

Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil

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Abstract The traditional shade cacao plantations (cabruças) of southern Bahia, Brazil, are biologically rich habitats, encompassing many forest-dwelling species. However, a critical question for the conservation management of this specific region, and the highly fragmented Atlantic forest in general, is to what extent the conservation value of cabruças relies on the presence of primary forest habitat in the landscape. We investigated the relative importance of cabruças and forests for the conservation of five diverse biological groups (ferns, frogs, lizards, birds and bats) in two contrasting landscapes in southern Bahia, one dominated by forest with some interspersed cabruças, and one dominated by cabruças with interspersed forest fragments. The community structure (richness, abundance and diversity) of all biological groups differed between cabruças and forests, although these differences varied among groups. A high number of forest species was found in the cabruças. However, there were pronounced differences between the two landscapes with regard to the ability of cabruças to maintain species richness. Irrespective of the biological group considered, cabruças located in the landscape with few and small

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forest fragments supported impoverished assemblages compared to cabruças located in the landscape with high forest cover. This suggests that a greater extent of native forest in the landscape positively influences the species richness of cabruças. In the landscape with few small forest fragments interspersed into extensive areas of shade cacao plantations, the beta diversity of birds was higher than in the more forested landscape, suggesting that forest specialist species that rarely ventured into cabruças were randomly lost from the fragments. These results stress both the importance and the vulnerability of the small forest patches remaining in landscapes dominated by shade plantations. They also point to the need to preserve sufficient areas of primary habitat even in landscapes where land use practices are generally favorable to the conservation of biodiversity.

Keywords Atlantic forest · Bats · Birds · Butterflies · Cabruça · Ferns · Frogs · Landscape context · Lizards · Shade cacao plantation

Introduction

The cacao-growing region of southern Bahia harbors most of what is left from the Atlantic forest of northeastern Brazil. These lowland remnant forests are known to be centers of endemism and diversification for animals and plants (e.g., Thomas et al. 1998), encompassing one of the richest pockets of biodiversity along the entire Atlantic coast (da Silva and Casteleti 2003). Today, the remaining forest cover in southern Bahia comprises a mosaic of a few native forest remnants immersed in a matrix dominated by shaded cacao plantations (Alger 1998). Although some plantations are shaded by planted exotic species such as erythras (*Erythrina* spp.) and rubber trees (*Hevea brasiliensis*), it is estimated that nearly 70% of the cacao from Bahia is cultivated under a thinned primary-forest canopy in the so-called “cabruça” system (Araújo et al. 1998). These cabruças are forest-like environments that partially maintain the native canopy and herbaceous species, and are simplified, though still stratified, habitats.

An increasing body of evidence has shown that complex agroforests, including the cabruça system, are used as habitat for several native species of plants and animals, including forest species (Schroth et al. 2004). Reports of native biodiversity thriving in cabruças include, for instance, the presence of some threatened species of snakes (Argôlo 2004), birds (Pacheco et al. 1996), primates (Dietz et al. 1996) and rodents (Oliver and Santos 1991). Canopy trees from the native flora add structure to the agroforest canopy. Brazilian cabruças represent important refuges for many heavily logged tree species which, today, are rarely found in native forest remnants (Johns 1999; Sambuichi 2002).

Although the cacao-producing landscapes are generally recognized as important habitats for wildlife, it is still unclear whether these agroecosystems serve as suitable, multi-strata forest habitats *per se* or if their importance is limited to providing permeable matrices of second-quality habitats that mitigate the deleterious effects of forest loss and fragmentation. Understanding this difference is crucial to establishing the real contribution of shade cacao and cabruças to the conservation of native biota. Matrix quality is one of the most important factors determining population persistence within fragments, and low contrasting habitats, such as cabruça agroforests, are expected to favor animal movements across fragmented landscapes (Ewers and Didham 2006; Kupfer et al. 2006).

Additionally, our current knowledge regarding the potential role played by cabruças in the conservation of the native biota results from a limited number of studies focusing on single species (Pinto and Rylands 1997) or particular taxonomic groups (e.g., Pardini 2004; Paciencia and Prado 2005a; Faria 2006). Recently, Faria et al. (2006) showed that cabruças provide shelter for rich communities of bats and birds, although assemblages of birds in cabruças were characterized by a loss of understory species and an increase of generalist, open area species, whereas the numbers of forest species of bats actually increased in cabruças when compared to surrounding forests. These authors also demonstrated that the ability of a given cabruça to harbor animal species might be influenced by the landscape context in which the cabruças are immersed. Cabruças located in a landscape interspersed by large forest tracts had more species—particularly of forest-dwellers—of birds and bats than plantations located in a landscape with few forest remnants, indicating the positive influence of native forest on the species richness and composition encountered in the cacao agroforests. It is not clear, however, whether the patterns reported for bird and bat assemblages also hold for other biological groups that have different ecological attributes and sensitivities to habitat disturbance. Multi-taxa inventories have reported variation in the response of species assemblages to habitat disturbance gradients (Lawton et al. 1998; Harvey et al. 2006) and agroforests (Schulze et al. 2004; Pineda et al. 2005), though none has assessed the effect of the landscape context on local biodiversity. In order to properly understand the potential of Brazilian cabruças to conserve plant and animal diversity and contribute to regional conservation strategies, it is important to conduct multi-taxa studies within these land use systems.

In this paper we present the results of a taxonomically diverse inventory conducted in forests and cabruças located in two contrasting landscapes of southern Bahia. Building on data presented by Faria et al (2006) for birds and bats, we investigate the impact of forest conversion to cabruças, and the influence of the total amount of native forest in the landscape (or landscape context) on species richness, abundance, diversity (within habitats) and composition of ferns and the leaf litter fauna of frogs and lizards within cabruça systems. We chose ferns and the litter herpetofauna because they are locally abundant in Neotropical forests, easy to sample, and often regarded as biological indicators of habitat disturbance (see Paciencia and Prado 2005b for ferns and Pough et al. 2001 for herpetofauna).

In a second step of the analysis we include the data for bat and bird assemblages and searched for potential differences in beta diversity (among habitats) of the five biological groups in cabruças and forest fragments from the two landscapes. Finally, we investigate the existence of relationships among the species compositions of the five communities relative to the sampling sites, and examine whether the five taxa display similar responses to different habitats and landscape contexts.

Methods

Study area

The cacao-growing region of southern Bahia, Brazil, overlaps with a high priority area for conservation. The region comprises one of the last remnants of what is left of the Atlantic forest in northeastern Brazil. It is estimated that the forest remnants represent only 3–5% of the Atlantic forest's original size (Thomas et al. 1998). This forest is classified as tropical lowland rainforest (Oliveira-Filho and Fontes 2000), with tall vegetation characterized by its stratification into lower, canopy and emergent layers, and abundant epiphytes, ferns,

bromeliads and lianas (Thomas et al. 1998). The mean rainfall for the town of Una, where part of the work was conducted, is 1918 mm year⁻¹ (from 1965 to 1973; Mori et al. 1983), while mean annual temperature is 24°C. Values for Ilhéus, the other study site, are very similar.

The spatial distribution of cacao plantations in southern Bahia is associated with the productive soils that predominate along a belt of 15–20 km from the coast. In this core region of the cacao production, cacao is the dominant land use, characterized by extensively managed shade plantations interspersed with a few forest remnants. Most of the remaining forest occurs along the coast, where the sandy and poor soils impeded the establishment of extensive plantations. In the coastal region, cacao is grown in only a few small plantations located on the more productive soils.

Site selection

This study was part of the RestaUna Project, a major research project designed to inventory part of the biota from southern Bahia (www.restauna.org.br). The investigation was undertaken in a total of 10 mature forests and 10 cabruças in two municipalities from southern Bahia, located in two landscapes, which differ in their relative amount of forest remnants and cabruças (Fig. 1). The present distribution and conservation status of the natural forest remnants in southern Bahia make it virtually impossible to use an experimental design that includes true replicates of real landscapes, which would be necessary to rigorously assess the influence of the total amount of forest on biological

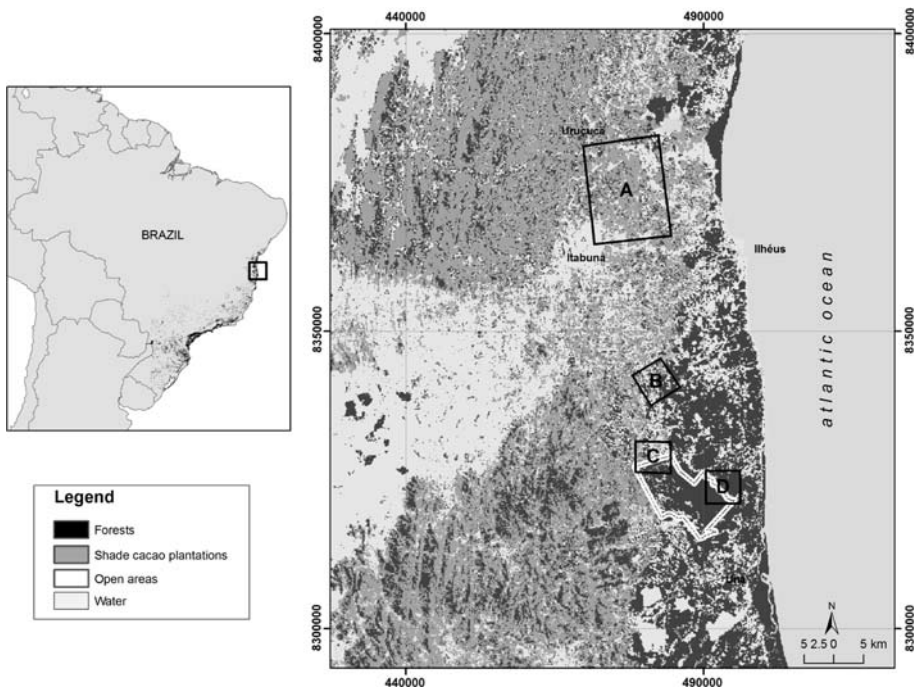


Fig. 1 Map of southern state of Bahia showing the areas covered by shade cacao plantations and forest. The landscape studied in Ilhéus (A) and the three sampling blocks from Una (B, C and D) are shown. The white polygon in Una represents the perimeter of the Una Biological Reserve (modified after Landau et al. 2003)

communities. However, both landscapes are very close (<40 km), occur in the same broad climatic conditions and have similar original vegetation and similar species assemblages of the five taxonomic groups considered here. The sampling of replicates of cabruças and forest fragments in the two landscapes was thus used as the best possible design for analyzing the influence of the surrounding forest cover, or landscape context, on the species assemblages within the cabruças.

The first landscape, Una, lies in the coastal zone. The region holds one of the largest forest remnants in northeastern Brazil, including the effectively protected 11,000 ha of the 'Una Biological Reserve', but with at least 14,216 ha of privately owned forest fragments contiguous to the forest reserve (Araújo et al. 1998). After mapping the vegetation of 14,300 ha, which included part of the Una Biological Reserve, it became clear that the landscape is composed primarily of a mosaic of forests in different successional stages, with nearly 50% of the land cover comprising mature forest fragments and an additional 16% in early secondary forests (Faria 2006). Cabruças cover only 6% of the landscape, and the majority of them are quite small (median value of 2.73 ha) and immersed in a forest-dominated landscape. In this landscape, we sampled six forest fragments (>200 ha) and six cabruças, from January 1998 to July 2001. The sampling sites in Una were distributed across three blocks of 6 km × 6 km, with two replicates of each habitat type (forest fragment and cabruça) located in each block (Fig. 2). This spatial arrangement of the sampling sites in Una took into account the proximity of small forest fragments to the larger (>1000 ha) forests, thus guaranteeing that the sampled sections of the landscape contained a significant amount of forest cover.

The second landscape was in the municipality of Ilhéus, located in the core region of cacao production. A map of 22,000 ha of the landscape in Ilhéus indicates that nearly 82% of the land cover consists of cacao agroforests, which are the predominant components of the matrix (Fig. 1). It was not possible in this analysis to separate accurately either the total amount or the locations of cabruças from cacao grown under rubber trees (*Hevea brasiliensis*) or the exotic *Erythrina* spp. However, most of the farms our team of researchers visited during the field work (February–May 2002) were predominantly cabruças. Forest fragments comprised nearly 5% of the total land cover and were small, highly disturbed remnants ranging from 1 to 300 ha in area (median 7.2 ha). The inventory in this second landscape was undertaken in eight selected areas comprising four cabruças and four forest fragments, from January to June 2002. Due to the shorter period of time available for mapping and sampling these areas in Ilhéus it was not possible to plan the same block design as in Una.

In each forest fragment and cabruça in both landscapes, a 200 m long, 1 or 2-m wide transect was established, placed at least 75 m from the surrounding habitats to avoid edge effect. All the surveys were conducted along the same 20 sampling transects: six forest fragments and six cabruças in Una and four forests and four cabruças in Ilhéus. The location of each transect took into account the logistical limitations including access to the site (e.g., proximity of dirt roads) and the permission of the landowners.

Fern sampling

Ferns were sampled in a 0.12 ha plot (120 m long × 10 m wide) placed along each sampling transect. In this plot, all individuals up to 2 m above the ground were identified and counted. We further categorized the species in guilds following the life-forms described in Poulsen and Nielsen (1995): epiphytes (ferns adhered to the bark of host plants), scandents (climbers still rooted in the soil), climbers (ferns adhered and dependent

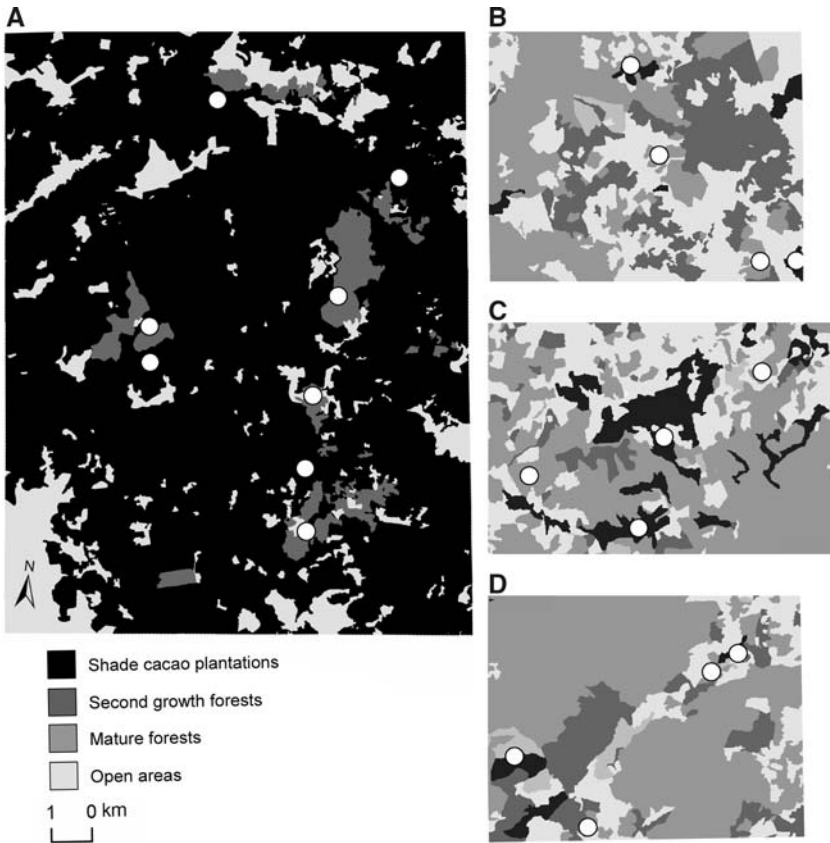


Fig. 2 A detailed map of the studied landscapes of Ilhéus (A) and Una (B, C, and D). In Ilhéus the map shows three categories of land cover: open areas, forests and shade plantations, predominantly cabucas. In the map of the three sampling blocks in Una it was possible to differentiate mature forests from second growth stands, and all the shade plantations were cabucas. The white circles mark the location of each sampling transect

on their host for survival), tree ferns (those that germinate and grow rooted in the soil, with their foliar buds located at more than 30 cm off the ground when the plant is an adult) and terrestrial ground herbs (ferns that germinate and grow fastened to the soil, with their foliar buds up to 30 cm above the soil).

All species were collected in triplicates and deposited at the Herbarium SP (Institute of Botany of São Paulo), at the CEPLAC Herbarium (Comissão Executiva para o Plano da Lavoura Cacaueira, municipality of Itabuna, Bahia), and at the UNIP herbarium (Universidade Paulista, São Paulo). Some duplicates can also be found at the New York Botanical Garden.

Frog and lizard sampling

Leaf litter frogs and lizards were sampled with pitfall traps and drift fences (Cechin and Martins 2000), with marking and release of animals. Three arrays of pitfall traps

containing four 35 L plastic buckets were installed along each sampling transect, with buckets connected by an 8-m long, 50-cm high fence. Each array was 25 m long, placed 50 m apart from each other along the transect. From October 1999 to February 2000 each transect in Una was sampled twice, for 12 consecutive days each, and in the Ilhéus landscape traps were kept open for 24 consecutive days from April to May 2002. Total sampling effort was thus similar across the two landscapes. In both landscapes traps were checked every 2 days since it was not possible to check all transects in a single day. Some specimens (maximum of 10 individuals of each species) were collected for identification, and vouchers were deposited at the Museum of Zoology from the University of São Paulo (MZUSP) and National Museum of Rio de Janeiro (UFRJ).

Bird sampling

Birds were monitored by point count surveys, establishing three points located 100 m apart along each 200 m transect. All points were sampled at five hourly intervals starting at sunrise. Points sampled in the same time interval were 200 m apart. Each point was sampled for 15 minutes, and all birds sighted or heard in a 30 m fixed-radius were recorded. Each transect was sampled over a period of 7–12 days. Nocturnal birds were not included in our data set. We considered as one record the detection of a single individual, a pair, a conspecific flock or a lek. In the Una region the survey was performed over two consecutive years (1999–2000) totaling 360 point counts, while the Ilhéus sampling was limited to July 2001, with 120 point counts. To standardize the sampling effort between the sites, we used the Indice Ponctuel d'Abondance (IPA) method (Blondel et al. 1970), i.e., instead of using the actual total number of records in each sampling transect as a measure of local species abundance, we calculated the ratio between the number of records of the species *i* and the total number of all species recorded in the sampling transect.

Bat sampling

Bats were sampled with ground mist nets deployed in all the 12 transects established in Una but in only six transects (3 cabruças and 3 fragments) in Ilhéus due to logistical constraints. Surveys were conducted from January 1998 to July 2001 in Una and from June to July 2002 in Ilhéus. On each sampling night, a set of eight 2.5-m high mist nets was deployed along each transect and remained open for 5 h after sunset. Each transect was equally sampled on four non-consecutive, moonless and rainless nights. Bats were sampled along the 12 transects in Una but, only in three cabruças and three forest fragments in Ilhéus, resulting in a total effort of 48 and 24 sampling nights in Una and Ilhéus, respectively. Once captured, each bat was identified, weighed, sexed and placed in a cloth bag to be released at the end of the sampling night. As bats were not tagged, the number of captures may include recaptures. Positive identification in the field was not possible in the case of seventy-eight specimens. These bats, representing less than 3% of the total captures (Faria et al. 2006), were collected and properly identified later at the laboratory. Vouchers are deposited in the Mammal Collection of the Universidade Estadual de Santa Cruz (UESC), Ilhéus, Bahia.

Data analysis

We used the first-order jackknife in order to estimate the species richness and evaluate the completeness of our inventory, by calculating the percent of the estimated richness that was actually observed. Two-way analysis of variance was used to investigate whether mean species richness (mean number of species in each treatment) and abundance (mean number of individuals in each treatment) differed among the two combinations of habitats (10 transects located in forest fragments vs. 10 located in cabrucas) and the landscape considered (12 transects located in Una versus 8 located in Ilhéus), and to search for possible interactions between these two factors (habitat vs. landscape). To allow comparisons across the two landscapes, transects within the different landscapes were considered as replicates of a given landscape type.

For each taxon, the raw data for each transect included the total species richness and the number of individuals observed. Data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene test); skewness and kurtosis of the residuals were also analyzed. Data were rank or log-transformed as needed, and differences were considered to be statistically significant at $P < 0.05$. Rarefaction curves were used to compare the expected number of species in samples of different sizes among the four treatments. This procedure was calculated with the package PAST (Hammer et al. 2001), using Krebs' algorithm (1989) and including standard errors.

Cluster analysis was used to compare similarities in species assemblages of each biological group among the combinations of habitats and landscapes. Clusters were constructed by the unweighted pair-group method using the arithmetic averages (UPGMA) algorithm and using the presence or absence with Sorensen's index as a measure of similarity (Ludwig and Reynolds 1988). To identify potential associations between the species assemblages of the five biological groups across the 20 sampling transects, we constructed a distance matrix for each of five biological groups sampled, based on Sorensen's index and calculated for each pair of sampling transects. Using the Mantel test, after 10,000 Monte Carlo permutations, a correlation [$r =$ standardized Mantel statistic, ranging from -1 to 1] between two matrices was calculated for each pair of the five biological groups investigated, with a significant level of $P < 0.05$. As bat surveys in Ilhéus were limited to only six of the eight transects (see above), the comparisons with bats and the other four biological groups were carried out using only the 18 commonly sampled transects.

Alpha diversity was calculated for each combination of habitat and landscape, using the Shannon diversity index. Beta diversity, a measure of the turn-over of species composition, was calculated for ferns, frogs, lizards, birds and bats, as $a + b + c / [(2a + b + c) / 2]$ (Whittaker 1960) where a is the total number of species found in both sites, b is the number of species present in site 1 but not in site 2, while c is the number of species present in site 2 but not in site 1. Using one-way analysis of variance, we investigated the significance of differences in the mean values of beta diversity between habitats in both landscapes (using pairs of the same habitat in both landscapes).

Results

Ferns, frogs and lizards: species richness, abundance, diversity and similarities

During the entire study we sampled a total of 7,196 ferns of 73 species, 827 frogs of 16 species and 431 lizards of 12 species (Table 1, Appendix 1). The first-order jackknife

Table 1 Summary of sampling effort, species richness, abundance and Shannon-Wiener diversity index (H') of ferns and the litter fauna of frogs and lizards sampled in forests and cabruças from two landscapes in southern Bahia, Brazil

Habitat	Landscape	Ferns				Frogs				Lizards			
		Sampling effort (ha) ^a	Richness	Abundance	H'	Sampling effort (days) ^b	Richness	Abundance	H'	Sampling effort (days) ^b	Richness	Abundance	H'
Forest	Una (6)	0.72	41	1,452	2.37	144	12	298	1.83	144	11	86	1.27
	Ilhéus (4)	0.48	26	1,045	2.51	96	11	145	1.38	96	8	88	1.32
	Total in forests (10)	1.30	51	2,497	2.76	240	17	443	1.85	240	11	257	1.39
Cabruca	Una (6)	0.72	26	1,019	2.16	144	12	217	1.97	144	9	148	1.72
	Ilhéus (4)	0.48	28	3,680	1.72	96	7	167	1.57	96	7	109	1.87
	Total in cabruca (10)	1.30	41	4,699	2.09	240	14	384	1.98	240	11	174	1.93
Total			73	7,196		16	827			13	431		

The number of sampling transects in each combination of habitat and landscape is given in parenthesis

^a An area of 0.12 ha were sampled in each transect, so the effort is calculated as $0.12 \times$ number of transects

^b Each transect was sampled twice during a 12 consecutive-day period in Una and in a 24 consecutive-day period in Ilhéus, so the effort is calculated as days \times number of transects

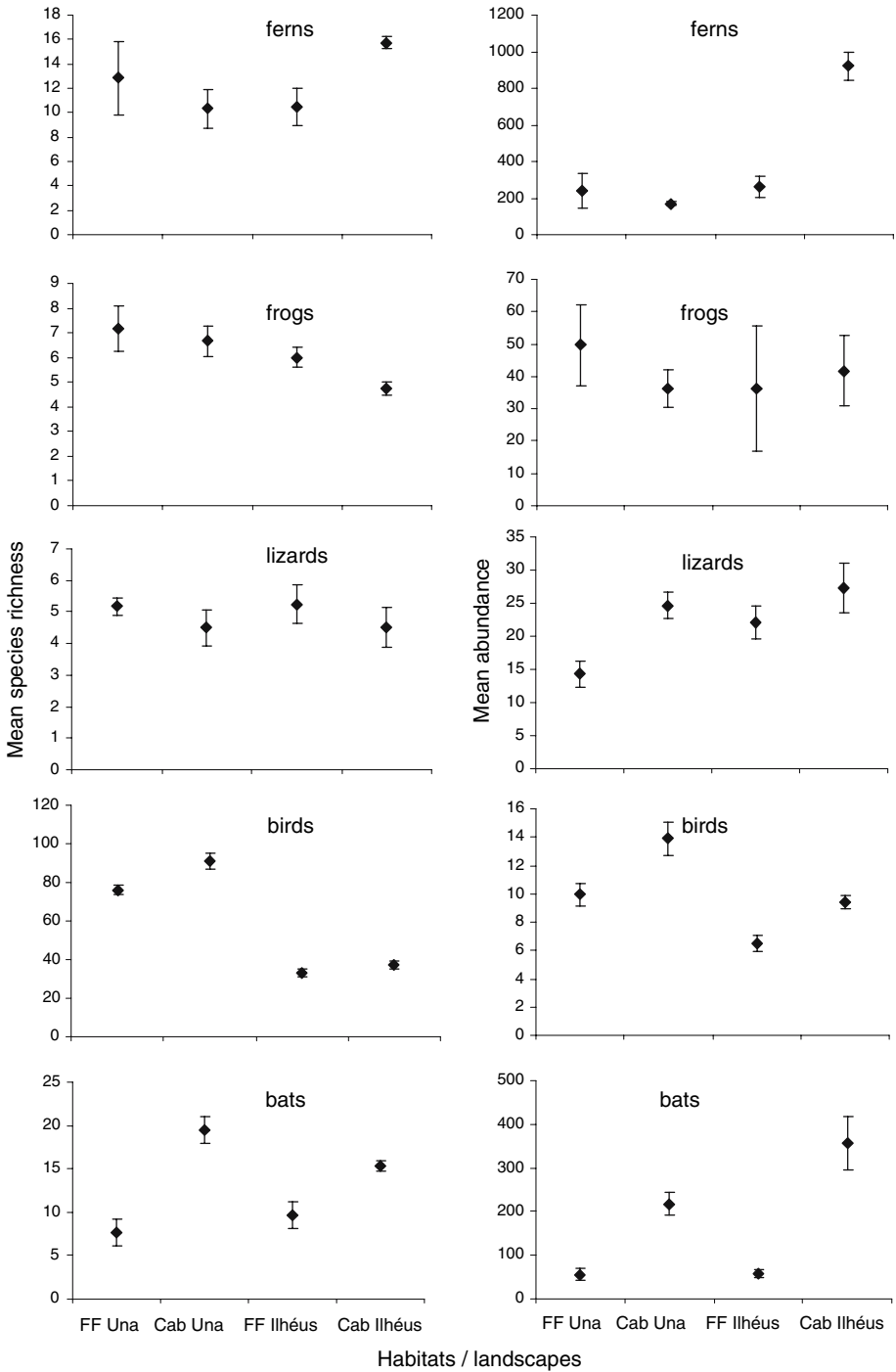
Fig. 3 Mean values (\pm SE) of species richness and abundance of ferns, frogs, lizards (from this study), birds and bats (from Faria et al. 2006) across the four combinations of habitats and landscape categories: forest fragments of Una (FF Una), cabruças of Una (Cab Una), forest fragments of Ilhéus (FF Ilhéus) and cabruças of Ilhéus (Cab Ilhéus)

estimates of total species richness were 113 species of ferns, 18.5 species of frogs and 13.5 species of lizards, indicating that we did not achieve a complete inventory of the local species assemblages for any of the three biological groups surveyed, with inventory levels of 65% for ferns, 92% for frogs and 96% for lizards. We reported the same trend in species richness observed and estimated by the first-order jackknife in the four combinations of habitats and landscapes for ferns ($r = 0.99$, $P = 0.008$) and frogs ($r = 0.96$, $P = 0.034$), but not for lizards ($r = 0.92$, $P = 0.07$).

Ferns, frogs and lizards showed different patterns of species richness and abundance among the four combinations of habitats and landscapes (Fig. 3). While mean species richness of ferns did not vary between habitats (two-way ANOVA, $F_{1,16} = 0.384$, $P = 0.544$) and across the two landscapes ($F_{1,16} = 0.483$, $P = 0.497$), rarefaction curves showed that, for a given number of individuals, forest fragments from Una presented the highest expected species richness, while cabruças from Una and fragments from Ilhéus had intermediate values and cabruças in Ilhéus had the lowest species richness (Fig. 4). A significant interaction of habitat and landscape was observed on the mean abundance of ferns ($F_{1,16} = 5.690$, $P < 0.030$), with ferns being significantly more abundant in cabruças in Ilhéus than in all other habitats (Fig. 3). With the same sampling effort for both habitats, 2,497 ferns were sampled in forests while 4,699 were reported in cabruças, with more than 51% of all the ferns observed occurring in cabruças from Ilhéus (Table 1). However, the cabruças from both landscapes showed lower species diversity than forests ($H' = 2.76$ for forest fragments versus $H' = 2.09$ for cabruças). For example, cabruças from Ilhéus were highly dominated by three species that together accounted for more than 81% of all individuals observed in these particular sites (*Adiantum latifolium*, *Thelypteris dentate* and *Blechnum occidentale*; Appendix 1).

Species assemblages of ferns were different in cabruças and forest fragments, a pattern clearly illustrated by the cluster analysis (Fig. 5). Cabruças had more herbaceous ground ferns ($\chi^2 = 6$; d.f. = 3; $P = 0.014$) but fewer climbers ($\chi^2 = 4$; d.f. = 3; $P = 0.045$; Fig. 6).

Mean abundance of frogs did not vary significantly between habitats ($F_{1,16} = 0.104$; $P = 0.751$) or across landscapes ($F_{1,16} = 0.100$; $P = 0.756$), nor was there an observed interaction between these two factors ($F_{1,16} = 0.589$; $P = 0.454$). A significant effect of the landscape was observed in the mean species richness of frogs ($F_{1,16} = 4.690$; $P = 0.046$), with transects of forest fragments and cabruças from Una showing, on average, more species of frogs than transects located in Ilhéus (Fig. 3). Three rare species reported in forests, each representing < 3% of the captures in forests, were not observed in cabruças (*Adelophryne pachydactyla*, *Cycloramphus migueli* and *Leptodactylus spixi*). Cabruças showed higher values of alpha species diversity ($H' = 1.98$) compared with forests ($H' = 1.85$), and the proportional representation of the three dominant species in forest also changed considerably in cabruças: the abundance of *Chiasmocleis* sp1 was only half that of forest sites, the numbers of *Bufo* aff. *margaritifera* doubled, while *Chiasmocleis gnoma* was only caught once in a cabruça in Una. The rarefaction curves highlight the changes in species richness at a landscape scale, with overall impoverished frog assemblages in the cabruças from Ilhéus compared with the other three habitats (Fig. 4). Cluster analysis revealed a greater similarity in species assemblages of both habitats in each landscape (Fig. 5).



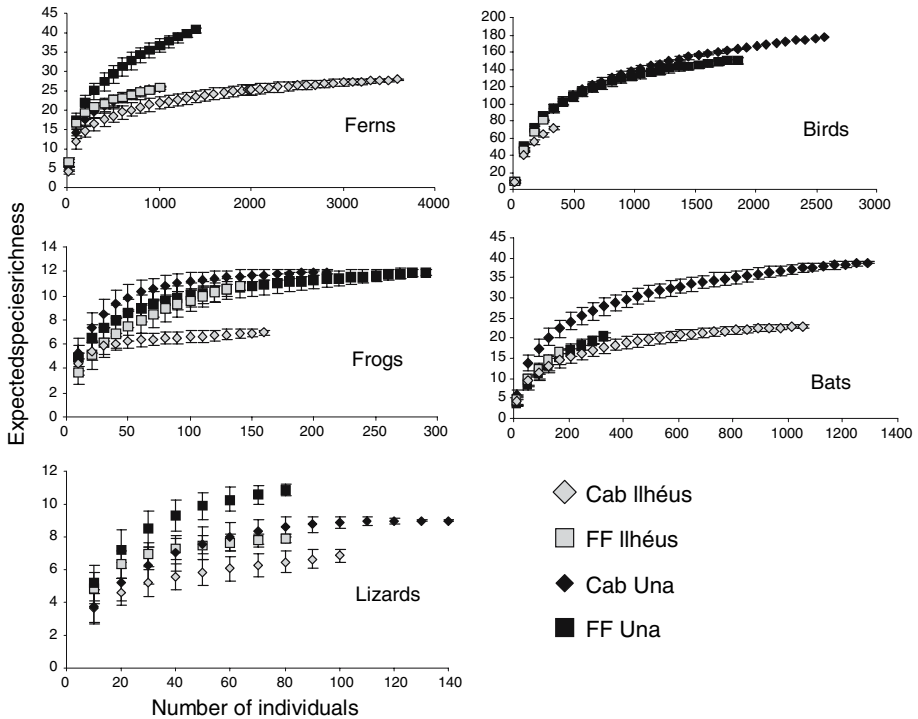
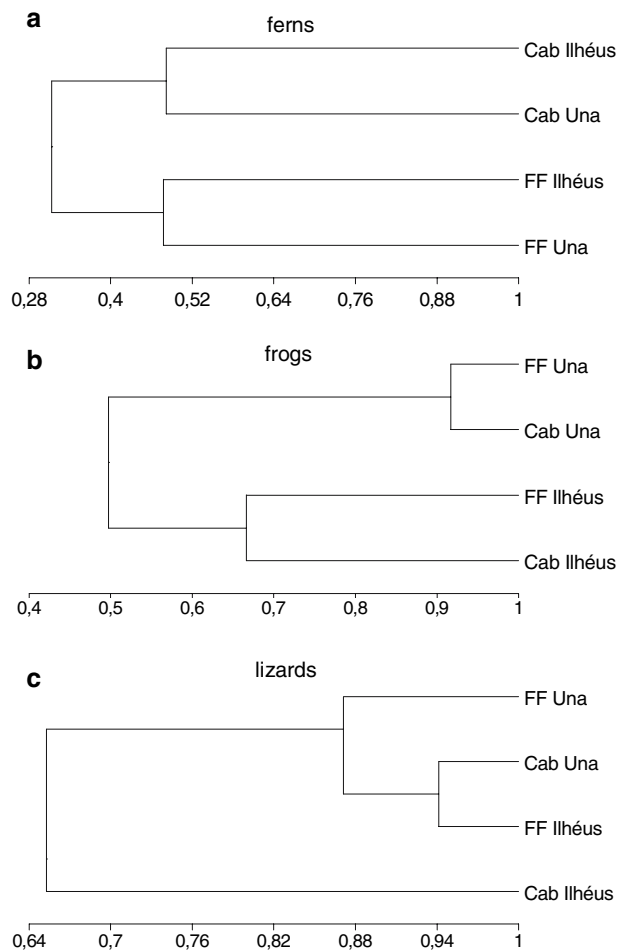


Fig. 4 Rarefaction curves of ferns, frogs, lizards (from this study), birds and bats (from Faria et al. 2006). Each curve represents the expected number of species from equal sample sizes taken from forest fragments and cabruças located in Una and Ilhéus landscapes. Abbreviations are: FF Una: forest fragments of Una, Cab Una: cabruças of Una, FF Ilhéus: forest fragments of Ilhéus and Cab Ilhéus: cabruças of Ilhéus. Bars are means ± 1 Standard Error

As observed for ferns, there were no significant differences in species richness of lizards between cabruça and forest habitats ($F_{1,16} = 1.28$; $P = 0.274$) or across the two landscapes ($F_{1,16} = 0.004$; $P = 0.948$); there was also no interaction between these two factors ($F_{1,16} = 1.81$; $P = 0.197$) (Fig. 3). With the same sampling effort (number of individuals), the rarefaction curves showed that lizard species richness was highest in forest fragments in Una, followed by cabruças from Una and forest fragments from Ilhéus. Cabruças in Ilhéus had the lowest lizard species richness (Fig. 4), sharing less than 65% of the species assemblages with the other treatments (Fig. 5). Additionally, the mean abundance varied across habitats ($F_{1,16} = 9.44$; $P = 0.007$), with lizards being more abundant in cabruças than in forest fragments. These shade plantations harbored 11 of the 12 species reported in forests, but were dominated by a single species, *Leposoma scincoides*, which comprised more than 60% ($n = 155$) of the total captures in cabruças. The cabruças therefore had lower values of species diversity ($H' = 0.36$) than the forest fragments ($H' = 0.63$). *Enyalius catenatus pictus* and *Leposoma annectans* were the most abundant species in forest fragments from both landscapes, with each species represented by 43 individuals. While the latter species was also common in cabruças, only three individuals of *E. c. pictus* were sampled in shade plantations from Una and no individuals were recorded in shade plantations in Ilhéus.

Fig. 5 Cluster analysis (UPGMA) for similarity of species composition calculated for (a) ferns, (b) frogs and (c) lizards, using the Sorensen index (presence/absence) for forest fragments and cabruças located in the Una (FF Una and Cab Una) and Ilhéus (FF Ilhéus and Cab Ilhéus) landscapes, in southern Bahia, Brazil



Beta diversity (w) and the similarity of response among ferns, frogs, lizards, birds and bats

Comparisons of beta diversity (w) among forest fragments in Una and Ilhéus revealed that bird composition was significantly more spatially variable in fragments located in Ilhéus than those in Una ($F_{1,19} = 30.227, P < 0.0001$), whereas no significant differences were observed for fern ($F_{1,19} = 0.20, P = 0.88$), frog ($F_{1,19} = 0.270, P = 0.60$), lizard ($F_{1,19} = 4.88, P = 0.40$) and bat assemblages ($F_{1,16} = 2.240, P = 0.631$). Conversely, the cabruças located in Una showed significantly more variation in species composition of ferns ($F_{1,19} = 4.106, P = 0.057$), lizards ($F_{1,19} = 7.482, P = 0.013$) and birds ($F_{1,19} = 111.50, P < 0.0001$) compared with cabruças from Ilhéus, with no differences observed for frog ($F_{1,19} = 0.369, P = 0.551$) or bat assemblages ($F_{1,16} = 2.281, P = 0.150$).

Except for frogs, positive and significant correlations were observed among the species assemblages of ferns, lizards, birds and bats present in the forest fragments and cabruças located in Una and Ilhéus, as shown by the significant values (P) reported by the Mantel-test for comparisons of dissimilarity matrices (Table 2). Significant correlations (r) between two

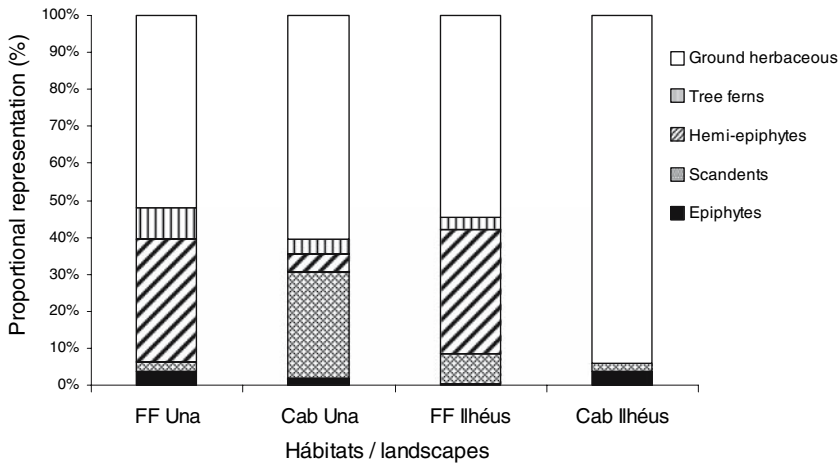


Fig. 6 Proportional representation (%) of the abundance of guilds of ferns in forest fragments and cabucas located in the Una and Ilhéus landscapes, southern Bahia, Brazil. The combinations of habitats and landscapes are as follows: FF Una; forest fragments of Una, Cab Una; cabucas of Una, FF Ilhéus; forest fragments of Ilhéus, and Cab Ilhéus; cabucas of Ilhéus

Table 2 Relationships of species assemblages of ferns, frogs, lizards, birds and bats inventoried in transects of four combinations of habitat (forest fragments and cabucas) and landscapes (Una and Ilhéus)

Biological group	Biological group			
	Ferns	Frogs	Lizards	Birds
Ferns	–	–	–	–
Frogs	0.034 (0.307)	–	–	–
Lizards	0.35 (0.0002)	–0.002 (0.507)	–	–
Birds	0.58 (0.0001)	0.039 (0.299)	0.34 (0.003)	–
Bats ^a	0.40 (0.0001)	0.02 (0.353)	0.25 (0.008)	0.53 (0.0002)

Values in each cell represent the correlation r (standardized Mantel statistic) of the distance matrices (Sorensen distances) followed by the level of significance P (in parentheses, with significant values of $P < 0.05$ in bold)

^a Distance matrices comparing bats with the remaining four biological groups were built with data from 18 of the 20 transects, as bat sampling in Ilhéus was limited to only 6 of the 8 transects

groups from the same set of sampling transects ranged from 0.25 (lizards and bats) to a maximum value of 0.58 (ferns and birds).

Discussion

Species richness, abundance, alpha diversity and composition of fern, frog and lizard assemblages

Ferns, frogs and lizards varied in their response to habitat modification. As noticed by previous studies on ants (Delabie et al. 1999), small mammals (Pardini 2004), birds (Alves

1990, Faria et al. 2006) and bats (Faria 2006; Faria et al. 2006; Faria and Baumgarten 2007), the cabruças in both landscapes harbored a substantial number of the overall species present in the landscape, containing 56% of the fern species, 81% of the frog species and 85% of the lizard species. However, the three taxa also showed significant changes in community structure of cabruças located in different landscape contexts, as previously reported for birds and bats (Faria et al. 2006).

Shade cacao plantations supported relatively impoverished fern assemblages compared with forest fragments. Furthermore, cabruças harbored a very particular pteridophyte species composition, with high abundance of invasive species, which are often common in open areas (Paciencia and Prado 2005a). The greater presence of open-area ferns in cabruças than in forests leads to a lower diversity in the cabruças. Fern assemblages in cabruças are also characterized by very low abundance of climbers, which mostly occurred in forested areas of the studied landscapes. The most important species representing this life form are the Dryopteridaceae, *Cyclodium meniscioides* and *Polybotrya cylindrica*, as well as the Lomariopsidaceae, *Lomagramma guianensis* and *Lomariopsis marginata*, which together comprise 12% of the total species recorded in all sites. These species are basically restricted to the dense forest areas and cannot maintain themselves in cabruças, probably as a consequence of weed control practices.

Pronounced differences in species richness and abundance of ferns were observed within cabruças located in Ilhéus. These extensive, shade plantations showed a reduction in species richness and an increased total abundance of ferns compared with forests and the shade plantations of Una. The greater abundance of ferns in the cabruças from Ilhéus is due to the high local abundance of *A. latifolium* (Pteridaceae), *T. dentata* (Thelypteridaceae) and *B. occidentale* (Blechnaceae), that together comprise nearly 82% of the observed individuals. These three open-area ferns also occur in cabruças of the Una landscape and in surrounding non-forested areas, but at low frequencies, and are apparently an indicator for the higher degree of disturbance of the cabruças around Ilhéus.

Cabruças still provide habitat for a major part of the forest species of leaf-litter frogs. However, compared to forests, cabruças lacked three species reported in forests and had fewer individuals of *Chiasmocleis gnomia*, a species that seems to be sensitive to forest alteration (Canedo et al. 2004). But due to a decrease in species dominance compared to forests, the cabruças had higher values of species diversity. A similar observation was made by Pineda et al. (2005) in shade coffee plantations in Mexico, which also harbored rich and diverse frog communities, but with fewer species compared to surrounding forest remnants. Interestingly, in both studies shade plantations harbored 20% fewer species of frogs than small forest patches. Pineda et al. (2005) suggested that the decrease of canopy cover that characterizes both types of shade plantations could be one of the main factors affecting the presence and abundance of frogs.

Considerable changes in frog species richness in southern Bahia were further observed at the landscape scale. On average, transects of cabruças and forests located in Una had significantly more frog species than the habitats in Ilhéus. The cabruças in Ilhéus had impoverished frog assemblages relative to forests and also to cabruças in Una. This pattern was consistent with the pattern observed for fern and lizard assemblages.

As observed for ferns, lizards were considerably more abundant and less diverse in cabruças than in forest. The cabruças in both Ilhéus and Una were characterized by a high dominance of a single species, *Leposoma scincoides*, which was also present in forests as well as other matrix habitats in Una, such as secondary forests (Dixo 2001). Only one rare species sampled in forest fragments (*Leposoma nanodactylus*) was not reported in cabruças. Although little information is available on the ecology of Gymnophthalmidae in

general, the preference of *Leposoma scincoides* for disturbed habitats such as forest edges, secondary forest and especially cacao groves was reported earlier (Rodrigues et al. 2002). These results are in accordance with those reported by Lieberman (1986) and Heinen (1992) for shade cacao plantations in Costa Rica, where the richness and evenness of lizards declined from primary forest to a disturbed site, resulting in an increase in the dominance of some species (like *L. scincoides* in this study) and the decline of others (such as *Enyalius catenatus pictus* in this study). *Enyalius catenatus pictus* was abundant in forest fragments, rare in the cabruças of Una and absent from cabruças of Ilhéus. This species was present in the forest leaf-litter and also on branches and trees, and may be considered sensitive to forest simplification caused by cacao management.

Species composition of ferns, frogs, lizards, birds and bats: relationships among biological groups and patterns of spatial variability (beta diversity)

Ferns, lizards, birds and bats showed a consistent response to habitat modification. In general, cabruças harbored: (1) very particular pteridophyte communities dominated by open-area species, (2) lizard assemblages highly dominated by a single, matrix-abundant species though still comprising most of the forest-dwellers, (3) bird communities represented by the juxtaposition of open-area and some of the forest-interior species (Laps et al. 2003; Faria et al. 2006), and (4) rich bat assemblages comprising a large number of forest-dependent, disturbance-sensitive species (Faria et al. 2006; Faria and Baumgarten 2007). Frog assemblages also responded to habitat modification but in a different way than ferns, lizards, birds and bats. The variability of frog abundance, particularly in forest sites (Fig. 3), made it more difficult to recognize patterns, but overall differences between landscapes seemed to be greater than the differences between habitat types.

Another important and consistent response among the different biological groups was the influence of the landscape context on the ability of a given cabruça to retain plant and animal species. Extensive plantations located in the landscape with few, small and scattered forest fragments (Ilhéus) had impoverished assemblages of ferns, frogs, lizards, birds and bats relative to plantations located in the landscape with greater forest cover (Una). This further supports the general notion that the community structure in cabruças, for a variety of biological groups, is influenced by the location and extent of native habitat in the landscape. Previous studies have demonstrated that the community structure of moths (Ricketts 2001), birds (Alves 1990; Greenberg et al. 2000), terrestrial mammals (Estrada et al. 1994) and bats (Estrada et al. 1993; Faria and Baumgarten 2007) in shade plantations, as well as other agricultural habitats, are strongly influenced by the proximity of forest remnants. In both landscapes investigated in the present study, the sampling sites of cabruças were located close to forest tracts (<1 km, see Fig. 2), so the impoverishment observed in the cabruças in Ilhéus compared with those in Una is likely to reflect differences in the relative area under forest and cabruças in the surrounding landscape. However, additional studies with true landscape replicates and a range of forest covers are needed to explore this relationship in greater detail.

The landscape context also appeared to influence the spatial variation of species composition. The higher beta diversity of birds in fragments in Ilhéus compared with Una probably reflects the dominance of cabruças in the Ilhéus landscape. The cabruças act as a permeable matrix for species typical of disturbed areas, while serving as a barrier to the dispersal of forest-interior species, which occur only at very low abundances in the cabruças. Using data from the same study, Faria et al. (2006) showed that

three forest-interior bird species (the scaled antbird *Drymophila squamata*, the black-capped antwren *Herpsilochmus pileatus* and the white-shouldered fire-eye *Pyriglena leucoptera*) which were present in both fragments and cabruças of Una, avoided cabruças in Ilhéus. As cabruças become more disturbed and the average distance between natural forest fragments increases, populations of forest-interior species in forest fragments become increasingly isolated, increasing their risk of random extinction. This, in turn, would result in a more variable composition of the assemblages of surviving species in the fragments (i.e., higher beta diversity). Lower dispersal rates and decreasing fragment size have previously been shown to result in increased beta diversity for small mammals in fragmented landscapes (Pardini et al. 2005; Ewers and Didham 2006).

By contrast, Una the landscape appears to be functionally connected for most of the biological groups investigated so far, as the small fragments (<100 ha) harbor the same values of species richness, abundance and diversity as the large forest tracts (>1000 ha) for ferns (Paciencia and Prado 2005b), butterflies (Accacio 2004), leaf litter herpetofauna (Dixo 2001), birds (Laps et al. 2003), bats (Faria 2006) and small mammals (Pardini 2004).

Implications for conservation

Studies have demonstrated that shaded tree crop plantations, including cabruças, are important landscape elements that provide habitat and dispersal pathways and help conserve local species assemblages (e.g. Estrada et al 1993, Estrada and Coates-Estrada 2002; Greenberg et al 2000). The present research, however, illustrated that the potential of cabruças in southern Bahia to provide suitable habitat for forest-dependent species varied with the biological group and the landscape context. These shade plantations represented poor habitat for forest-dependent ferns, intermediate quality habitat for birds, but high quality habitat for many forest-associated species of frogs, lizards and bats.

Irrespective of the biological group considered, the ability of cabruças to support a high diversity of forest species decreased with decreasing extent of natural forest habitat in the landscape. Under present management practices the habitat quality of cabruças for forest species is likely to decline over time as the cabruças become increasingly dominated by pioneer and secondary vegetation (Alves 1990; Alger 1998; Rolim and Chiarello 2004). These results reinforce the notion that the conservation of forest biodiversity, and especially of disturbance sensitive species that are of greatest conservation concern, ultimately depends on the conservation of natural habitat within the landscape.

Although cabruças are not surrogates for native habitats and cannot alone sustain the region's entire species pool, these agroforests should be viewed as complementary habitats in a broader conservation scheme in which the native forest functions as the backbone (Schroth et al. 2004). In order to enhance the probabilities of conserving more species within the cabruça system, it will be critical to maintain the forest mosaic in Una and increase the amount of native habitat in Ilhéus. In Ilhéus and other cabruça-dominated landscapes, the few small forest remnants are important reservoirs of vulnerable populations of some forest species and their disappearance at a local scale may have profound consequences at a regional scale. Thus, these small fragments should be incorporated in the current scheme of conservation units that, today, encompasses only the larger remnants along the coast.

It is important to also stress that even the future of cabruças themselves is no longer guaranteed. In response to the witches' broom disease (*Crinipellis pernicioso*) that devastated cacao production in southern Bahia in the nineties, cacao cultivation is becoming more intensified, with the use of more resistant cacao varieties, an overall depletion of the shade canopy, more intense pruning and weeding and a higher agrochemical input (CE-PLAC 2006). Numerous studies have shown that increasing intensification of management leads to a simplification of the local biodiversity, and overall changes toward species associated with disturbance (Perfecto et al. 2003). The substitution of vast areas of cabruças with more intensified cultivation, coupled with the reduction of the few remaining forest tracts and the constant human pressure, is likely to jeopardize the conservation of a greater number of the region's species.

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Appendix 1 Species abundance of ferns and the litter fauna of frogs and lizards sampled in four combinations of habitats (forest fragments and cabruças) located in two landscapes (Una and Ilhéus) of southern Bahia, Brazil

Species	Forest		Cabruca		%	Guild ^a
	Una	Ilhéus	Una	Ilhéus		
Ferns						
<i>Adiantum diogoanum</i>	0	0	51	102	2.13	TGH
<i>Adiantum dolosum</i>	2	17	0	0	0.26	TGH
<i>Adiantum latifolium</i>	0	14	53	1,722	24.86	TGH
<i>Adiantum lucidum</i>	1	1	0	0	0.03	TGH
<i>Adiantum obliquum</i>	0	53	2	0	0.76	TGH
<i>Adiantum</i> sp.	0	83	0	0	1.15	TGH
<i>Anemia phyllitidis</i>	3	123	1	0	1.76	TGH
<i>Anemia</i> sp.	0	0	3	1	0.06	TGH
<i>Asplenium serratum</i>	26	0	0	1	0.38	EPI
<i>Asplenium</i> sp.1	0	6	0	0	0.08	TGH
<i>Asplenium</i> sp.2	0	0	0	2	0.03	TGH
<i>Blechnum brasiliense</i>	1	0	39	0	0.56	TRE
<i>Blechnum occidentale</i>	0	19	15	535	7.91	TGH
<i>Campyloneurum</i>	2	0	0	0	0.03	EPI
<i>Ctenitis</i> sp.1	0	0	0	142	1.97	TGH
<i>Ctenitis</i> sp.2	0	0	0	8	0.11	TGH
<i>Cyclodium heterodon</i>	478	6	1	0	6.74	TGH
<i>Cyclodium meniscioides</i>	42	0	0	0	0.58	CLI

Appendix 1 continued

Species	Forest		Cabruca		%	Guild ^a
	Una	Ilhéus	Una	Ilhéus		
<i>Danaea elliptica</i>	2	2	0	0	0.06	TGH
<i>Dicranoglossum desvauzii</i>	1	0	0	0	0.01	EPI
<i>Elaphoglossum pteropus</i>	3	0	0	0	0.04	EPI
<i>Elaphoglossum macrophylla</i>	1	0	0	0	0.01	EPI
<i>Hemionitis tomentosa</i>	0	0	2	0	0.03	TGH
<i>Lindsaea lancea falcata</i>	15	0	0	0	0.21	TGH
<i>Lindsaea lancea lancea</i>	50	28	0	0	1.08	TGH
<i>Lindsaea macrophylla</i>	11	0	0	0	0.15	TGH
<i>Lomagramma guianensis</i>	201	232	13	0	6.20	CLI
<i>Lomariopsis marginata</i>	86	65	0	0	2.10	CLI
<i>Macrothelypteris torresiana</i>	0	0	10	11	0.29	TGH
<i>Lygodium volubile</i>	42	87	293	84	7.03	SCA
<i>Metaxya rostrata</i>	4	0	0	0	0.06	TGH
<i>Microgramma geminata</i>	2	1	1	2	0.08	EPI
<i>Microgramma lycopodioides</i>	1	0	3	0	0.06	EPI
<i>Microgramma squamulosa</i>	0	0	2	1	0.04	EPI
<i>Microgramma vacciniifolia</i>	0	1	7	21	0.40	EPI
<i>Nephrolepis multiflora</i>	0	0	220	24	3.39	TGH
<i>Nephrolepis pectinata</i>	0	0	0	7	0.10	TGH
<i>Nephrolepis rivularis</i>	14	0	58	1	1.01	TGH
<i>Pecluma ptilodon</i>	1	0	3	0	0.06	EPI
<i>Pecluma plumula</i>	0	0	0	43	0.60	EPI
<i>Pleopeltis angusta</i>	0	0	0	58	0.81	EPI
<i>Pleopeltis</i> sp.	0	0	0	4	0.06	EPI
<i>Polybotrya cylindrica</i>	153	52	36	0	3.35	CLI
<i>Polypodium catharinae</i>	0	0	1	0	0.01	EPI
<i>Polypodium meniscioides</i>	8	0	0	0	0.11	EPI
<i>Polypodium trisseriale</i>	0	0	8	0	0.11	TGH
<i>Polypodium polypodioides</i>	0	0	0	2	0.03	EPI
<i>Pteris splendens</i>	1	0	0	0	0.01	TGH
<i>Pteris biaurita</i>	0	0	0	23	0.32	TGH
<i>Pteris</i> sp.	0	0	0	5	0.07	TGH
<i>Pteris</i> sp.2	0	5	0	0	0.07	TGH
<i>Schizaea elegans</i>	1	1	0	0	0.03	TGH
<i>Selaginella flexuosa</i>	14	0	0	0	0.19	TGH
<i>Stygmatopteris</i> sp.	0	1	0	0	0.01	TGH
<i>Thelypteris macrophylla</i>	0	7	0	0	0.10	TGH
<i>Thelypteris dentata</i>	1	11	170	734	12.73	TGH
<i>Thelypteris longifolia</i>	2	0	0	0	0.03	TGH
<i>Thelypteris hispidula</i>	0	0	0	5	0.07	TGH
<i>Thelypteris</i> sp.1	0	0	22	3	0.35	TGH

Appendix 1 continued

Species	Forest		Cabruca		%	Guild ^a
	Una	Ilhéus	Una	Ilhéus		
<i>Thelypteris</i> sp.2	0	0	0	4	0.06	TGH
<i>Thelypteris</i> sp.3	0	144	0	91	3.27	TGH
<i>Tectaria</i> sp.	0	0	0	44	0.61	TGH
<i>Trichipteris corcovadensis</i>	71	0	0	0	0.99	TRE
<i>Trichipteris phalerata</i>	43	38	0	0	1.13	TRE
<i>Trichipteris procera</i>	6	0	0	0	0.08	TRE
<i>Trichipteris</i> sp.	2	0	0	0	0.03	TRE
<i>Trichomanes crispum</i>	2	0	0	0	0.03	EPI
<i>Trichomanes elegans</i>	4	0	0	0	0.06	TGH
<i>Trichomanes pedicellatum</i>	2	0	0	0	0.03	EPI
<i>Trichomanes pinnatum</i>	21	1	0	0	0.31	TGH
<i>Trichomanes polypodioides</i>	1	0	0	0	0.01	EPI
<i>Triplophyllum funestum</i>	130	47	2	0	2.49	TGH
<i>Vittaria lineata</i>	1	0	3	0	0.06	EPI
Total	1.452	1.045	1.019	3.680	100%	
Frogs						
<i>Adelophryne pachydactyla</i>	3	9	0	0	1.45	
<i>Adenomera hylaedactyla</i>	1	1	5	0	0.85	
<i>Bufo</i> aff. <i>margaritifera</i>	46	36	71	68	26.72	
<i>Bufo crucifer</i>	0	6	0	9	1.81	
<i>Bufo granulatus</i>	4	0	3	0	0.85	
<i>Chiasmocleis carvalhoi</i>	7	0	5	0	1.45	
<i>Chiasmocleis gnomia</i>	63	0	1	0	7.74	
<i>Chiasmocleis</i> sp1	106	79	48	37	32.65	
<i>Colostethus olfersioides</i>	0	3	10	21	4.11	
<i>Cycloramphus migueli</i>	0	1	0	0	0.12	
<i>Hyophryne histrio</i>	7	0	17	0	2.90	
<i>Leptodactylus spixi</i>	0	1	0	0	0.12	
<i>Macrogenioglottus alipioi</i>	1	1	6	0	0.97	
<i>Physalaemus</i> cf. <i>crombiei</i>	9	2	13	22	5.56	
<i>Proceratophrys laticeps</i>	25	0	27	1	6.41	
<i>Stereocyclops incrassatus</i>	26	6	11	9	6.29	
Total	298	145	217	167	100%	
Lizards						
<i>Ameiva ameiva</i>	3	1	3	0	1.62	
<i>Coleodactylus meridionalis</i>	3	9	3	0	3.48	
<i>Enyalius cateatus pictus</i>	34	9	3	0	10.67	
<i>Gymnodactylus darwini</i>	9	10	7	15	9.51	
<i>Gymnophthalmidae</i> spn	6	6	3	18	7.66	
<i>Kentropyx calcarata</i>	3	3	9	4	4.41	
<i>Leposoma annectans</i>	7	36	24	7	17.17	
<i>Leposoma nanodactylus</i>	3	0	0	0	0.70	

Appendix 1 continued

Species	Forest		Cabruca		%	Guild ^a
	Una	Ilhéus	Una	Ilhéus		
<i>Leposoma puk</i>	0	0	0	1	0.23	
<i>Leposoma scincoides</i>	16	14	92	63	42.92	
<i>Mabuya macrorhynca</i>	1	0	0	1	0.46	
<i>Tropidurus torquatus</i>	1	0	4	0	1.16	
Total	86	88	148	109	100%	

Ferns were further classified by guilds representing different life-forms (see methods)

^a Codes for guilds of ferns are: (EPI) epiphytes, (SCA) scandents, (CLI) climbers, (TRE) tree ferns and (TGH) terrestrial ground herbs

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