

Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil

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Abstract. In the core region of Brazilian cocoa production, shade cacao plantations (so-called cabruças) are important components of regional landscapes, constituting potential habitat for a vast array of the regional biota. This research focuses on the ability of cabruças to harbor bird and bat species in two nearby districts – Una and Ilhéus – with contrasting landscapes. At Una, cabruças represent less than 6% of the land and are surrounded by large tracts of forest, whereas at Ilhéus these shade plantations are the landscape's dominant feature. Bird and bat communities were richer in cabruças located in Una compared to nearby forest, while cabruças from the Ilhéus landscape were significantly poorer in species than nearby forest fragments. However, bird assemblages in cabruças were characterized by the loss of understory specialists and the increase of more open area and generalist species, whereas forest dwellers still comprised most of the bat species reported in cabruças. Species richness and composition differed between the two landscapes. Forest fragments and cabruças from Ilhéus harbored fewer forest-dwelling species than similar habitats in Una. Our study shows that cabruças support high species richness of birds and bats from the native assemblages but are no surrogates for intact forests, since the presence and representativeness of some forest species apparently depends on the existence of nearby forests. A landscape dominated by cabruças with a minor portion of native forest is unlikely to ensure long-term conservation of many target species, particularly those of major conservation concern.

Introduction

An increasing body of evidence has shown that the nature of the matrix, defined as the modified habitats surrounding forest fragments, greatly influences the dynamics of fragmented landscapes (Gascon et al. 1999; Ricketts 2001; Fahrig 2003). In this context, agroforests might play a crucial role as elements of the matrix in tropical landscapes (Perfecto et al. 1996). These systems provide a more structurally complex habitat compared with land uses

devoid of arboreal vegetation (Pimentel et al. 1992; Estrada et al. 1993a, b, 1994; Perfecto et al. 1996; Greenberg et al. 1997; Rice and Greenberg 2000; Sherry 2000; Estrada and Coates-Estrada 2002; Schroth et al. 2004), conferring a greater permeability to local biotas.

Within the array of the agroforestry systems that comprise significant portions of areas once covered by tropical forests, an emblematic example can be found in eastern Brazil, at the southern tip of the state of Bahia. This region is considered the country's main cocoa (*Theobroma cacao*) production area, and the present forest cover, including the largest remnants of coastal rainforests of northeastern Brazil, is a mosaic of native patches and areas of shade cacao plantations (Alger and Caldas 1996; May and Rocha 1996; Alger 1998). Nearly 70% of its cocoa production originates from the rustic agroforestry system locally known as cabruca (Araújo et al. 1998), in which the cacao shrubs completely replace the original understory and grow under the shade of a thinned layer of native canopy species (Alves 1990). Although cabruças are highly disturbed and represent more simplified habitats compared to native forests (Mori et al. 1983; Alves 1990; Sambuichi 2002; Rolim and Chiarello 2004), they offer a greater potential to include a significant part of the native forest assemblages than most other agricultural systems. Previous studies undertaken in southern Bahia have shown that cabruças support many forest-dwelling species of butterflies (Accacio 2004), frogs and lizards (Dixo 2001), snakes (Argôlo 2004), birds (Alves 1990; Laps et al. 2003) and non-volant small mammal species (Pardini 2001, 2004).

The conservation value of these cacao agroforests gains a significant weight by the presence of endemic, threatened species of the Atlantic Forest that include, among others, the pink-legged graveteiro (*Acrobatormis fonsecai*; Pacheco et al. 1996), the thin-spined porcupine (*Chaetomys subspinosus*; Oliver and Santos 1991) and primates such as the golden-headed lion tamarin (*Leontopithecus chrysomelas*) and the yellow-breasted capuchin (*Cebus xanthosternos*) which both use cabruças as secondary or transitory habitats (Dietz et al. 1996).

In spite of these promising findings, little is known about the extent to which cabruças are serving as habitat for the native, forest-dwelling biota. It has been shown that the nature of shade plantations (e.g. tree species and canopy structure), the intensity of their management and their proximity to native forest remnants strongly determine the diversity and abundance of local species present in them (Alves 1990; Greenberg 1998; Moguel and Toledo 1999; Rice and Greenberg 2000). Organisms also vary in their use of cabruças, since some species may explore and thrive in these agroecosystems, using them as forest surrogates, whereas others are absent from them, or still depend on the surrounding natural habitats (e.g. Alves 1990). Furthermore, the true role of cabruças in supporting biodiversity is likely influenced by the overall landscape in which they are immersed, as has been suggested for shade coffee plantations (Somarriba et al. 2004).

Birds and bats are two faunistic groups with comparable dispersal abilities, responsible for most of vertebrate species richness in Neotropical forests at a local scale, and important for the functioning of tropical ecosystems (e.g. Haila 1985; Wiens 1989; Findley 1993). Most of the present knowledge of bird and bat faunas thriving in shade plantations comes from studies in shade coffee, an agricultural habitat resembling the *cabruca* though often with a simpler structure. These shade crops are known to support a high species richness and diversity of birds (Greenberg et al. 1997; Wunderle and Latta 1998) and bats (Estrada et al. 1993a; Estrada and Coates-Estrada 2002), with particular importance for the Neartic bird migrants (Greenberg et al. 1997; Wunderle and Latta 2000). The abundance of omnivore and nectarivore bird species contributes to the observed high diversity in shade coffee plantations (Greenberg et al. 1997). Bird communities in shade cacao plantations have been less studied, but some results indicate that patterns of species richness are similar to the assemblages known for shade coffee plantations (Alves 1990; Greenberg 1998; Reitsma et al. 2001; Laps et al. 2003).

Shade coffee and cacao plantations have been shown to host fewer species of bats than nearby forest remnants (Estrada et al. 1993a; Medellín et al. 2000; Estrada and Coates Estrada 2002), but some generalist and specialist species coming from forest tracts are known to exploit these agricultural landscapes in Mexico (Estrada et al. 1993a; Estrada and Coates Estrada 2002).

In the present paper, we evaluate the ability of *cabruca*s to harbor assemblages of bats and birds at a landscape scale. We undertook this biological assessment in forest fragments and *cabruca*s located in Ilhéus and Una, two districts of the southern Bahia cacao region representing two different landscapes, that vary in the amount of forest remnants versus cacao plantations as the dominant land use. Extensive shade plantations and few forest fragments characterize the landscape of Ilhéus, while the opposite situation – small *cabruca*s immersed in a landscape dominated by forest remnants – is found at Una. Our goal was to detect possible differences in community and species-level responses for both taxonomic groups regarding habitat type (forest or *cabruca*) and landscape considered, thereby shedding some light on the potential role of the *cabruca* ecosystem as a conservation tool at a landscape scale.

Methods

Study area

The cacao region of southern Bahia is located between the Atlantic coast and 41°30' W and between 13°00' and 18°15' S, covering an area of nearly 91,819 km². The national cocoa production, mostly under the form of shade plantations, is currently concentrated in this region (Mori and Silva 1979). Mean annual temperature is 24 °C and the rainfall averages 2000 mm year⁻¹,

with no identified seasonality, though a rainless period of 1–3 months may occur from December to March (Mori et al. 1983; Thomas et al. 1998). The vegetation is classified by Oliveira-Filho and Fontes (2000) as tropical lowland rainforest, harboring tall vegetation characterized by a stratification in lower, canopy and emergent layers, and abundant in epiphytes, ferns, bromeliads and lianas (Thomas et al. 1998).

The cacao from southern Bahia is grown under a wide range of management systems, varying in the composition of shade trees (exotic or native species) and in the shade intensity. According to a recent estimate, of the 650,000 ha of cacao plantations in southern Bahia, only a minor part is shaded by either rubber trees (*Hevea brasiliensis*) or the exotic *Erythrina* spp., whereas nearly 70% are cabruças (Araújo et al. 1998). The establishment of the cacao plantations in southern Bahia followed the distribution of more productive soils, mostly located 15–20 km away from the coastal zone (Alger 1998). In these chief producing areas, cabruças occupy a larger proportion of land use types, while the native forest fragments are often small and highly disturbed (Alger 1998). Most of the largest native forest fragments in southern Bahia are nowadays concentrated along the coastal region, where the poor sandy soils served as a major barrier to deforestation, preventing the conversion of forest into agricultural production, including cacao. Cabruças can also be found in this coastal zone, though they are often restricted to river valleys and are often represented by small, scattered patches surrounded by either mature or secondary native forests. Therefore, broadly speaking, the core region of cacao production is characterized by extensive shade plantations interspersed with a few, scattered forest fragments, while the coastal zone shows the opposite distribution of small cabruças scattered in a matrix of mature or secondary forest (Figure 1).

Sites selection and experimental design

The current study is part of the RestaUna Project, a biological inventory carried out in southern Bahia (<http://www.restauna.org.br>). The field work for the present study was carried out from January 1998 to July 2002. The study was performed in mature forests and cabruças located in two districts from southern Bahia, one in the core region of cacao production and the other along the coast (Figure 1). Forest fragments and cabruças in the core region of cacao cultivation were located in the district of Ilhéus. A map of an area of 21,742 ha in Ilhéus shows that agroforestry systems predominate in the matrix, comprising nearly 82% of the land cover (Figure 2a). At this scale, it was not possible to separate accurately cabruças from cacao shaded by either rubber trees or *Erythrina* spp. However, during the field work it was confirmed that cabruças were predominant in most of the visited private properties. Only 4.8% of the landscape was covered by forest remnants, often being small, ranging from 1 to 300 ha in area (mean of 63.8 ± 37 ha), distant from one

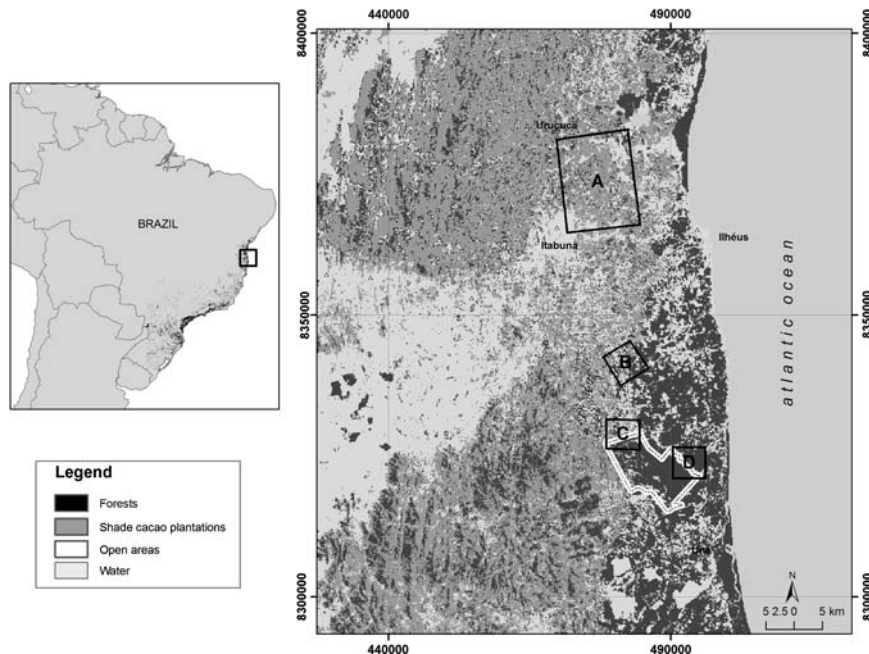


Figure 1. Map of southern Bahia showing the areas covered by shade plantations and forest tracts. The landscape studied in Ilhéus (A) and the three sampling blocks from Una (B, C and D) are shown, and the white polygon in Una represents the perimeter of the Una Biological Reserve (modified after Landau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

another (see Figure 2a) and highly disturbed. In this landscape, bird sampling was undertaken in four replicates of each habitat (cabruças and forest fragments), while bat sampling was carried out in three replicates of each habitat (Figure 2a).

In the coastal zone, where most of the forest remnants are concentrated, we undertook the bird and bat sampling in the district of Una, which holds one of the largest forest remnants of northeastern Brazil, including the 11,000 ha Una Biological Reserve which was officially established in 1980 (Coimbra-Filho et al. 1993). Additionally, at least 14,216 ha of other privately owned forest fragments and reserves are contiguous to the Biological Reserve (Araújo et al. 1998). A detailed study of 14,300 ha of Una landscape revealed that it is composed primarily of a mosaic of forests in different successional stages, with nearly 50% dominated by mature forest fragments, and an additional 16% of early secondary forests (Pardini 2001; Faria 2002). Most forest remnants are physically connected by other modified forested habitats such as second growth vegetation or by narrow strips of primary forests, as well as by cabruças, which comprise only 6% of the land cover. With a few exceptions, cabruças are quite small (mean of 35.7 ± 24.8 ha) and scattered within the matrix, often established close or adjacent to forest patches.

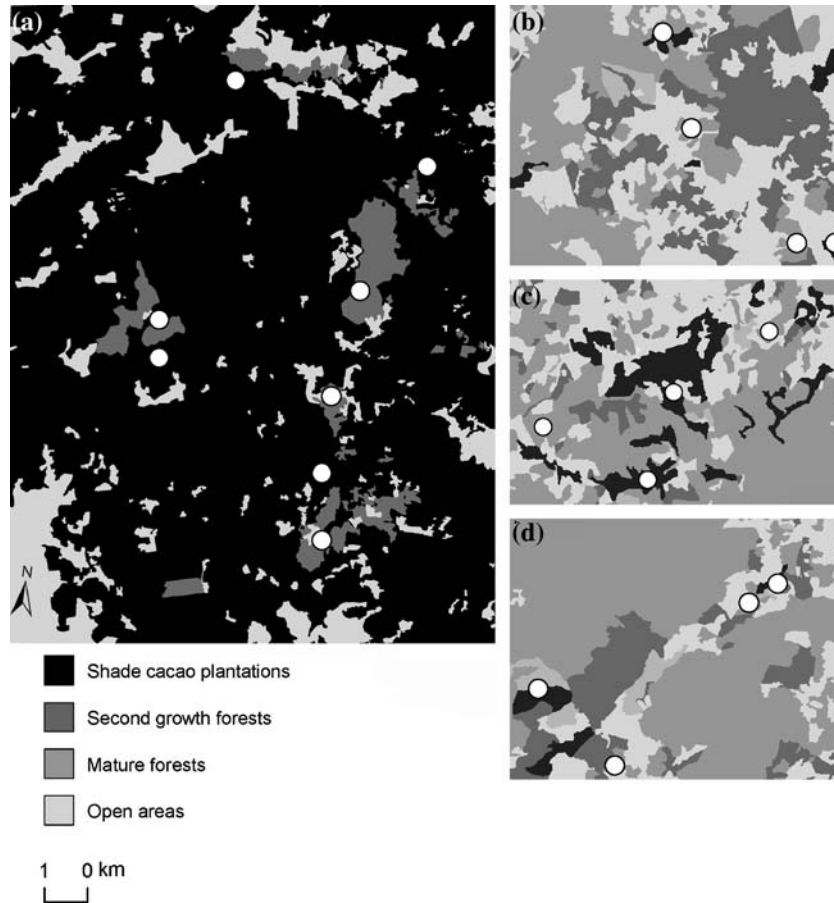


Figure 2. A detailed mapping of the studied landscapes of Ilhéus (a) and Una (b, c, and d). In Ilhéus the map considered the presence of three categories of land cover: open areas, forests and shade plantations, which included cabruca. In the map of the three sampling blocks in Una it was possible to differentiate mature forests from second growth stands, and all the shade plantations represented cabruca. The position of each sampling transect is shown by a white circle.

Birds and bats were sampled in Una in six small forest fragments (< 100 ha) and six cabruca. These habitats were located in three sampling blocks of 6 by 6 km, with two replicates of each habitat type located in each block (Figure 2b, c, d). The blocks also contained large forest remnants (> 1000 ha; Pardini 2004).

The selected cabruca from both landscapes are actively managed plantations, with a high degree of shade, mostly determined by the presence of native canopy trees, although some exotics were present (e.g. jackfruit – *Artocarpus heterophyllus*, rubber trees, *Erythrina* spp.). In each selected cabruca and natural forest, a 200 m long, 1 to 2-m wide transect was established, positioned at

least 100 m from surrounding habitats to avoid edge effects (Figure 2). Surveys of birds and bats were conducted along the same transects.

Sampling of birds and bats

We monitored birds using point count surveys (Ralph et al. 1995), establishing three sampling points located 100 m apart along each 200 m transect. All points were sampled at hourly intervals starting at sunrise to 5 h later. Points sampled in the same time interval were 200 m apart. Each point was sampled during 15 min, and all birds detected (sighted or heard) in a 30 m fixed-radius were registered. 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 carried out along two consecutive years (1999–2000) totaling 360 point counts (total survey time of 90 h), while the Ilhéus sampling was limited to July 2002, with an effort of 120 point counts (total survey time of 30 h). To standardize the sampling effort among the sites, we applied the Indice Ponctuel d'Abondance (IPA) method (Blondel et al. 1970, 1981), i.e., instead of using the 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 surveys in Una were conducted from January 1998 to July 2001, with samplings regularly distributed on a bi-monthly basis, while in Ilhéus the total sampling occurred from June to July 2002. Bats were sampled with ground mist nets placed along transects. Like any other sampling technique, the use of ground mist nets gives a biased picture of local bat assemblages, readily sampling most of Phyllostomidae bats, but often underestimating the presence or abundance of the remaining species (Fenton et al. 1992). Nevertheless, sampling with mist nets was chosen because it is the most widespread methodology used to assess bat biodiversity (Kunz 1982).

In each sampling night, a set of eight 2.5-m high mist nets was established along the transect, totaling a sampling area of 165 m². Nets remained open for 5 h after sunset, resulting in a sampling effort of 825 m² per night per site. Each transect was equally sampled during four non-consecutive, moonless and non-rainy nights, resulting in a total sampling effort of 39,600 m² for sites in Una and 19,800 m² in Ilhéus. Nets were checked every 30 min and all captured bats were identified, weighed, sexed and kept inside cloth bags until the end of the sampling night, after which they were released. Bats were not tagged during the study, so the number of captures probably includes recaptures. However, studies have shown that recapture rates of Neotropical bats are low (Thomas and La Val 1988; Bernard and Fenton 2003), and the capture frequency has been used as an index of abundance (Gorresen and Willig 2004).

Data analysis

We first tested for differences in bird and bat species richness between habitats (cabruças vs. forest fragments) and landscapes (Ilhéus vs. Una) as well as interactions between these two factors, by Analysis of Covariance (ANCOVA), using sample size (captures in bats, registers of calls for birds) as a covariate because of its well-known effect on species richness (Willott 2001). We confirmed the existence of linear relationships between species richness and sample size (log transformed data) of bats ($n = 18$; $r^2 = 0.615$; $p < 0.001$) and birds ($n = 20$; $r^2 = 0.660$; $p < 0.001$). Rarefaction curves, used to compare the expected number of species in samples of different sizes, were calculated for bats and birds with the package PAST (Hammer et al. 2001), using the algorithm of Krebs (1989) and including standard errors. The Shannon diversity index (H') for each combination of habitat type and landscape was also calculated using the PAST package.

The similarity of species composition of each biological group among the combinations of habitats and landscapes was compared by cluster analysis using the presence/absence Sorensen index as a measure of similarity. Clusters were constructed by the unweighted pair-group method using the arithmetic averages (UPGMA) algorithm.

We categorized bats and birds into broad feeding guilds. Based on literature (Bonaccorso 1979; Kalko et al. 1996; Fenton et al. 1999), bats were assigned as aerial insectivores (AI), carnivores (CA), frugivores (FR), gleaning insectivores (GI), nectarivores (NE), omnivores (OM) and sanguinivores (SA). Birds were classified according to literature (Stotz et al. 1996; Sick 1997) and own knowledge into guilds described by Greenberg et al. (1997) according to foraging strata (canopy, ground and understory) and main dietary category (omnivores, nectarivores, insectivores, granivores and frugivores). The class of insectivore habitat-generalists was also included, to consider those generalist insectivores related to disturbed areas and edges. The number of species in each feeding guild was compared by Chi-square statistics.

As most conservation efforts focus on conserving sensitive, forest dependent species, we categorized birds and bats as forest interior species by selecting those commonest species reported in the interior areas (> 75 m from the edge) of large forest tracts (> 1000 ha) of the Una region, which possibly represents one of the most pristine habitats left in southern Bahia. This species list was obtained from the data bank of Projeto Resta Una (<http://www.resta-una.org.br>), and was collected under the same sampling protocol as the data of the present study. We examined the presence and the variation in the average number of captures and IPA values (for bats and birds, respectively) of these forest interior species among habitats and landscapes and the possible effect of interaction between these two factors, using a two-way ANOVA. This analysis was restricted to the 10 most common bird species and the three most common bat species from the interior of large forest tracts in Una because of the low number of observations for the remaining species. The 10 bird species, which

together comprised 42% of the registers, included (in descending order of dominance) the scaled antbird (*Drymophila squamata*), the screaming piha (*Lipaugus vociferans*), the reddish hermit (*Phaethornis ruber*), the bananaquit (*Coereba flaveola*), the grayish mourner (*Rhytipterna simplex*), the rufous-capped antthrush (*Formicarius colma*), the white-shouldered fire-eye (*Pyriglena leucoptera*), the olivaceous woodcreeper (*Sittasomus griseicapillus*), the black-capped antwren (*Herpsilochmus pileatus*) and the black-cheeked gnateater (*Conopophaga melanops*; R.R. Laps, unpublished). The three bat species were *Rhinophylla pumilio*, *Carollia perspicillata* and *Artibeus obscurus* and contributed 87.4% of all captures from forest interiors in Una (Faria 2002).

The assumptions of the ANCOVA and ANOVA models were checked with Kolmogorov-Smirnov and Levene tests; skewness and kurtosis of the residuals were also analyzed (Zar 1999). For all analyses, differences were considered to be statistically significant at $p < 0.05$, and the analyses were run using the software SPSS 10.0.1 (SPSS 1999).

Results

General aspects

Both habitats and landscapes surveyed comprised rich and diverse assemblages of birds and bats. During the entire study, we detected 5,081 birds from 197 species and 44 bat species from 2,908 captures, which probably included recaptures (see Methods). With the same sampling effort in each habitat (Table 1), bird and bat richness was higher in cabrucas than in forests. These shade crops harbored 87.8% of bird and 93.2% of the bat species recorded, and the majority of bird records (58.2%) and bat captures (82.1%) were obtained in cabrucas (Table 1). Sixty-four percent of bird and 56.8% of bat species were recorded in both habitats. Bird species diversity was slightly higher in forests than cabrucas; in contrast, cabrucas, particularly those located in the Una region, showed the highest overall value of bat species diversity (Table 1).

Species richness and faunal similarities

The applied linear models explained a large amount of the variance in species richness of birds ($r^2 = 0.804$) and bats ($r^2 = 0.972$) with sample size explaining part of the variation of species richness in birds ($p = 0.003$) and bats ($p = 0.05$). Both biological groups showed similar variation of species richness (Figure 3), with marked interactions between habitats and landscapes (birds: $F = 6.9$, $p = 0.018$; bats: $F = 6.3$, $p = 0.025$). Bird and bat communities were richer in cabrucas located in Una compared to nearby forest, while cabrucas from the Ilhéus landscape were significantly poorer in species than nearby forest fragments (Figure 3). Overall, bird assemblages were poorer

Table 1. Summary of sampling effort, number of species, sample size (records for birds and captures for bats) and Shannon–Wiener diversity index (H') of bird and bat assemblages sampled in forests and cabruças from two landscapes in southern Bahia, Brazil.

Habitat	Landscape	Birds			Bats			Capture frequency	H'
		Sampling effort (point counts)	Number of species observed	Number of registers	H'	Sampling effort (nights)	Number of species reported		
Forest	Una	180	139	1852	4.37	24	21	345	1.63
	Ilhéus	60	78	263	3.88	12	17	175	1.82
	Total in forests	(240)	(150)	(2115)	(4.32)	(36)	(27)	(520)	(1.77)
Cabruca	Una	180	187	2577	4.33	24	39	1314	2.34
	Ilhéus	60	74	383	3.73	12	23	1074	1.61
	Total in cabruca	(240)	(173)	(2960)	(4.28)	(36)	(41)	(2388)	(2.12)
Total			197	5081			44	2908	

Numbers in parenthesis refers to the totals obtained in each habitat type from both landscapes.

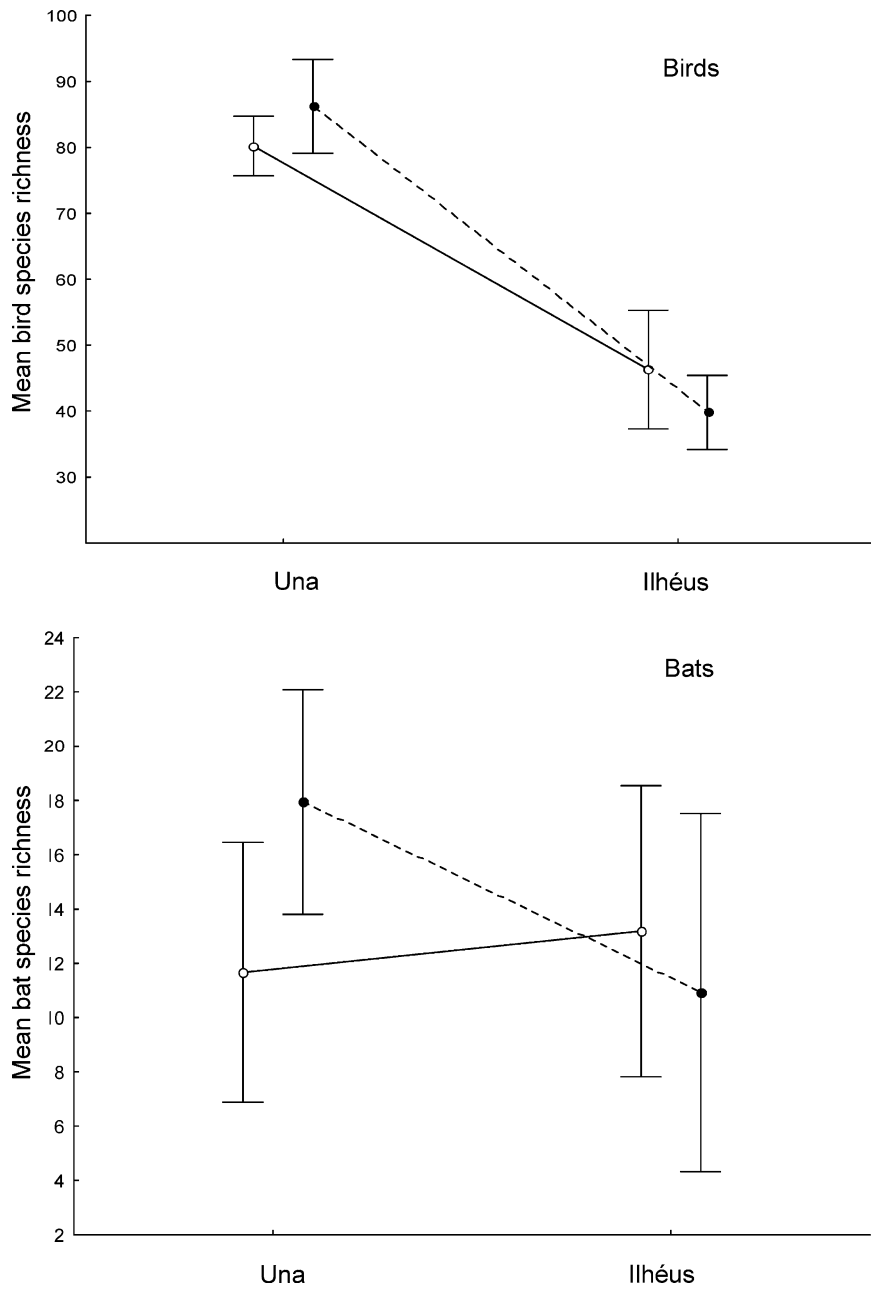


Figure 3. Least square means of bird and bat species richness in forest fragments (open circles) and cabruças (solid circles) located in Una and Ilhéus landscapes respectively, in southern Bahia, Brazil. Vertical bars denote 0.95 confidence intervals.

in Ilhéus than in Una, and this tendency was also noticed for bat communities, though differences were not significant (birds: $F = 101.5$, $p < 0.0001$; bats: $F = 2.5$, $p = 0.137$; Figure 3).

For both groups, rarefaction curves also illustrate the differences in species richness among habitats and landscapes (Figure 4). For a given sample size, higher bird and bat species richness are expected for the cabruças from Una compared to the forest fragments, and lower species richness is expected from cabruças than forest fragments of Ilhéus.

Cluster analysis showed a similar bird species composition between cabruças and fragments from Una, as they formed a single cluster, while no consistent similarities were found between these two habitats in Ilhéus (Figure 5). For bats, the landscapes formed two distinct groups, each one comprising forests

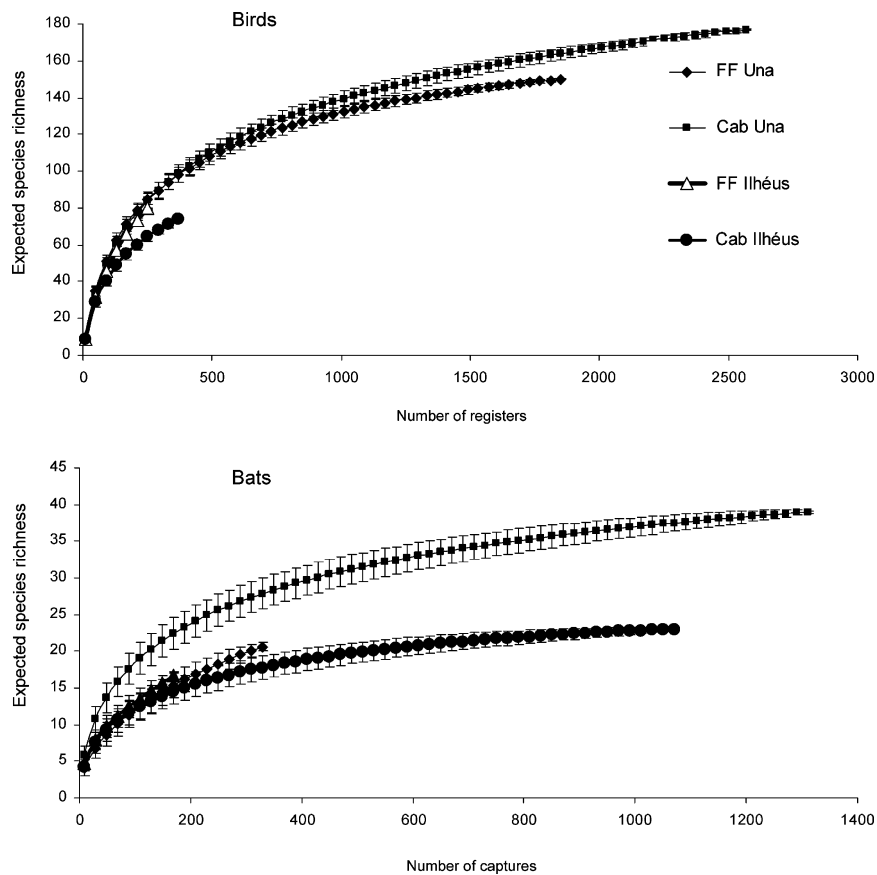


Figure 4. Rarefaction curves for the expected number of bird and bat species from equal sample sizes taken from forest fragments and cabruças located in Una and Ilhéus landscapes, FFUna: forest fragments of Una, CabUna: cabruças of Una, FF Ilhéus: forest fragments of Ilhéus and Cab Ilhéus: cabruças of Ilhéus. Bars are ± 1 standard error.

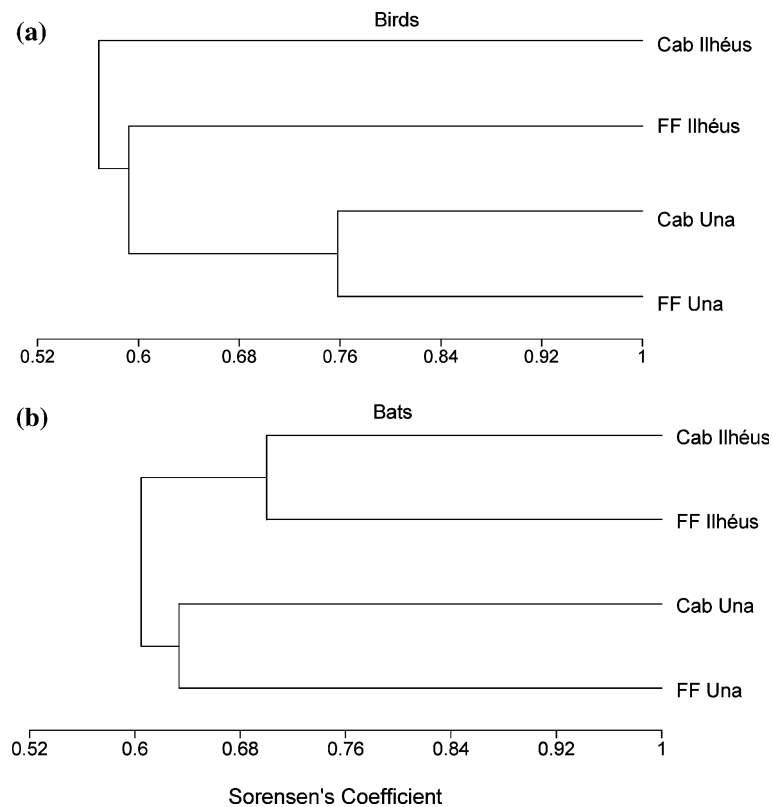


Figure 5. Cluster analysis (UPGMA) for similarity of species composition calculated for birds (a) and bats (b) using the Sorensen index (presence/absence) for forest fragments and cabruças located in Una (FFUna and CabUna) and Ilhéus (FFIlhéus and CabIlhéus) landscapes, in southern Bahia, Brazil.

and their nearby cabruças, with higher similarity between the Ilhéus habitats than those located in Una (Figure 5).

Feeding guilds

The most pronounced differences in bird and bat feeding guilds were reported between the two habitats in both landscapes. Bird faunas in cabruças, of both landscapes, were characterized by proportionally fewer understory insectivore ($\chi^2 = 17.09$, $p = 0.0007$, $df = 3$) and frugivore species ($\chi^2 = 9.368$, $p = 0.0248$, $df = 3$) and more generalist feeders, such as nectarivores ($\chi^2 = 9.186$, $p = 0.02$, $df = 3$), omnivores ($\chi^2 = 27.857$, $p < 0.00001$, $df = 3$) and insectivores from open areas than the forest bird fauna ($\chi^2 = 18.586$, $p = 0.0003$, $df = 3$) (Figure 6). Ground granivores, representing eight species in Una, were represented in Ilhéus only by a single species reported in forest fragments ($\chi^2 = 10.571$, $p = 0.01$, $df = 3$).

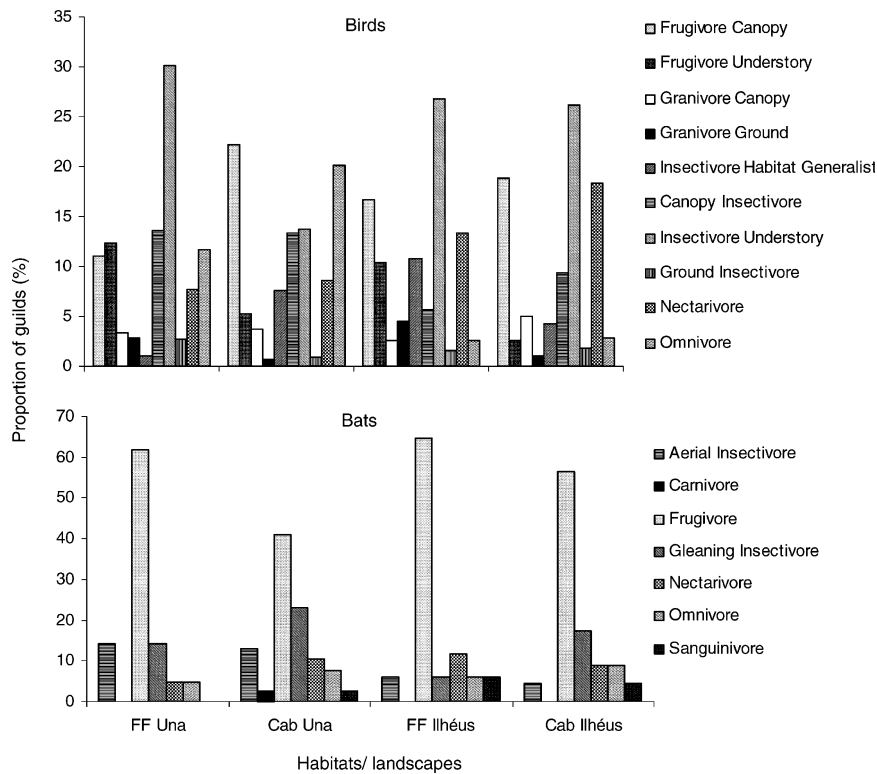


Figure 6. Proportional representation (%) of the species richness in each feeding guild of birds and bat assemblages in forest fragments and cabruças located in Una and Ilhéus landscapes, southern Bahia, Brazil. The combinations of habitats and landscapes are as follows: FF Una: forest fragments of Una, Cab Una: cabruças of Una, FF Ilhéus: forest fragments of Ilhéus and Cab Ilhéus: cabruças of Ilhéus.

Frugivorous bats were the most speciose guild, followed by the gleaning insectivores (Figure 6). The remaining guilds had too few species to allow statistical comparisons. Overall, the number of frugivorous species did not differ statistically among the combination of habitats and landscapes ($\chi^2 = 0.962$, $p = 0.81$, $df = 3$), but a higher number of species classified as gleaning insectivores was reported in the cabruças from Una ($\chi^2 = 8.176$, $p = 0.04$, $df = 3$). The latter cabruças were composed of bat species from all feeding guilds, including a single carnivore (*Chrotopterus auritus*) capture.

Comparisons of individual species

From the ten bird species categorized as common forest-dwellers, the understory frugivore *L. vociferans* was exclusively reported in fragments from Una, *D. squamata*, *H. pileatus* and *P. leucoptera* were absent from the cabruças of

Ilhéus, while the remaining six forest interior species were present in forests and cabruças of both landscapes (Table 2). The hummingbird *P. ruber* was present in all study sites and did not show any effect of habitat, landscape or interaction between these two factors (Table 2), while all the remaining forest species presented marked and significant differences regarding their abundance among the combination of habitats and landscapes (Table 2). Eight species showed significant or marginally significant effect of habitat type: one restricted to fragments (*L. vociferans*), six being more commonly observed in forest fragments than cabruças (the understory insectivores *D. squamata*, *H. pileatus*, *P. leucoptera*, *R. simplex* and the ground insectivores *C. melanops* and *F. colma*) and one more frequent in cabruças than forest fragments (the nectarivore *C. flaveola*). Seven forest bird species showed significant or marginally significant differences between the two landscapes, with one species (*L. vociferans*) restricted to Una, most species more common in Una than Ilhéus (the understory insectivores *D. squamata*, *R. simplex*, *S. griseicapillus* and the ground insectivores *C. melanops* and *F. colma*) and only the nectarivore *C. flaveola* more abundant in Ilhéus than in Una (Table 2).

The three dominant bat species from the interior of large forest tracts were present in both habitats and landscapes. The understory frugivore *C. perspicillata* was the dominant species everywhere, with a significant increase in its capture frequency in cabruças compared to forest fragments, particularly in Ilhéus where this species accounted for nearly 60% of all captures (Table 3). *Artibeus obscurus* was more frequent in cabruças than in forest fragments for both landscapes (Table 3). A significant interaction between habitat and landscape was found to influence the abundance of *R. pumilio* (Table 3). In Una, this species was clearly more abundant in cabruças than forest patches, while in Ilhéus it occurred more in forests than cabruças, following the same pattern of variation as the total bat species richness (Figure 3). In Ilhéus, *R. pumilio* was among the three dominant species in forest fragments (22.3% of all captures), but in cabruças it represented less than 2% of the total captures.

Discussion

The cabruça as habitats for birds and bats

Our study supports the general notion that the cabruça system can harbor a significant part of the native bird and bat fauna in southern Bahia forests, including species usually associated with more pristine forests. However, the extent to which a given cabruça can support forest species assemblages clearly varies between biological groups and also differed between the two landscapes considered in this research.

Structural complexity of shade plantations, such as the cabruças of southern Bahia, is probably the main feature influencing their use by wild species at a local scale (Perfecto and Snelling 1995; Moguel and Toledo 1999; Reitsma

Table 2. Mean values and standard deviations of the Indice Ponctuel d'Abondance (IPA) of forest interior bird species in small forest fragments and cabruças in Una (FF Una and Cab Una) and in small forest fragments and cabruças in Ilhéus (FF Ilhéus and Cab Ilhéus), southern Bahia, Brazil.

Species	Habitat and landscape						Significance level (p)					
	FF Una		Cab Una		FF Ilhéus		Cab Ilhéus		Habitat	Landscape	Interaction	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation				
<i>C. flaveola</i>	0.310	0.076	0.6898	0.0619	0.6042	0.1042	0.9792	0.0924	0.000	0.003	0.978	
<i>C. melanops</i>	0.199	0.067	0.0138	0.0062	0.0208	0.0208	0	0	0.029	0.040	0.073	
<i>D. squamata</i>	0.435	0.097	0.0139	0.0139	0.2083	0.1102	0	0	0.001	0.008	0.086	
<i>F. colma</i>	0.213	0.081	0.0138	0.0095	0.0208	0.0208	0	0	0.050	0.065	0.106	
<i>H. pileatus</i>	0.217	0.050	0.0833	0.0351	0.1458	0.0625	0	0	0.007	0.109	0.901	
<i>L. vociferans</i>	0.088	0.044	0	0	0	0	0	0	*	*	*	
<i>P. ruber</i>	0.389	0.054	0.3981	0.1026	0.4792	0.0208	0.625	0.1423	0.916	0.089	0.484	
<i>P. leucoptera</i>	0.176	0.051	0.046	0.0137	0.125	0.0538	0	0	0.005	0.234	0.954	
<i>R. simplex</i>	0.204	0.041	0.097	0.0224	0.0417	0.024	0.0417	0.024	0.065	0.002	0.201	
<i>S. griseicapillus</i>	0.231	0.010	0.324	0.1028	0.0625	0.0398	0.1041	0.0625	0.363	0.015	0.727	

Significance levels for the two-way ANOVA is presented for comparisons of habitat (forests and cabruças), landscapes (Una and Ilhéus) and the effect of interaction between habitats and landscapes, with values in bold indicating significant probabilities ($p < 0.05$).

*The understory frugivore *L. vociferans* was restricted in forest fragments of Una, precluding statistical comparisons.

Table 3. Mean values and standard deviations of the capture frequency of forest interior bat species in small forest fragments and cabruças in Una (FF Una and Cab Una) and small forest fragments and cabruças in Ilhéus (FF Ilhéus and Cab Ilhéus), southern Bahia, Brazil.

Species	Habitat and landscape						Significance level				
	FF Una		Cab Una		FF Ilhéus		Cab Ilhéus		Habitat	Landscape	Interaction
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard Deviation	Mean	Standard deviation			
<i>A. obscurus</i>	4.5	2.3	25.0	8.3	4.6	1.5	27.3	3.7	0.001	0.570	0.910
<i>C. perspicillata</i>	23.6	22.2	77.3	44.2	24.6	13.3	209.6	91.3	0.001	0.049	0.150
<i>R. pumilio</i>	19.5	10.2	33.1	15.5	13	7.5	6.0	6.2	0.580	0.120	0.010

Significance levels for the two-way ANOVA is presented for comparisons of habitat (forests and cabruças), landscapes (Una and Ilhéus) and the effect of interaction between habitats and landscapes, with values in bold indicating significant probabilities ($p < 0.05$).

et al. 2001; Schroth et al. 2004). Compared to the original forest, structural and floristic simplification of cabruacas impacted birds and bats in different ways. The complete suppression of native understory vegetation and the thinning process of the canopy layer that characterizes cabruacas allowed the influx of edge and open field bird species (e.g. seedeaters and swallows) and omnivores. Nectarivore records (e.g. *C. flaveola*) also increased in cabruacas relative to forests, possibly because of the composition of shade trees that includes, among others, some attractive flowering plant species for this group such as the legume *Erythrina* sp. In the Dominican Republic, *C. flaveola* was also very common in shade coffee plantations, foraging mainly on flowers of the legume *Inga* sp. (Wunderle and Latta 1998).

Losses of forest interior bird species in cabruacas included the frugivore Screaming Piha (*Lipaugus vociferans*), a very common representative of the understory of pristine, large forest tracts in Una, that was virtually absent from cabruacas. The significant decrease of six common understory, forest interior species further highlights the significant alterations in the bird community structure of cabruca plantations. Nevertheless, cabruacas harbored nearly 90% of the bird species reported in the present study, with 64% of the species also reported from forest fragments, which includes nine out of ten most common forest interior species investigated here. For birds, the cabruca system is most likely to be characterized as an ecotone, comprising the juxtaposition of the invaders from more open, disturbed areas (those forest species that are enhanced by local disturbance regimes, e.g. gap specialists), and a subset from the forest-dwelling species supplied by the surrounding forests tracts.

Bat assemblages in cabruca were even richer, more diversified and abundant than in forests and encompassed nearly all the species and the bulk of bat captures. Cabruacas included almost all species from forest tracts and from all categories of feeding guilds, including the gleaning insectivores, a feeding guild known to harbor species usually regarded as sensitive to habitat disruption (Fenton et al. 1992) and overall disturbances (Medellín et al. 2000). The three dominant species from nearby forest tracts actually increased or maintained their frequencies in cabruacas. The overwhelming richness, diversity and frequency of bats in cabruacas is also likely to be influenced by the structural and floristic features of the cabruacas. Tropical forests represent complex habitats, and bats are known to show a consistent pattern of use of this vertical stratification, with species foraging preferably or exclusively in specific forest heights (Handley 1967; Bernard 2001). The simplification of the vertical structure, with a thinned canopy and a less dense stratum below (Alves 1990; Johns 1999; Faria 2002), is likely to facilitate movements of bats in these shade plantations, resulting in an increased ability to catch bats by the mist nets placed 1–2 m from the ground. This might explain the higher capture rates in the cabruacas of some well known Phyllostomidae canopy species in ground mist nets, such as *Artibeus jamaicensis*, *Artibeus lituratus*, *Chiroderma villosum* and *Phyllostomus hastatus* (Faria 2002). Frugivorous and nectarivorous bats are known to feed on fruiting plants in both canopy and herbaceous layers in

shade plantations elsewhere (Estrada et al. 1993, 2002). Plants from the genus *Piper* are amongst the most abundant and widespread species growing in the herbaceous layer of cabruças, and are the main food source for *C. perspicillata* (Fleming 1991; Thies and Kalko 2004) and, to a minor extent, for *R. pumilio* (D. Faria, unpublished), both dominant forest species in cabruças. Hence, the combination of a less dense though still vertically stratified, multilayered habitat with the maintenance of food resources may explain the presence and the high frequency of many bat species in cabruças.

Additional observations suggest that birds and bats use cabruças not only as stop-overs or foraging habitats, but also as breeding grounds and roosting sites. Several bird species have been recorded as breeding in cabruças (e.g. tyrants, furnariids), among them the endangered white-necked hawk (*Leucopternis lacernulatus*) was observed regularly singing while perched in cabruças from Una. The endangered and endemic *Acrobatornis fonsecai* was observed nesting in cabruças in Ilhéus, showing the importance of cabruças for certain endangered bird species. Bats were reported in day roosts inside cabruças, including hollow trees (*C. perspicillata*, *Phyllostomus discolor*, *Phyllostomus hastatus*, *Trachops cirrhosus*), termite nests (*Lophostoma silvicolium*) and leaves of herbaceous plants of *Heliconia* spp. (*Thyroptera tricolor*; Faria 2002).

Cabruças as matrix components

Important differences were observed in the structure and composition of bird and bat communities from cabruças in Una and Ilhéus, and the contrasting pattern of the landscapes is likely to be a key factor influencing these changes. The fragmented landscape of Una still combines the existence of large and small forest patches that are physically connected by a net of narrow strips of mature vegetation and the presence of small patches of second growth and forest crops, which include the cabruças. Under this situation, data from butterflies (Accacio 2004), frogs (Dixo 2001), birds (Laps et al. 2003), small mammals (Pardini 2001) and bats (Faria 2002; Vieira et al. 2003) show that the landscape from Una, although fragmented, is still functionally connected for these biological groups, with small fragments generally supporting most of the species reported for the large, nearby forest tracts. In the Una landscape, all the 13 species regarded as common in interior areas of large, pristine forest fragments were reported in small forests, and except for a single understory bird species (*L. vociferans*), they were also present in the local cabruças. Bird and bat assemblages in cabruças from Una harbored most of the species reported to occur in the local forest fragments, showing similar or even higher species richness and diversity compared with the local forest fragments.

In spite of changes in the overall representation of feeding guilds and forest interior species already discussed, the species composition of the cabruças from Una resembled those of the local fragments for both biological groups, indicating that the mosaic comprising cabruças, forest fragments and the larger

forest tracts present at Una, in some way, provides sufficient resources to maintain bat and bird populations. Although we have no data regarding the persistence of populations in cabruças, the presence of breeding and roosting species in this habitat may indicate that some populations can rely on cabruças as resident areas and, possibly, form self-sustaining populations. On the other hand, populations of some species that were seen in cabruças may be the result of constant recolonization from larger forest tracts.

By contrast, in Ilhéus, where the native forest remnants are reduced and cabruças dominate the entire landscape, these shade plantations supported overall impoverished bird and bat communities compared to Una, with four bird forest interior species not being reported in these cabruças (*D. squamata*, *H. pileatus*, and *P. leucoptera*) or from the entire landscape (*L. vociferans*). In addition, the bird species whose population increased in cabruças from Ilhéus were the generalist insectivores and nectarivores (like *C. flaveola*) or those that could take advantage from second-growth vegetation (like *P. ruber*).

Forest species composition of both biological groups in Ilhéus differed from those forest fragments in Una, even considering the short distance between the two sampling landscapes (< 20 km). Some forest species of birds were missing (*L. vociferans*) or greatly reduced in Ilhéus. The endemic black-capped antwren (*Herpsilochmus pileatus*) is restricted to a narrow band of coastal forest in southern Bahia (see Whitney et al. (2000) for a redefinition of the taxon and conservation issues). It deserves special attention because of its presence in forest fragments, but the sharp decline in cabruças (mainly in Ilhéus) suggests that landscapes dominated by cabruças may not support large populations of this species unless sufficient forest cover remains.

Differences in bat and bird species composition between the two landscapes and the overall impoverishment of both assemblages in the cabruças at Ilhéus are probably related to differences in landscape structure. While both landscapes present matrices dominated by forested areas, the presence of large forest tracts in Una is possibly a key factor allowing the maintenance of larger populations of forest species that can, throughout a connected landscape, constantly supply both small fragments and cabruças. In Ilhéus by contrast, because native forest area is reduced to less than 5% of the land cover and large forest areas (>1000) are missing, the small forest remnants are the only habitat available for more strictly forest-dependent species, and possibly the source of populations of many forest-dependent species that are able to exploit the cabruças. Reduction in the effective size of forest-dependent populations is expected to occur in smaller forest habitats (Wiens 1989), restricting the potential of these patches to support viable populations or to supply other habitats with colonizers. For instance, four forest interior species of birds that were less common in cabruças in Ilhéus were also less common in forest fragments in Ilhéus than in Una (*C. melanops*, *F. colma*, *R. simplex* and *S. griseicapillus*). Also, we observed broad variations in the number of records of some forest interior birds among the fragments sampled in Ilhéus, as reflected by large standard deviations (see Table 2). For example, *D. squamata*

was recorded in three forest fragments in Ilhéus, but 60% of all records were reported only from the largest fragment (300 ha), showing a heterogeneous representation of presence and abundance of this species among the sampled fragments.

For bats, cabruças in both landscapes showed a similar species composition to that found in local forest fragments, but as for birds, bat communities in cabruças from Ilhéus were impoverished compared with those from Una. Notable changes in the proportional representation of two common forest interior bat species occurred in cabruças from Ilhéus. These shade plantations were highly dominated by *C. perspicillata*, which comprised nearly 60% of local captures. A remarkable result is the decrease in the proportional representation of *R. pumilio* in cabruças from Ilhéus compared with those in nearby forests. *Rhinophylla pumilio*, the most frequent bat species from forest interiors of large fragments in Una and in forest fragments from Ilhéus, but it represented less than 2% of the captures in the cabruças from Ilhéus. In a previous study also conducted in Ilhéus, the frugivores *R. pumilio* and *A. obscurus* were seldom caught in cabruças when the sampling site was located more than 2 km away from the closest forest tract (Ortiz et al. 2002; Britez et al. 2003), indicating that the presence of both species, despite their high frequencies, is probably influenced by the closeness of those cabruças to forest tracts.

Additionally, the small forest remnants sampled in Ilhéus, although showing a size range similar to those sampled in Una (> 300 ha), are usually more disturbed than the fragments from Una, probably as a result of earlier fragmentation and overall exploitation (Eduardo Mariano, unpublished). For birds, these disturbed forest fragments may favor generalist/opportunist species, further increasing their supply for the surrounding cabruças.

Conclusions

The wet forests of southern Bahia represent some of the world's highest levels of species richness and endemism, but the native forest cover is fragmented and sharply reduced, with 5–7% of its original extent remaining (Thomas et al. 1998). Our results have demonstrated that cabruças can provide habitat for a substantial number of native bird and bat species from this biodiversity rich, Neotropical region.

Matrices comprising complex agroforests, which includes cabruças, are more desirable from a conservation perspective than other agricultural land uses that are more structurally simplified or devoid of tree cover (Schroth et al. 2004). Certainly many more species from the local biota would have declined or even disappeared if the areas covered by cabruças were represented by cattle-pastures or by intensified agricultural use. Bearing in mind that cabruças represent the bulk of the forested areas in southern Bahia (May and Rocha 1996; Figure 1), these shade crops are certainly playing a paramount role in

conserving part of the regional biodiversity, especially in places where cabruças are the only forested areas available. The replacement of the cabruças by other more structurally simplified land uses would likely have negative impacts on many species and populations of the regional biota.

However, important differences in bat and bird community structure between the two landscapes outline the key role played by natural habitats as population sources of forest species to cabruças, pointing out that these shade plantations *per se* are not true substitutes for the original forest (Alves 1990; Greenberg 1998; Schroth et al. 2004a, b). The potential of cabruças to provide habitat for forest-dwelling species seems to be closely linked to the presence and abundance of these target species in the nearby forest. For instance, when forest remnants are impoverished, as in Ilhéus, so are the surrounding cabruças. In contrast, when small forests harbor rich species assemblages – because of connectivity with larger remnant forests in the landscape – then the nearby cabruças also maintain a substantial portion of the forest biodiversity of both bats and birds, as well as elements of more open bird faunas.

In the Una landscape, and possibly in other larger remnants along the coast of the cacao region, cabruças are important complementary habitats for many species reported from the native forests, and may contribute to landscape connectivity as well as serve as buffers for the forest itself. From our data, it is unlikely that a dominant cabruça matrix and the small, highly disturbed forest fragments as found in Ilhéus are adequately conserving forest-dependent bird and bat species at a landscape scale, including some target species of major conservation concern. Increasing and reinforcing actions to preserve and restore native forest remnants are necessary steps to ensure an adequate representation of the native biota, and the long-term persistence of the remnant populations. Therefore, in order to effectively conserve the original species assemblages in Ilhéus, and probably throughout the core region of cocoa production where shade cacao plantations represent most of the forest cover left, we need to consider the role of cabruças as habitats for the local biota, but also keep in mind the imperative to conserve and increase the representation of native forest remnants within the landscape without which the conservation impact of the cabruças will be severely restricted.

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