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Research Article

Richness and abundance of *Aechmea* and *Hohenbergia* (Bromeliaceae) in forest fragments and shade cocoa plantations in two contrasting landscapes in southern Bahia, Brazil

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Abstract

The intensification of agricultural activity can have profound impacts on biodiversity. We evaluated the influence of the landscape's percentage of forest cover and shaded cocoa plantations on the community of zoochorous bromeliads in southern Bahia, Brazil. We selected two contrasting landscapes, one dominated by Atlantic tropical rainforest and the other by traditional cocoa plantations. In each landscape we sampled three forest fragments and three areas of cocoa plantation, where we conducted a survey of epiphytic bromeliads of the genera *Aechmea* and *Hohenbergia* in eight plots of 400 m^2 in each area. The number of trees differed between landscapes and habitats, and was higher in forest fragments than in shade cocoa plantations, but the number of phorophytes was similar between landscapes and habitats. Highest richness of *Aechmea* and *Hohenbergia* species was found in forest fragments in landscapes where forests are predominant. Contrary to expectations, the richness in the other areas was relatively low, and extremely low in the landscape dominated by cocoa plantations, ranging from zero to four species per fragment. Bromeliad abundance was not different among landscapes and habitats, but the shade cocoa plantations located in predominant agroforest landscape showed the higher number of stands. Moreover, the species found in the cocoa plantations were more drought-tolerant species. These results suggest that the conservation of species of these genera depends on factors such as the conservation status of each forest fragment and the microclimatic alterations in the habitats, and not only on the percentage of forest in the landscape *per se*.

Keywords: Atlantic Forest, Anthropogenic disturbances, Bromeliads, Forest Cover.

Resumo

Considerando a intensificação da atividade agrícola e o seu impacto sobre a biodiversidade, este estudo avaliou a influência da quantidade de floresta e agroflorestas de cacau sobre a comunidade de bromélias zoocóricas no sul da Bahia. Para isso, foram selecionadas duas paisagens contrastantes, uma dominada por floresta e a outra em que as plantações de cacau são predominantes. Em cada paisagem foram amostrados três fragmentos florestais e três plantações de cacau e realizado um levantamento das espécies de bromélias dos gêneros *Aechmea* e *Hohenbergia* em oito parcelas de 400 m^2 em cada área. O número de árvores foi diferente entre as paisagens e os habitats, sendo maior nos fragmentos florestais do que nas áreas de plantio, ao contrário do número de forófitos que não diferiu entre as paisagens ou habitats avaliados. Foi encontrada maior riqueza de espécies de *Aechmea* e *Hohenbergia* nos fragmentos florestais da paisagem onde as florestas são predominantes. Ao contrário do esperado nas outras áreas, a riqueza foi relativamente baixa e nos fragmentos florestais da paisagem dominada por cultivo foi extremamente baixa, variando de zero a quatro espécies por fragmento. A abundância dos grupos de bromélias não diferiu entre as paisagens e habitats, embora as cabrucas da paisagem predominantemente agrícola tenham apresentado o maior número de grupos. As espécies encontradas nas plantações de cacau compreenderam espécies mais tolerantes à seca. Estes resultados sugerem que a conservação de espécies desses gêneros depende de fatores como a o estado de conservação dos fragmentos florestais e alterações microclimáticas nos habitats e não apenas do montante de floresta na paisagem *per se*.

Palavras-chave: Mata Atlântica, Bromélias, Cobertura Florestal, Distúrbios Antrópicos

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Introduction

A large proportion of the surface of the planet is undergoing rapid and dramatic changes due to human activities [1]. The intensification of agricultural practice is a major cause of land use change and of biodiversity loss [2]. In many tropical landscapes, agroforestry systems are the ecosystems that most resemble forests [3-6]. Agroforestry can help both rural livelihoods and biodiversity conservation [4], as well as mitigating changes in temperature and precipitation [7]. Together, coffee and cocoa are the most common crops grown under shade trees, a technique used to reduce the physiological stress affecting the longevity of these plants [8]. In Brazil, the region with the largest area of cocoa cultivation is the south of Bahia, with approximately 400,000 hectares [9].

The Atlantic Forest of southern Bahia is a tropical rainforest, with high diversity of plant and animal species and high levels of endemism [10, 11]. It is one of the most preserved areas and still presents large patches of original vegetation, compared to the rest of the biome [12]. This characteristic is partly due to the cultivation of cocoa (*Theobroma cacao*), the main local agricultural product. Evidence has shown that cocoa agroforestry areas are used as habitat for many species of plants and animals, including forest species [3, 13]. The cultivation of cocoa in this region is traditionally performed by the thinning of the understory while maintaining part of the native trees to shade the crop, a system that is locally known as *cabruca* [14]. The shaded cocoa plantations also harbor trees of comercial value that currently are rarely found in forest remnants [15].

Although shaded cocoa plantations have the potential to maintain part of the local biodiversity [16], this capacity may be influenced by landscape scale [17, 18]. The hypothesis that the percentage of forest cover in the landscape influences the maintenance of taxonomic groups was previously tested for birds, bats, frogs, and ferns [17, 18]. In those studies, it was found that the role of shaded cocoa plantations as supporters of biodiversity varies according to the landscape in which the plantations are located. Bomfim et al. [19] also found the same pattern for fruit consumption by birds, and suggested that landscapes with higher percentage of forest cover had higher potential for maintaining ecological processes than landscapes with less forest cover.

A large proportion of the plant diversity in neotropical areas is represented by vascular epiphytes [20-23]. In traditional plantations, part of the epiphytic flora can be preserved because some of the large trees are kept for shading the crop [24, 25]. There is evidence that in modified habitats, the structure and diversity of the epiphytic communities differ from those of undisturbed forests [26-32]. These changes are usually attributed to microclimatic conditions such as light and humidity [33, 34] and factors related to seed dispersal [35]. However, the influence of the percentage of forest cover in the landscape was never tested for epiphytic plants, which are sensitive to habitat modifications [36, 37].

We therefore evaluated the influence of two contrasting landscapes on the richness and abundance of epiphytic species of *Aechmea* and *Hohenbergia* in southern Bahia. The first is dominated by Atlantic forest, in which a Conservation Unit of approximately 9,000 ha is located, and the second is predominantly agricultural, where the few remaining forests (5% of the landscape) are immersed in cocoa plantations [17]. The two studied genera are represented by zoochorous species, which are present in forest fragments and shaded cocoa plantations, and have a large number of species endemic to the state of Bahia [38]. Specifically, the following questions were addressed: (i) How do the richness and abundance of the species of both genera vary between the two landscapes? and (ii) Does the species composition differ between the two landscapes? Due to anthropogenic alterations such as fragmentation, removal of large trees, and the possible decrease in diversity of seed dispersers, we expected that the landscape with the greatest amount of forests would have the highest diversity of these bromeliads. We also expected that within each landscape, forest fragments would present higher richness due to less microclimatic change and loss of microhabitats than shaded cocoa plantations. On the other hand, due to the high level of incident light and the availability of large phorophytes, we expected that the abundance of some xerotolerant species within both genera would be higher in areas of cocoa plantations.

Methodos

Study area

The study was conducted in the cocoa plantation region of southern Bahia, northeastern Brazil, where two contrasting landscapes were selected (Fig.1): one being predominantly forest (LA) and the other predominantly cocoa plantations (LB). In landscape A is located the Serra do Conduru State Park (SCSP), which is a Conservation Unit established in 1997. It has an area of approximately 9,000 hectares and includes the cities of Ilhéus, Itacaré, and Uruçuca [39]. The SCSP is composed of a mosaic of forests in different successional stages, including areas of forest in advanced regeneration stage [40]. The SCSP is immersed in a matrix of shaded cocoa plantations, rubber tree plantations, banana plantations, pasture, and other crops.

In the landscape of the city of Ilhéus (LB), shaded cocoa plantations are prevalent, occupying soils with medium to high fertility [42]. In addition, there are several cocoa plantations shaded by exotic species of the genus *Erythrina* [15]. The shade cocoa plantations from landscape B are more than 50 years old, older than those of landscape A, which are less than 20 years old (J. G. Z. Calixto, pers. com.). In landscape B, the few remaining forest fragments (1-300 ha) cover approximately 4.8% of the landscape and are located far from each other, being immersed in large areas of cocoa plantations [17]. This landscape is considered relictual due to the scarcity of forest cover in a matrix of agricultural habitat (*sensu* [43]).

Aechmea and Hohenbergia (Bromeliaceae)

The two studied genera belong to the subfamily Bromelioideae, which comprises 35 genera and approximately 940 species [44], all of them producing fleshy fruits dispersed by animals [45, 46]. *Aechmea* is the largest genus in the subfamily, with about 276 species distributed in tropical

America [44, 45]. In Brazil, it is represented by about 136 species, 55 of which are endemic to the state of Bahia [38]. The species are distributed in eight subgenera, and the pattern of inflorescence is one of the most variable in the subfamily [45]. The genus *Hohenbergia* comprises about 65 species [44] distributed from Central America to Brazil, and most of the species, 21 of which are endemic [38], are found in the state of Bahia [47].

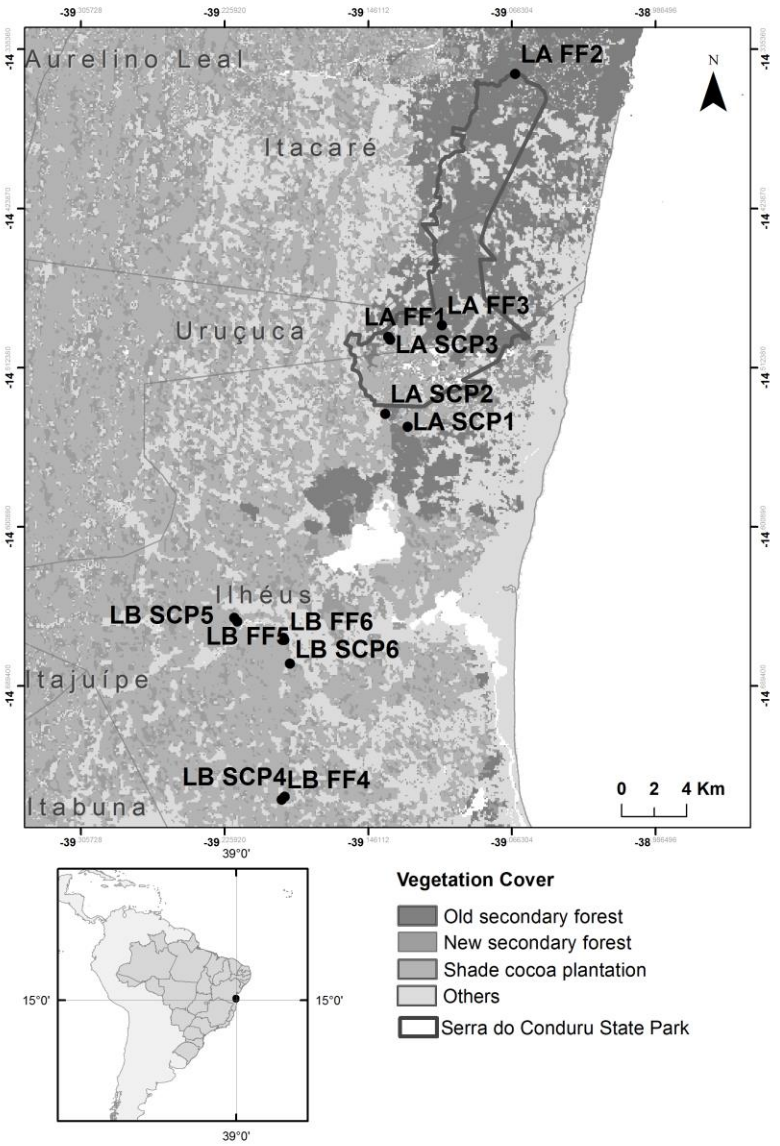

Fig.1. Study map showing the two landscapes evaluated: landscape A (LA), located in the north and dominated by forest fragments and landscape B (LB) located in the south and dominated by shade cocoa plantations. The circles represent the sample sites within each landscape (FF – forest fragment; SCP – shade cocoa plantation). Modified from [41].

Studies of bromeliad fruit consumption are scarce [48, 49]. Some studies in southern Bahia identified the golden-headed lion tamarin (*Leontopithecus chrysomelas*) as one of the dispersers of the genus *Aechmea* [50-52]. However, considering that this genus has different types of infructescences [39, 45, 46], it is possible that other animals, such as birds, consume their fruits. As far as we know, there are no studies on frugivory with the genus *Hohenbergia*; however, the type of infructescence and fruit size indicate that the dispersion is probably carried out mainly by birds.

Sampling design

In each landscape, we selected three areas of shaded cocoa plantation and three forest fragments, where a transect of 900 meters was set up, excluding 80 meters from the edge, in order to minimize potential microclimate interferences. Along each transect, we installed eight plots of 20 x 20m, at least 100 meters apart from each other. The plots were assembled around a large tree with circumference at breast height (CBH) ≥ 100 cm (adapted from [53]). These trees are rich in epiphytes due to their large and complex canopy, and they were available for epiphyte colonization for a long period of time [30, 54, 55]. Thus, it was possible to maximize the amount of recorded information about *Aechmea* and *Hohenbergia*. In each plot, all trees with CBH ≥ 25 cm were counted and marked, and their diameter at breast height was measured.

We recorded the abundance of each bromeliad species by counting the number of stands in all branches and trunks of phorophytes. The stands were defined as any cluster of rosettes of bromeliads, whether they were formed by one or by several rosettes [56]. The recording of the stands was conducted using binoculars. All collected plants were deposited in the Herbarium of the State University of Santa Cruz (HUESC).

Data analyses

We performed permutational multivariate analyses of variance (PERMANOVA) to compare the number of trees and phorophytes, the mean CBH of the trees and phorophytes, and the mean number of species and stands of *Aechmea* and *Hohenbergia* between the landscapes and habitats (forest fragments and shaded cocoa plantations) in the studied sites. We performed the analyses in the software R [57].

We constructed diversity profiles to assess diversity in the studied sites, using the Rényi series in order to compare the communities. For the Parameter $\alpha = 0$, the value of diversity is equal to the number of species in the landscape. For α trending to 1, the value of diversity is equivalent to the Shannon index; for $\alpha = 2$, the value is equal to that obtained by the inverse of the Simpson index (1/D); and for high values of α, the weights for rare species decrease and the value is equal to the Berger-Parker index [58].

We analyzed the similarity between the habitats of *cabruca* and forest fragments of the landscapes A and B with cluster analysis, using the Jaccard similarity coefficient. The cluster analysis was processed by the UPGMA method (Unweighted Pair Group Method with Arithmetic Mean) [58].

Results

Trees and phorophytes

The forest fragments of landscape A had 54.8% (N=1,222) of the total of the sampled trees (N=2,229), and the trees of the shaded cocoa plantations of this landscape represented only 3.6% (N=81). In landscape B, the trees of the forest fragments accounted for 35.7% (N=795), and the trees of the shaded cocoa plantations represented 5.9% (N=131) of the total. The mean number of trees differed between the landscapes and between the habitats within each landscape. There was also an interaction between habitat and landscape (Table 1, 2; Fig. 2).

Table 1. Mean number of trees and phorophytes, DBH of trees and phorophytes, and number of species and groups of *Aechmea* and *Hohenbergia* in two contrasting landscapes (LA and LB) in southern Bahia, Brazil (SCP=shade cacoa plantation, and FF=forest fragment).

	LAFF	LASCP	LBFF	LBSCP
Nº trees	407.33±36.53	27±1	265±19.92	43.67±8.08
Nº phorophytes	45±25.24	8.67±5.68	2.33±2.08	20.67±5.51
Trees CBH (cm)	53.09±2.66	148.17±26.67	54.31±5.36	135.62±17.15
Phorophytes CBH (cm)	87.96±18.64	180.67±11.37	110.17±95.42	202.83±20.05
Species *(Aechmea and Hohenbergia)*	9.33±3.78	4.33±1.52	1.67±1.53	4.33±0.58
Groups (*Aechmea and Hohenbergia)*	63.33±36.47	19.33±12.89	3±2.64	70.67±23.09

Of the total of the sampled trees in the forest fragments of landscape A, 11.05% were phorophytes (N=135), whereas in the shaded cocoa plantations, the phorophytes accounted for 32.1% (N=26) of the trees. In landscape B, the phorophytes present in the fragments represented 0.88% (N=7) of the trees in this habitat, whereas, in the cocoa agroforests, they represented 47.33% (N=62) of the trees. The number of phorophytes did not differ statistically between the landscapes nor between the habitats. However, there was an interaction between habitat and landscape, indicating that the number of phorophytes in the forest fragments and shaded cocoa plantations was dependent on the landscape in which they were inserted (Table 2, Fig. 2).

Table 2. Permutational multivariate analyses of variance (PERMANOVA) on the mean number of trees and phorophytes, mean CBH of trees and phorophytes, and mean number of bromeliad species and groups in the landscape, habitat (forest fragment x shade cocoa plantation, and the interaction between factors (landscape x habitat). * P<0.05

	Landscape	Habitat	Habitat*Landscape
Nº tress	P<0.01*	P<0.01*	P<0.01*
Nº phorophytes	P=0.080	P=0.273	P<0.01*
CBH trees	P=0.560	P<0.01*	P=0.481
CBH phorophytes	P=0.463	P=0.012*	P=0.999
Nº species	P=0.016*	P=0.384	P=0.016*
Nº groups	P=0.738	P=0.390	P<0.01*

The CBH of the trees and phorophytes did not differ between landscapes A and B. However, there were differences between the analyzed habitats; both trees and phorophytes were larger in the shaded cocoa plantations than in the forest fragments (Table 1, Table 2). There was no interaction between habitat and landscape in relation to the CBH of trees and phorophytes (Table 2, Fig. 2).

Richness and abundance of Aechmea and Hohenbergia

We sampled 20 bromeliad species in the studied areas (see Appendix 1), of which 80% belong to *Aechmea* (S=16) and 20% to *Hohenbergia* (S=4). Most of the 469 recorded stands belong to *Aechmea* (66.5%, S=305), and the highest abundances occurred for *A.* cf. *lingulata* and *H. blanchetii* with 157 (33.5%) and 88 stands (18.8%), respectively.

The forest fragments of landscape A presented the highest species richness (S = 16), and only 4 species in 9 stands were recorded in the fragments of landscape B (Table 1). The mean species richness differed between the landscapes (Table 2), and there was no difference between the forest fragments and plantations within each of the landscapes; however, there was a significant interaction between habitat and landscape.

Similarly, the fragments of landscape A presented more stands of bromeliads, ca. of 41% (N=190), than the fragments of landscape B that presented only 2% (N=9) of the total of recorded stands. Regarding shaded cocoa plantations, the number of stands of bromeliads was higher in landscape B, with approximately 45% (N=212) than in landscape A, with 12% (n=58) of the total of stands (Table 1). No difference was found between landscapes A and B nor between the habitats. However, there was an interaction between habitat and landscape (Table 1, 2; Fig. 2).

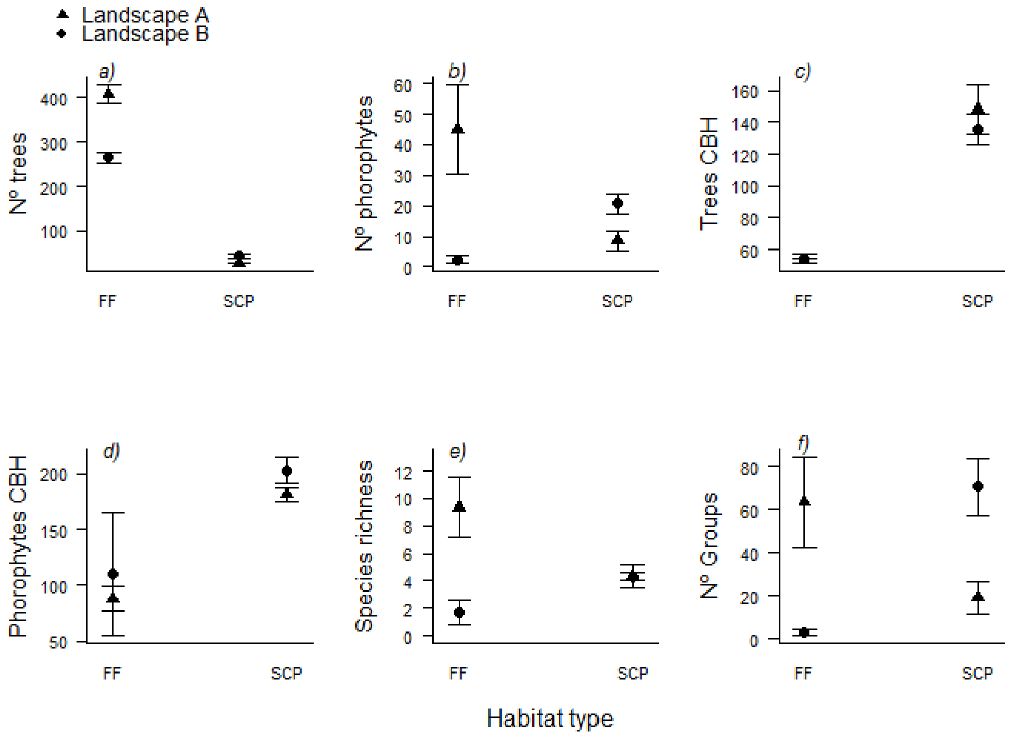

Fig.2. Comparisons between the mean number of trees (a) and phorophytes (b), mean CBH of trees (c) and phorophytes (d), and the mean number of species (e) and stands (f) of *Aechmea* and *Hohenbergia* in forest fragments (FF) and shade cocoa plantations (SCP) in landscape A and B. Vertical bars represent the standard error.

The analysis of similarity showed the formation of two groups, with forest fragments of landscape A dominated by forests apart from all the other areas. All cocoa agroforestry areas (landscapes A and B) and forest fragments of landscape B were clustered with similarity index around 50% (Fig. 3).

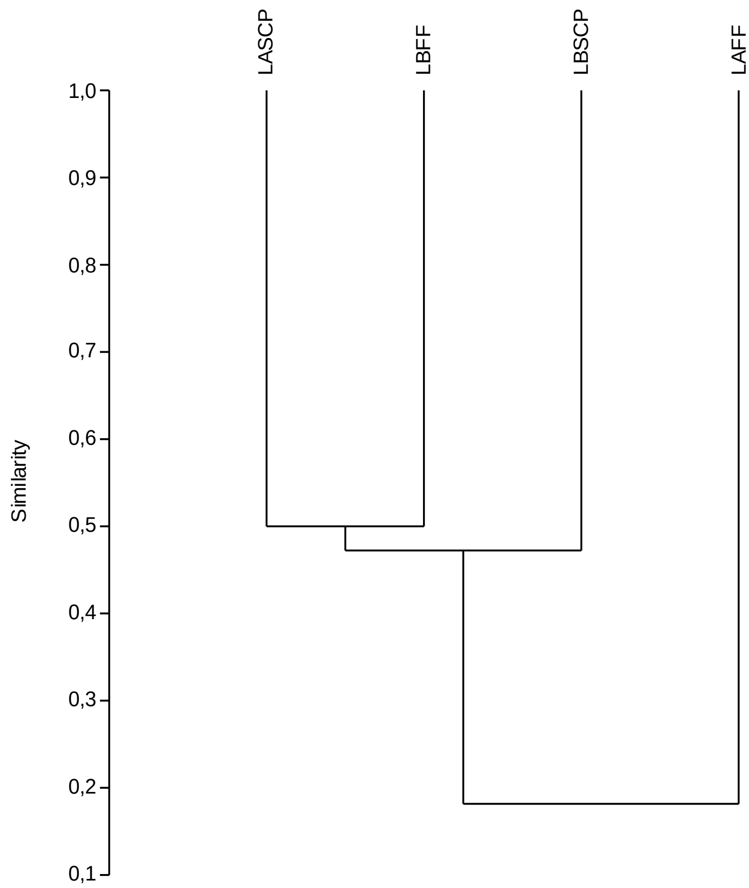

Fig.3. Cluster analysis using Jaccard similarity coefficient among the habitats (forest fragment and shade cocoa plantations) and landscapes A and B (LASCP = landscape A shade cocoa plantation, LAFF = landscape A forest fragment, LBSCP = landscape B shade cocoa plantation, LBFF = landscape B forest fragment). The values were generated after 10000 randomizations.

The analysis of the diversity profile also showed that the fragments of landscape A were the most diverse, regardless of the diversity index (Fig. 4). The least diverse habitat corresponded to the forest fragments in landscape B, independently of the value of alpha. The shaded cocoa plantations of landscape A were more diverse than those of landscape B (Fig. 4).

In landscape A, dominated by forests, approximately 60% of species that occurred in the cocoa plantations were also present in the forest fragments (Fig. 5; Appendix 1). These species represented approximately 30% of the total of the species in the fragments (Fig. 5; Appendix 1). In landscape B, species composition is similar between the habitats; however, the abundance of species in the shaded cocoa plantions was approximately 20 times higher than in the forest fragments (Fig. 5; Appendix 1).

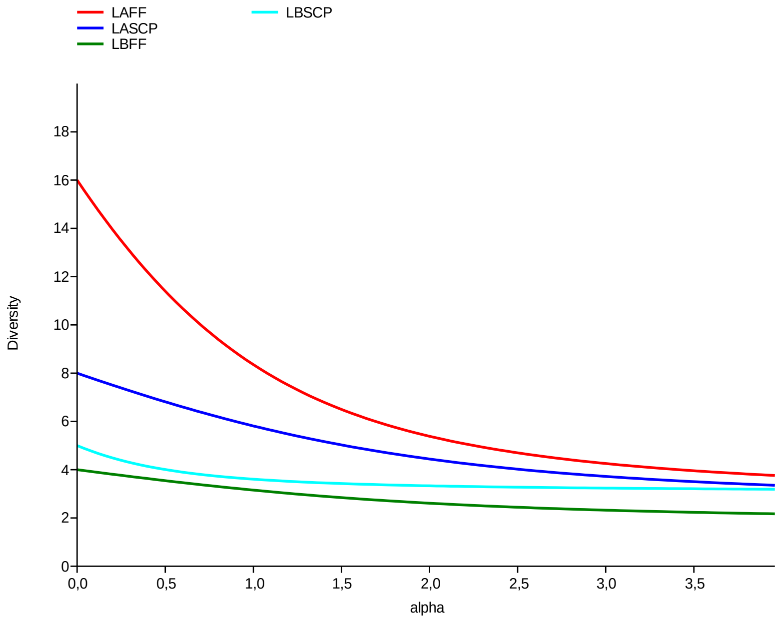

Fig.4. Diversity profile using the Rényi series representing the communities located in forest fragments and shade cocoa plantations from landscape A and B in southern Bahia, Brazil (LASCP = landscape A shade cocoa plantation, LAFF = landscape A forest fragment, LBSCP = landscape B shade cocoa plantation, LBFF = landscape B forest fragment).

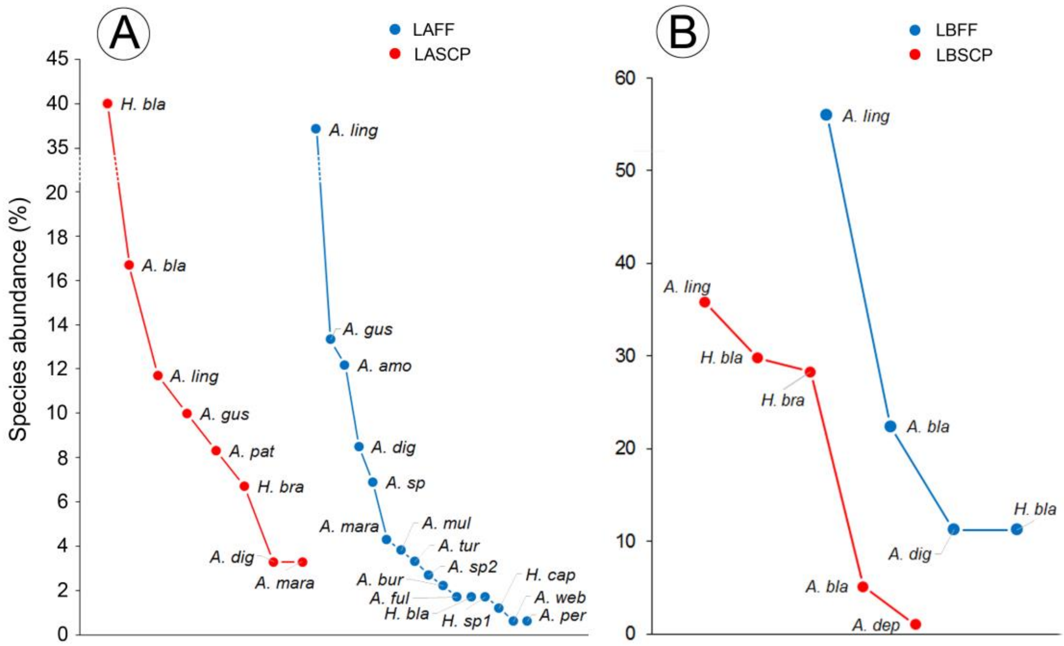

Fig. 5. Rank abundance curve of the bromeliad species from the forest fragments and shade cocoa plantations in each landscape (LASCP = landscape A shade cocoa plantation, LAFF = landscape A forest fragment, LBSCP = landscape B shade cocoa plantation, LBFF = landscape B forest fragment). A. ling- *Aechmea* cf. *lingulata*, H. bla- *Hohenbergia blanchetii*, H. bra- *Hohenbergia brachycephala*, A. bla- *Aechmea blanchetiana*, A. dep- *Aechmea depressa*, A. dig- *Aechmea digitatta*, A. gus- *Aechmea gustavoi*, A. amo- *Aechmea amorimii*, A. sp- *Aechmea sp1*, A. mara- *Aechmea marauensis*, A. mul- *Aechmea multiflora*, A. tur- *Aechmea turbinocalyx*, A. sp2- *Aechmea* sp2, A. bur- *Aechmea burle-marxii*, A. ful- *Aechmea fulgens*, H. sp1- *Hohenbergia* sp1, H. cap- *Hohenbergia captata*, A. web- *Aechmea weberi*, A. per- *Aechmea perforata*, A. pat- *Aechmea patentissima*.

Discussion

Trees and phorophytes

The highest number of trees found in forest fragments compared to cocoa plantations was expected, considering that in the traditional shaded cocoa plantations, most of the smaller trees characteristic of the forest understory are cut for cultivation management [15]. The difference in the mean number of trees between the landscapes is mainly due to the higher number of trees in the forest fragments of landscape A dominated by forests, which corresponds to approximately twice the number of individuals present in the fragments of landscape B dominated by shaded cocoa plantations. The lower number of trees in the fragments of landscape B is partly due to timber exploitation, to which the region was subjected from the 1970s on [15]. First, timber was cut for the cultivation of cocoa itself, and later, after the collapse of cocoa cultivation due to the fungus *Moniliophthora perniciosa*, deforestation occurred for timber sales, establishment of pastures, and crop diversification [59]. It is possible that selective logging coupled with deforestation made the forest remnants in the region more vulnerable to an intensive edge effect, as observed by Laurance et al. ([60, 61]) for Amazon forests.

It is noteworthy that the interaction between habitat and landscape was due to the higher number of trees in the fragments of landscape A than in landscape B, in contrast to trees in the plantations which had the opposite pattern. We suggest that differences in management practices might explain the pattern observed. Cocoa plantations in landscape B are older [42], with longer availability for the arrival of propagules and subsequent colonization [62, 63]. These plantations are poorly managed, being less sparse than the plantations of landscape A, which receive intense management and less intense shading of the crop (V. Souza, pers. obs.) Moreover, in landscape B, some farmers use natural regeneration of native tree species in the plantations to assist in shading the crop [64].

Although differences were found in the number of trees between the landscapes and between the habitats within each landscape, the number of phorophytes was not different. This suggests that there is an environmental filter – which was not evaluated in this study – influencing the colonization of the studied habitats by the bromeliads of both genera. Considering that shaded cocoa cultivation is characterized by the selection of tall trees with large diameters to remain in the culture [14], as expected, the cocoa plantations presented trees with larger circumference at breast height than those of forest fragments. The phorophytes in the former habitat also followed the same pattern of circumference at breast height, since they represent the trees available for bromeliads colonization in the cocoa plantations.

Abundance and richness of Aechmea and Hohenbergia

The species richness of *Aechmea* and *Hohenbergia* was much higher in the forest fragments in the landscape A. Contrary to expectations, all other areas were relatively similar in relation to the species diversity. It is noteworthy that the richness in these areas was relatively low and, in the fragments of the landscape dominated by shaded cocoa plantations, it was extremely low, ranging from zero to four species per fragment.

The influence of the landscape on species richness, and the effect of the interaction between habitat and landscape on richness and abundance of bromeliads suggest that, although the species of *Aechmea* and *Hohenbergia* may occur in habitats embedded in a predominantly forested landscape, the formation of stands of these bromeliads and consequent conservation of the species only occur under certain specific microclimatic conditions, not evaluated here (e.g. vapor pressure deficit [65]). Further investigation of the distance between fragments and large patches of forest and/or the type of cocoa plantation management (see [24]), and how they influence these specific microclimatic conditions, may elucidate which variables contribute more to conservation of the species. Our results also contradict one of our initial hypotheses and contrast with previous studies conducted in the region for different taxonomic groups such as birds, bats [17, 18], ferns, frogs, and lizards [18] in which the amount of forest in the landscape was the predominant factor explaining the richness of these groups.

Another factor that may explain the higher number of species found in the fragments of landscape A is the conservation status of these areas, which are located in the SCSP. It is a Conservation Unit protected by law since 1997 [39], and has experienced a decrease in illegal logging that caused loss of epiphytes, similarly as found by [31]. Finally, the forest fragments within the SCSP have a high diversity of epiphytes probably due to increased diversity in available phorophytes, which was previously shown to increase epiphyte diversity [66]. Martini et al. ([40]) identified 283 species of trees in only 0.3 hectare, which represents one of the highest densities of tree species in the world, many of which are endemic to southern Bahia.

The species composition of landscape B, dominated by cocoa plantations, represents a subset of the Bromeliads occurring in landscape A, dominated by forest. The only exception is *Aechmea depressa*, which occurs only in the predominantly agricultural landscape. Similarly, in the landscape dominated by forests, the species contained in the cocoa agroforestry habitats constitute a subset of the species occurring in the fragments. The exception is *Hohenbergia brachycephala*, which occurs only in plantation areas. It is noteworthy that in general the subset of species that persist in the agroforests is composed mainly of drought-tolerant species. Toledo et al. ([25]) also showed that after perturbation, some xeromorphic *Tillandsias* species dominate the coffee plantations and replace mesomorphic species. In our study areas, the higher relative humidity in forests than in cocoa plantations [67] may have influenced the species composition and richness. Changes in the canopy microclimate could explain why the communities of epiphytes in modified habitats, such as cocoa or coffee plantations and secondary forests, comprise mostly drought-tolerant species [29-31, 34].

The mean species richness was significantly higher in the landscape dominated by forest fragments, and no differences were observed between habitats within each of the landscapes. This is partly due to the intense crop management in landscape B. Even though these plantations are older and more trees were recorded in the plantations of this landscape, the richness of both habitats remained significantly lower, suggesting that older plantations will not necessarily harbor more epiphytic species (but see [37]). Some other factor may influence species richness and composition. For instance, the conversion of the forests into cocoa plantations implies alteration in the arboreal community composition and forest structure [68], which may adversely affect these genera.

Studies have demonstrated that the abundance and richness of some epiphyte groups, such as orchids and filmy ferns, tend to be lower in forest environments with intense disturbance [26, 28, 30, 34, 37, 69]. Furthermore, the small amount of forests in the landscape exposes the fragments therein to dryness, to invasion of ruderal plants [70], and to collection of plants for ornamental use [71]. These factors may have directly or indirectly affected the abundance of epiphytes and have influenced the low number of trees colonized by *Aechmea* and *Hohenbergia* in the fragments of the landscape dominated by cocoa plantations. With the modification of the original landscape, the small fragments are probably functioning as edge areas with modified forest dynamics and microclimate conditions [72]. Considering the epiphytes' preference for humid environments [20, 23, 33], only plants that are more resistant to desiccation such as

Aechmea cf. lingulata and *Hohenbergia blanchetii* have advantage in the colonization of these habitats.

Moreover, in relation to landscape B (predominantly agricultural), the plantations had higher abundance of stands of bromeliads than the forest fragments. Cocoa plantations with more stratified canopy, as in landscape B, have a higher diversity of organisms – especially those dependent on forest – than plantations with simplified canopy [16]. However, this abundance corresponds to many groups composed of few species. The species represented in the cocoa plantations and the forest fragments of landscape B are generalist/common species with wide geographical distribution (see [38]) that probably adapt easily to different environments.

The high density of these specific bromeliads in plantation areas may be due to the greater vegetative reproduction and the increased germination of new individuals that occur when some bromeliad species are subjected to higher intensities of light [73, 74]. In addition, larger trees provide food and shelter for disperser animals, increasing the probability of being colonized [75, 76]. The large trees had also enough time for colonization of propagules [77]. Although studies of frugivory for epiphytes are scarce, the golden-headed lion tamarin (*Leontopithecus chrysomelas*) has been documented as a consumer and disperser of seeds of some species of the genus *Aechmea* [50, 52, 78]. These primates are endemic to southern Bahia and have been recorded in Ilhéus and surrounding cities. However, in spite of being located in this region, there are no reports of such animals in the Serra do Conduru State Park region or in the areas of cocoa cultivation in the surroundings (L. Oliveira, pers. com.). In contrast, the tamarins have the ability to inhabit cocoa plantations and secondary forests, nevertheless preferring the plantations as sites of foraging, sleeping, and feeding [51, 52, 78]. They possess the skills necessary to consume and disperse the fruits of these bromeliads [50, 51], which could explain the higher abundance of *Aechmea depressa* in the plantation areas of landscape B, considering that this primate is a disperser of this species.

In the predominantly agricultural landscape, the remaining forest fragments were not able to support a representative diversity of the bromeliads under study. The combination of the forest remnants with the matrix dominated by traditional cocoa plantation seems essential to conserve what remained of these two genera in the landscape, since the species are found in greater quantity in the shaded cocoa plantations. However, we must emphasize that the richness in landscape B is much lower than that recorded in landscape A, highlighting the need for forests in advanced successional stage to maintain the species of both genera.

Implications For Conservation

This study evaluated for the first time the role of the percentage of forest cover and shade cocoa plantations on bromeliad diversity. The rarity of the genera *Aechmea* and *Hohenbergia* in places where disturbance is more intense highlights the need for conservation of forest fragments. The shade cocoa plantations can only maintain a sub-sample of the species diversity present in forest fragments, which suggests the former habitats work as sinks for these species. It is noteworthy that, since the mid-1990s, the traditional cocoa plantations have been threatened by the fungus *Moniliophthora perniciosa*, known as witches' broom disease (WBD), which attacks cocoa plantations and causes great financial losses to the cocoa farmers of the region [14]. The replacement of these traditional plantings by systems of more intensive management, such as cocoa plantations exposed to the sun, presents another threat to the conservation of *Aechmea* and *Hohenbergia* in the region due to the resultant structural simplification. Disturbed areas of forest or agriculture are not able to maintain *Aechmea* and *Hohenbergia* diversity, which reinforces the dependence of these genera on large preserved areas.

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Appendix 1) Species names and number of stands of *Aechmea* and *Hohenbergia* sampled in forest fragments (LAFF1, LAFF2, LAFF3) and shade cocoa plantations (LASCP1, LASCP2, LASCP3) from landscape A; and forest fragments (LBFF1, LBFF2, LBFF3) and shade cocoa plantations (LBSCP1, LBSCP2, LBSCP3) from landscape B in the Atlantic Forest in southern Bahia, Brazil.

Species	**LAFF1**	**LAFF2**	**LAFF3**	**LASCP1**	**LASCP2**	**LASCP3**	**LBFF1**	**LBFF2**	**LBFF3**	**LBSCP1**	**LBSCP2**	**LBSCP3**
***Aechmea amorimii* Leme**	1	0	22	0	0	0	0	0	0	0	0	0
***Aechmea blanchetiana* (Baker) L.B.Sm.**	0	0	0	0	10	0	0	0	2	5	5	3
***Aechmea burle-marxii* E. Pereira**	0	0	4	0	0	0	0	0	0	0	0	0
***Aechmea depressa* L.B.Sm.**	0	0	0	0	0	0	0	0	0	1	0	1
***Aechmea digitatta* L.B.Sm. & R.W. Read**	9	5	2	1	0	1	1	0	0	0	0	0
***Aechmea fulgens* Brongn.**	2	0	1	0	0	0	0	0	0	0	0	0
***Aechmea gustavoi* J.A. Siqueira & Leme**	13	5	7	6	0	0	0	0	0	0	0	0
***Aechmea cf. lingulata* (L.) Baker**	32	8	30	4	3	0	4	0	1	14	38	23
Aechmea* sp. *1	6	0	7	0	0	0	0	0	0	0	0	0
***Aechmea marauensis* Leme**	5	3	0	0	0	2	0	0	0	0	0	0
***Aechmea multiflora* L.B.Sm**	3	0	4	0	0	0	0	0	0	0	0	0
***Aechmea patentissima* (Mart.ex Schult. & Schult. f.) Baker**	0	0	0	5	0	0	0	0	0	0	0	0
***Aechmea perforata* L.B.Sm.**	0	1	0	0	0	0	0	0	0	0	0	0
Aechmea* sp. *2	0	0	5	0	0	0	0	0	0	0	0	0
***Aechmea turbinocalyx* Mez**	3	0	3	0	0	0	0	0	0	0	0	0
***Aechmea weberi* (E. Pereira & Leme) Leme**	1	0	0	0	0	0	0	0	0	0	0	0
***Hohenbergia blanchetii* (Baker) E. Morren ex Mez**	0	0	3	6	16	0	0	0	1	12	24	26
***Hohenbergia brachycephala* L.B.Sm.**	0	0	0	1	1	2	0	0	0	12	17	31
Hohenbergia captata Schult. & Schult.f.	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Hohenbergia* sp.*1	**0**	**0**	**3**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**