisture and intensity of light (Oishi 2009). For instance, bryophyte life-forms related to arid environments are, from less to more tolerant, tuft, cushion, and mat (Gimingham & Birse 1957; Glime 2015). This suggests that the occurrence of a life-form, and thus a specific species, in an area is related to microhabitat conditions, such as moisture. Consequently, the degree of habitat heterogeneity or the number of substrates available can influence community assemblage (Jansová & Soldán 2006; Delgadillo *et al*. 2012), and life-form diversity. Therefore, since bryophytes depend on substrate conditions for colonization and successful establishment (Lloret & González-Mancebo 2011), their richness is expected to be related to the variety of microhabitats available more so than to island area.

Using bryophytes and soil islands on rocky outcrops in a xeric environment as models to study the processes acting on SAR, we: (1) tested the relationship between soil island area and habitat heterogeneity (i.e. number of substrates and soil depth); (2) tested the relationship between bryophyte richness, soil island area and habitat heterogeneity; and (3) investigated if life-form richness is related to island area or habitat heterogeneity. We hypothesized that bryophyte and life-form richness of soil islands are more related to the habitat heterogeneity than to island area.

Materials and methods

Study area

The present study was carried out on four rocky outcrops in the states of Paraíba and Pernambuco in northeastern Brazil (Fig. 1). The region experiences a pronounced dry season of more than six months (Wilby 2008), with mean annual precipitation ranging from 393 mm to 623 mm, and mean annual temperature ranging from 21.7 °C to 24.7 °C. All the studied outcrops were located in Brazilian Seasonally Dry Tropical Forest of the Caatinga domain. According to Silva *et al*. (2014), elevation does not influence species richness or community composition of bryophytes of xeric rocky outcrops, and so macroclimate variables were not considered in the present study.

Sampling design

Soil islands are considered soil agglomerations larger than 10 cm^2 in size, regardless of the presence of vascular plants (concept modified from Conceição *et al*. 2007), and surrounded by a rocky matrix. We selected 15 to 20 soil islands on each rocky outcrop that were colonized by bryophytes, for a total of 59 soil islands. The soil islands chosen were more than 20 m apart to ensure that each was statistically independent of each other. During the dry season we sampled all bryophyte species living on the soil, rocks, and live trunks of the islands following the standard techniques for collection and herbarium preservation of bryophytes described in Yano (1984) and Frahm (2003).

Each soil island had one or two substrate types present (rock or live trunk) other than the soil. The soil islands differed in size and shape (see Silva *et al*. 2014), and varied in soil depth (Tab. S1 in supplementary material). We calculated the area, mean depth, and number of substrates for each of the 59 soil islands as a proxy for habitat heterogeneity. To calculate the area of each soil island we took photos that encompassed the entire perimeter and analyzed them using ImageTool software (Dove 2002). For islands smaller than 100 cm^2, depth was estimated using a scaled ruler buried in the center of the island. For larger islands, depth was determined by calculating the mean soil depth for measurements made using a scaled ruler placed at three random points equally distant from the center. Although soil depth is likely not to act directly on species or life-form richness of bryophytes, since they can be fixed in shallow substrates on the order of millimeters, this variable serves as a proxy for density of vascular plants, which is higher in deeper soils (Scarano 2002), and which can increase the amount of available substrates for bryophytes.

Data analyses

In order to evaluate the independence of the explanatory variables (island area, soil depth and number of substrates) we calculated Spearman correlation coefficients (R_s) (Zar 2010). This analysis was also used to determine whether variation in species richness is accompanied by variation in the diversity of life-forms. Spearman correlation analysis assumes that the variables are normally distributed (Zar 2010), so the data were ln-transformed to achieve normality and homogeneity of variances (Ayres *et al*. 2007).

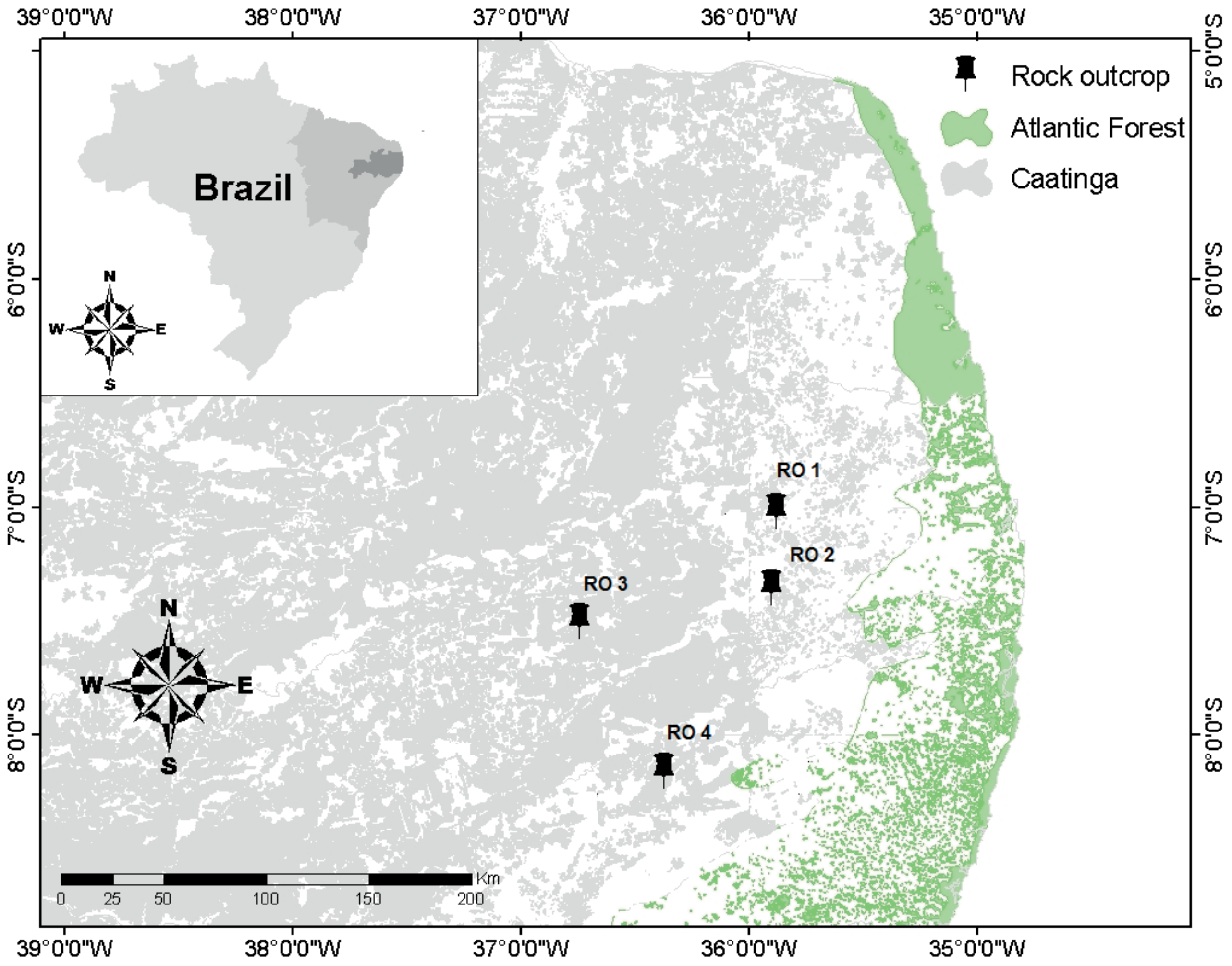

Figure 1. Rock outcrops (RO) in Brazilian dry forests (Caatinga), each of which had 15-20 soil islands selected for study. Map adapted from Silva & Pôrto (2016).

We used Generalized Linear Models (GLM) to test for a species-area relationship (SAR) (Zar 2010) for two models: one with bryophyte species richness as the dependent variable, and the other with bryophyte life-form richness as the dependent variable. We used the mean and standard deviation for evaluating the distribution of species and their life-forms (Gotelli & Ellison 2011). We exclude outliers from all analyses.

Results

We found 19 bryophyte species (14 mosses and five liverworts) (Tab. 1). Among the five life-forms recorded, tuft had the higher species richness, whereas only one species was found as a thalloid mat (Fig. 2). Bryophyte species richness varied among the islands from one to seven species, with approximately 70 % of the islands containing only one or two species (2 ± 0.9). The most diverse island containing five. Most of the islands had only one life-form present while around 30 % had two or more (1.0 ± 0.6).

Island area ranged from 0.3 m^2 to 36 m^2, with most being smaller than 10 m^2 (Fig. 3). Soil depth ranged from 0.5 to 20 cm, with most islands being shallow (i.e., less than 10 cm) (Fig. 2). Approximately 51 % (28) of the islands contained two substrates, while 49 % (26) had three.

Regarding the relationship between soil island area and habitat heterogeneity, only the number of substrate types was positively correlated with island area, although weakly so ($R_s = 0.40$; $p = 0.001$; Tab. 2). However, we found a positive correlation between species richness and life-form richness ($R_s = 0.60$; $p = 0.0008$). Nevertheless, our model using GLM with species richness as the dependent variable and soil island area as the explanatory variable and soil depth as covariate, and the same model using bryophyte life-form richness as the dependent variable, did not show a significant relationship (Tab. 3).

Table 1. Bryophyte species and their life-forms, according Mägdefrau (1982), on soil islands of rocky outcrops. The numbers between parentheses indicate, respectively, number of genera and species per family. We used Goffinet *et al*. (2009) and Crandall-Stotler *et al*. (2009) as the basis for classifying the moss and liverwort species, respectively.

Phylo/Family/species	Life-forms					
	Tuft	Cushion	Fan	Weft	Mat	Thalloid mats
BRYOPHYTE						
Archidiaceae (1/1)						
Archidium ohioense Schimp. ex Müll. Hal.	X					
Bartramiaceae (1/1)						
Philonotis hastata (Duby) Wijk et Margad.	X					
Bryaceae (2/3)						
Bryum argenteum Broth.		X				
Bryum exile Dozy & Molk.		X				
Rosulabryum billarderi (Schwägr.) J.R. Spence	X					
Calymperaceae (2/2)						
Octoblepharum albidum Hedw.		X				
Syrrhopodon prolifer (Brid.) Besch.	X					
Fissidentaceae (1/3)						
Fissidens lagenarius Mitt. var. *lagenarius*			X			
Fissidens serratus Müll. Hal.			X			
Fissidens submarginatus Brusch.			X			
Leucobryaceae (1/3)						
Campylopus pilifer Brid.	X					
Campylopus richardii Brid.	X					
Campylopus savannarum (Mull.Hal.) Mitt.	X					
Pottiaceae (1/1)						
Tortella humilis (Hedw.) Jenn.	X					
MARCHANTIOPHYTA						
Cephaloziellaceae (2/2)						
Cephalozia crassifolia (Lindenb. et Gottsche) Fulford				X		
Odontoschisma longiflorum (Taylor) Steph.				X		
Frullaniaceae (1/1)						
Frullania kunzei (Lehm. et Lindenb.) Lehm. et Lindenb.					X	
Lejeuneaceae (1/1)						
Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe					X	
Ricciaceae (1/1)						
Riccia vitalii Jovet-Ast						X

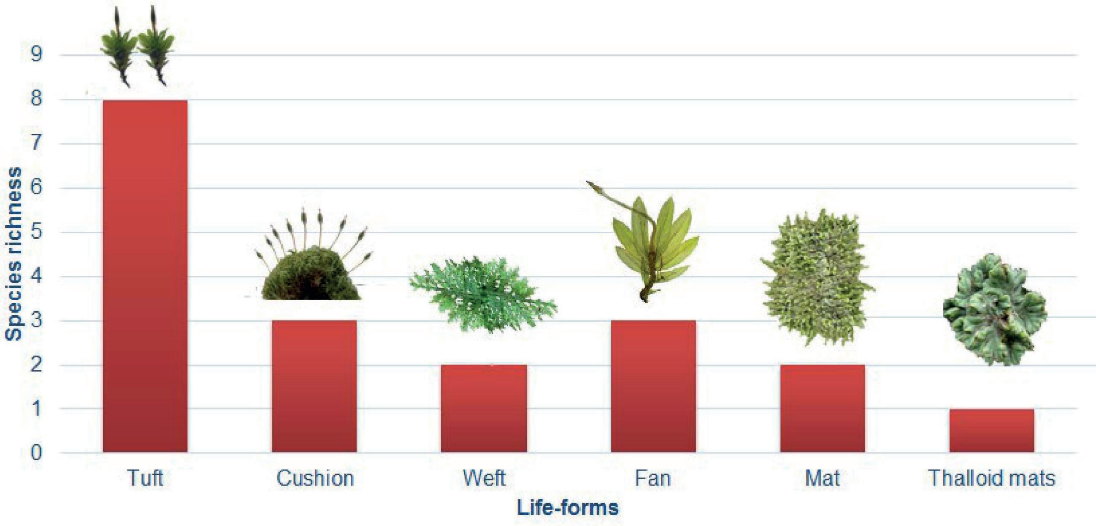

Figure 2. Distribution of life-forms among soil islands of rocky outcrops, with the life-forms with the largest number of species indicated. We used pictures from Mägdefrau (1982) and Bordin (2011).

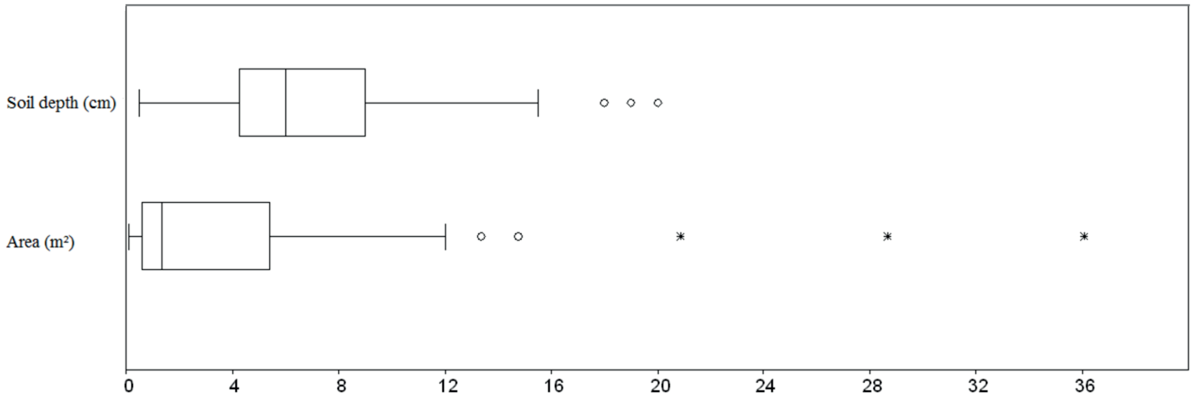

Figure 3. Box-plot illustrating the distribution of soil islands according to soil depth and island area, and the outliers.

Table 2. Spearman (Rs) correlation coefficients for microhabitat variables showing that the dependence on substrate varies according to area. P-values in italics, Spearman coefficients (Rs) not italicized.

	Area	Soil depth	Number of substrata
Area	-	*0.056*	*0.001*
Soil depth	0.245	–	*0.797*
Number of substrata	0.395	0.033	–

Table 3. Generalized Linear Models (GLM) testing for a species-area relationship (SAR) in two models: one with species richness as the dependent variable and the other with life-form richness as the dependent variable. DF = 54.

	SQ (Aj.)	QM (Aj.)	F-value	P-value
Species richness ~ soil island area + soil depth				
Area	0.66	0.66	0.49	0.49
Soil depth	25.02	0.71	0.53	0.94
Error	23.08	1.35		
Total	50.14			
Life-forms richness ~ soil island area + soil depth				
Area	0.61	0.61	1.70	0.20
Soil depth	16.22	0.46	1.28	0.29
Error	6.13	0.36		
Total	22.83			

Discussion

SAR is an important ecological theory due to its ability to predict species diversity (Harte *et al*. 2008). It has been corroborated for various biological groups including vascular plants (Flores-Palacios & García-Franco 2006; Magalhães & Lopes 2015) and bryophytes (Kimmerer & Driscoll 2000). Part of SAR can be explained by habitat heterogeneity, which can also vary according to island area (Coleman *et al*. 1982). Here, our results did not corroborate these previous findings, since neither species richness nor the richness of functional groups (i.e., life-forms) were related to soil island area or habitat heterogeneity. This is also inconsistent with other previous studies (Groot *et al*. 2012; Patiño *et al*. 2013), in which the contribution of environmental heterogeneity was more important than factors such as degree of isolation of an area. Thus, our results seem to indicate that species richness of bryophyte communities of soil islands in arid environments may be related to other processes not related to area and habitat heterogeneity, such as limitations to dispersal.

Bryophytes have greater species richness in wet tropical forest than in dry tropical forests (see Delgadillo & Cárdenas 1990; Pôrto *et al*. 1994; Pôrto & Bezerra 1996; Glime 2007; Silva & Germano 2013; Silva *et al*. 2014). Despite soil islands being one of the richest microhabitats of rocky outcrops of xeric environments (Silva *et al*. 2014), the richness of bryophytes is naturally low in these habitats (Silva & Germano 2013; Silva *et al*. 2014), probably because of the low tolerance of bryophytes to water deficit. This low level of species richness could decrease the predictive power of SAR (Patiño *et al*. 2014), but this was not corroborated by other studies (e.g. Diamond & May 1977; Maly & Doolittle 1977; Abbott & Black 1980). This further reinforces the hypothesis that other variables not related to island area or heterogeneity can influence bryophyte richness in the study area. In fact, Kimmerer & Driscoll (2000) found that soil island size, isolation and microhabitat heterogeneity had no influence on bryophyte richness, and suggested that species richness may be the result of intrinsic traits, such as population level processes that govern dispersal and establishment.

Bryophyte spores are dispersed passively, which, according to the Target Area Hypothesis, should favor their interception by islands with larger areas (Lomolino 1990). However, many factors influence soil islands, such as the amount of litter. Larger islands are often shallow and do not support shrub or tree species, thus decreasing the amount of potentially colonizable substrates. In addition, shallow islands often have greater exposure to high solar irradiation, thus intensifying the influence of this environmental filter on the island and decreasing the number of bryophyte species.

We argue that bryophytes can respond to some environmental constraints, such as micro-climatic variables, with (1) taxon-specific life-history traits (e.g. light demands; Drakare *et al*. 2006; Franzén *et al*. 2012; Gerstner *et al*. 2014); and (2) their long-distance dispersal capacity (LDD) (Schaefer 2011). Bryophyte richness may be more related to the variety of microhabitats on an island than to island area because they are very small plants that depend on substrate conditions for colonization (Lloret & González-Mancebo 2011). This importance of local conditions is further supported, for example, by Jansová & Sondán (2006), who showed that the species composition of bryophytes on dead trunks was related to local conditions such as humidity, diameter of the trunk and texture of the bark. Some species colonize specific substrates (Tng *et al*. 2009), such as *Campylopus pilifer*, a species of moss typically recorded on soil (Frahm 2002; Imbassahy *et al*. 2009), which is a drier micro-environment than trunks. Nevertheless, in the studied area, the soil islands usually support shrubs or small trees and their litterfall production limits the establishment of bryophytes on the soil. Thus, *C. pilifer* was repeatedly recorded as an epiphyte, suggesting that although there are substrate options, including preferred substrates, the condition of each substrate is more important to it being colonized than simply their presence in the habitat.

We expected to find a positive relationship between soil island area and bryophyte species and life-form richness because larger areas would be more heterogeneous (MacArthur & Wilson 1967; Coleman *et al*. 1982), and thus possess a more diverse array of habitat conditions for bryophyte establishment. Among the habitat heterogeneity variables studied, soil depth could be very important for bryophyte richness, since deeper soils support fixation of more robust trees and shrubby species (Scarano 2002; Oliveira *et al*. 2004) and because these islands have higher soil humidity, more shadows and greater protection against desiccating winds by vascular flora than shallower soils. Therefore, the higher humidity of deeper soils would favor conditions for vascular plant growth (Keever *et al*. 1951). In our study most of the deeper islands (50 %) had small areas (≤ 5 m²) – which is consistent with other studies (e.g. Oliveira & Godoy 2007) – because these islands were formed by soil deposition in deep depressions in the rock, in contrast to other soil islands that were formed by soil deposition in shallow depressions. These shallow islands are constantly undergoing separation and unification, a process that increases or decreases island area, but not soil depth. Thus, these shallower islands are very dynamic for bryophyte colonization, resulting in a high degree of variation in the number of species.

Although our results did not reveal a significant relationship with the assumptions of SAR, we did identify a significant positive relationship between species richness and richness of life-forms. Oishi (2009) found that life-form is a good predictor of species richness. Different life-forms (i.e. different functional groups) mean different strategies for acquiring resources such as water and light (Frey & Kürschner 1995; Kürschner *et al*. 1998), the main environmental filters for bryophytes on soil islands in xeric environments (Silva *et al*. 2017). Even in an environment with pronounced environmental filters, such as soil islands on rocky outcrops in the Caatinga, bryophytes may exhibit this niche partitioning in order to avoid competition. On the other hand, the dry environment of the Caatinga favors the development of life-forms such as tuft and cushion, which are functionally the most important life-forms for species of bryophytes (Glime 2007). This relationship is due to the fact that several species can grow the same life-form and use the same strategy to access water and protect against heat stroke.

In a recent study, Patiño *et al*. (2014) showed that SAR depends not only on neutral factors, but also on characteristics intrinsic to the organism, such as dispersion capacity, which involves specialized sexual diaspore production and frequency of sexual reproduction. Despite finding no SAR and no relationship between richness and environmental heterogeneity in the studied area, it is probable that intrinsic characteristics of bryophytes blur the effect of environmental factors on richness. Not only are the effects of micro-climatic factors likely to be important, such as temperature and air moisture, but opportunistic colonization is also probably an important factor influencing species richness of bryophytes in soil islands in xeric environments.

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