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Slow death of Atlantic forest trees in cocoa agroforestry in southeastern Brazil

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Abstract. Cocoa (Theobroma cacao) is cultivated in the states of Bahia and Espírito Santo in eastern Brazil under the so-called 'cabruca system', where the understorey of native Atlantic forest is cleared and the canopy is thinned out to provide adequate shading for the cocoa trees. Apart from its economic and social role, the cabruca system is said to be important for the conservation of Atlantic forest biodiversity. In this paper we studied tree species richness and forest structure of cabrucas to examine the demographic health of these forests and discuss their long-term survival. Data were collected in 20 farms located alongside a 30 km track of the northern margin of the Rio Doce, in northern Espírito Santo. All trees \geq 5 cm DBH were identified and their diameter was measured in 80 plots (600 m²), totalling 4.8 ha of sampled area. Recorded trees were also allocated to four different regeneration phases (pioneers, early secondary, late secondary and climax). The inventory resulted in 507 trees belonging to 105 species in 39 families. This species richness is much lower than in less disturbed forests located in the region. Pioneers and early secondary species dominate the cabruca forest in terms of number of species (56.2%), density (71.0%) and basal area (72.3%). The distribution of diameter frequency showed an imbalance in tree regeneration. Most trees in the range of 5–30 cm DBH were pioneers (40.7%), or early secondary species (32.6%), while late secondary and climax trees were less frequent (10.2 and 16.5% of the sampled trees, respectively). The dominance of species of early regeneration phases was also observed for trees >30 cm DBH (69.0% of pioneers or early secondary and 31.0% of late secondary or climax species). The results indicated that the cabruca forests are not only less diverse and less dense than secondary or primary forests of the region, but also, and more importantly, their natural succession and gap dynamics are being severely impaired. As a consequence, cabrucas present a structure where tree species of late successional phases are becoming increasingly rare while pioneers and early secondary species are becoming dominant. If current management practices of thinning and clearing of native trees are not improved, the long-term survival of these forests is questionable and their role in maintaining biodiversity in the long run is limited.

Introduction

Anthropogenic disturbances alter the ecology of tropical forests in several ways (Phillips 1997). Deforestation represents the greatest potential loss of species (Myers 1989; Whitmore and Sayer 1992), but other disturbances such as hunting (Chiarello 2000a; Cullen et al. 2000; Peres 2000) and forest fragmentation (Terborgh 1992; Lawrence et al. 2000), for example, can lead to 'empty forests' (Redford 1992), which may have their structure and dynamics affected due to the absence or reduced abundance of seed predators, dispersers and pollinators (Chiarello 2000b; Silva and Tabarelli 2000).

In the Atlantic coastal forests of the states Bahia and Espírito Santo, Brazil, about 4% of the world production of cocoa (Theobroma cacao L.), and 75% of the Brazilian production is obtained in what is locally called 'cabruca systems', a special type of agroforestry where the understorey is drastically suppressed to make room for cocoa trees and the density of upper storey trees is greatly reduced. This is done because the cocoa tree needs some shading, ideally between 30 and 60% of incident radiation (Batista and Alvim 1981), for fruit development and production (Cunningham and Burridge 1960). The retention of some native trees is also needed as a protection against winds throughout the life of the cocoa plant. In the Atlantic forest the cabruca systems allow the retention of native trees varying in density from 76 (Alvim and Pereira 1965) to 201 trees/ha (Fernandes and Vinha 1984).

Cocoa is one of the major economic activities in Bahia, extending over 650,000 ha and involving about 2 million workers (Alvim and Nair 1986). About 500,000 ha of production are under the cabruca systems and in 150,000 ha cocoa is cultivated under Erythrina fusca, Hevea brasiliensis, or other introduced tree species (Alvim and Nair 1986; Sena Gomes 1992). In Espírito Santo, cabruca systems extend over 17,000 ha along both banks of the lower Rio Doce, in the municipality of Linhares. Comparing the cabruca system with land use under other agricultural systems, the advantages of the former are obvious due mainly to the higher indirect economic value generated by the environmental services it provides (see Constanza et al. 1997, 1998). Additionally, agroforestry systems allow far better nutrient cycling, erosion control (water and soil retention), richer biological diversity and more complex trophic interactions than pastures or traditional field crops (Nair 1989; Montagnini 1992; Fassbender 1993; Parrish et al. 1998). These facts alone would justify the maintenance of the cabruca system as a better alternative to deforestation or establishment of more conventional agriculture.

The Atlantic forest in southern Bahia and northern Espírito Santo is a very important center of endemism and diversity of flora (Mori et al. 1983; Prance 1987; Peixoto and Silva 1997; Thomas and Carvalho 1997; Thomas et al. 1998) and fauna (Kinzey 1982). One of the main plants cultivated in the Atlantic forest, cocoa has historically contributed to the conservation of considerable forest cover in this biome, forming important refuges and forest corridors for the movements of animals and dispersion of propagules between fragments (Alves 1990; Hummel 1995; Johns 1999; Moura 1999; Pardini 2001; Saatchi et al. 2001; Sambuichi 2002). Additionally, a number of farmers and producers keep forest areas for the establishment of future cocoa plantations. A review of economic, cultivation and historic aspects of cocoa agroforestry was presented by Johns (1999), and its importance as a sustainable agroforestry system was stressed by Alger (1998), Duguma et al. (1998), Greenberg (1998), Parrish et al. (1998), and Power and Flecker (1998), among others. In this paper we present data that show, however, that the long-term survivorship of native forest trees under cabruca systems are under threat if the current management practices continue, mainly due to severe reductions in tree diversity and regeneration imbalances. This, in turn, results in a drastically

simplified forest structure where secondary species are benefited in detriment of primary species.

Study site and methods

The main cocoa-producing region in Brazil extends from the Rio Doce basin in the municipality of Linhares, Espírito Santo $(19°35' S)$, to the region of northern Ilhéus and Itabuna, in southern Bahia ($13^{\circ}00'$ S), a strip of approximately 700 km along the Atlantic coast (Vinha et al. 1983). In this region the predominant relief varies from flat to slightly undulated, always within the domain of the Atlantic forest. Cocoa was first introduced in this region in 1746, brought from Pará in the Amazon. In Espírito Santo the first saplings came from Bahia in the late 19th century and were planted in the valley of the Rio Doce. Thanks to government policies of land donation, cocoa cultivation expanded during the 1930s with production under cabruca systems. This epoch coincided with a crisis in coffee cultivation, which contributed to the expansion of cocoa as an economic alternative. The study area encompasses the northern margin of the Rio Doce in Linhares, where farms are distributed along approximately 30 km (Figure 1). The climate of this region is hot and humid, tropical with rainy summers and drier winters (Aw in Köppen's classification). Average annual precipitation is 1202 mm and the driest period occurs from May to August (average of 47.8 mm/month . The study area is located in a coastal lowland with average altitude of 20–30 m over sediments of both marine (sand) and fresh water (sand-clay) origins (Suguio et al. 1982). The soil along the Rio Doce is predominantly a eutrophic Cambissol with a moderate A horizon and clay texture.

Data collection

Data were collected from November to December 2000. The systematic sample technique was used for analysis of vegetation (Cochran 1977). A strip of land along the Rio Doce between the municipalities of Linhares and Povoação was divided in 60 equal parts, each 0.5 km wide. One of such parts was randomly chosen to be the first one to be sampled and the next ones were selected every 1.5 km from the first sampling part, totalling 20 systematic samples. Access to the area was possible due to existing dirt roads paralleling the margins of the river. In each farm, four 600 m^2 plots $(20 \text{ m} \times 30 \text{ m})$ were sampled between 100 and 500 m from the nearest dirt road. In case a sample was located in a farm whose owner/administrator denied entrance, the nearest farm was used instead for sampling. In each 600 m^2 plot, the diameter at breast height (DBH at 130 cm) of all trees was recorded, all native trees with DBH \geq 5 cm were identified by specialists (CVRD Herbarium) and all cocoa trees were counted. In total, the 20 systematic samples of four plots each resulted in 4.8 ha of sampled area. Density, basal area and frequency were estimated for all species and the 95% confidence interval (CI) was computed according to the formula (Cochran 1977): 95% CI = mean \pm ($t_{0.05}$) \times mean standard error.

Figure 1. Cocoa agroforestry in Rio Doce, Brazil, showing the study area (sample location in black points paralleling the margins of the river). Source: http://www.sosmatatlantica.org.br.

The rarefaction method (Simberloff 1978; Gotelli and Colwell 2001) was utilized to generate the expected number of species in cocoa agroforestry and in primary forest (plots in Vale do Rio Doce Forest Reserve, located 30 km to the north of the study site) in a collection of 500 individuals. The free software EcoSim 7.0 (Gotelli and Entsminger 2003) was utilized for construction of individual-based rarefaction curves and confidence intervals for species richness after about 1000 resamplings (Gotelli and Colwell 2001).

For the analysis of natural regeneration (tree saplings), $9 \text{ m}^2 (3 \text{ m} \times 3 \text{ m})$ subplots were sampled within the 600 m^2 plots mentioned above. All plants located within these subplots with DBH <5 cm were identified and counted. Four ecological groups (regeneration phases) were used to categorize trees and saplings following the classification with modifications by Budowski (1965): pioneer (PI: very fast growth rates, low wood density, light demanding, gap colonizer, seed bank, short life-span, ability to colonize disturbed sites), early secondary (ES: fast growth rates, low wood density, seedling bank, medium life-span), late secondary (LS: slow growth rates, high wood density, shade-tolerant, gap-opportunist, seedling bank), and climax (CL: slow growth rates, high wood density, shade-tolerant, seedling bank, large seed, long life-span).

Results

Overall, 507 trees (DBH $>$ 5 cm) of 105 species in 39 families were recorded in the sampled area (4.8 ha). Of the total number of species, six were classified only to the genus level. The richest families were Myrtaceae (8 species), Leg. Faboideae (7), Moraceae (6), Lauraceae (6), Euphorbiaceae (6), Meliaceae (5), Anacardiaceae (5), Sapotaceae (4), Leg. Mimosoideae (4), Lecythidaceae (4) and Cecropiaceae (4). Of the recorded species, four are introduced and do not naturally occur in the basin of the Rio Doce: E. fusca, Leucaena leucocephala, Albizia falcataria and Artocarpus heterophylla. It is not known if these species were intentionally introduced or if they were dispersed in the farms by natural dispersion agents. Table 1 presents the floristic composition of the area.

Considering that each sample (four plots of 600 m^2) was located in every sampled farm, on average, 14.8 (\pm 3.2) tree species/farm were recorded throughout the north margin of the Rio Doce and tree density in each farm varied from 50.0 to 279.2 trees/ha. The estimates of populational parameters for the sampled tree species are presented in Table 1. Overall, the estimated basal area and density were $24.2~(\pm 3.8)~\text{m}^2/\text{ha}$, and 105.6 (± 28.5) trees/ha, respectively. These values include trees standing dead (1.25 trees/ha and 0.34 m²/ha). About 41.3% of the species recorded ($n = 43$) had only one tree and 76.9% ($n = 80$) had less than 1.04 tree/ha (i.e., up to five trees in 4.8 ha).

The populational density of *Joannesia princeps* was slightly higher than that of Gallesia integrifolia, however, the latter presented larger trees and many of them had forked trunks (trunk bifurcations were not considered as an additional tree). Other high-density species were: Alchornea iricurana, Spondias mombin, Guarea guidonia and Cecropia glaziovii. The populations of G. integrifolia and A. iricurana were widely distributed along the bank of the Rio Doce (frequency of 80%) and other species with slightly lower frequency (40–65%) were S. mombin, Dialium guianense, C. glaziovii, J. princeps, G. guidonia and Rollinia laurifolia. Among the tree species of highest densities, the occurrence should be mentioned of E. fusca, an introduced species recorded in 25% of the sampled farms. About 56.2% of the species, 71.0% of the overall density and 72.3% of the basal area are from pioneers and early secondary trees (Table 2).

The diameter distribution shows that the density of the 5–10 cm DBH class is lower than that of the larger diameter class (Figure 2). The analysis of the species occurring in the 5–29.9 cm DBH class shows an overwhelming dominance of pioneers (40.7% of the trees) and early secondary trees (32.6%), and a smaller proportion of late secondary (10.2%) or climax trees (16.5%). Above 30 cm DBH 22.5% are pioneers, 46.5% early secondary, 19.9% late secondary, and only 11.1% climax trees.

The overall density observed in the regeneration subplots $(9 \text{ m}^2 \text{ plots})$ for tree saplings $\langle 2.5 \text{ cm} \text{ DBH} \rangle$ was 11,597 (\pm 5198) plants/ha (Table 1). No plant in the 2.5–5 cm DBH class was observed within the plots, although some were found growing in abandoned places outside the plots. Micropholis sp. was the most dominant species, followed by *L. leucocephala, Cryptocarya aschersoniana*,

Table 1. Summarized information record from 4.8 ha of cocoa agroforestry systems (DBH \geq 5 cm) and 720 m2 (DBH <5 cm) in Rio Doce, Linhares, Brazil. Ecological groups (EG): pioneer (PI), early secondary (ES), late secondary (LS) and climax (CL).

Species/family		EG DBH >5		DBH < 5	
			$n \, \text{ha}^{-1} \, \text{m}^2 \, \text{ha}^{-1} \, F\% \, \text{n} \, \text{ha}^{-1}$		
Joannesia princeps Vell. (Euphorbiaceae)	PI	8.96	1.151	40	388.9
Gallesia integrifolia (Spreng.) Harms (Phytolaccaceae)	ES	7.29	7.02	80	27.8
Alchornea iricurana Casar. (Euphorbiaceae)	PI	7.08	0.805	80	83.3
Spondias mombin L. (Anacardiaceae)	ES	5.83	0.963	65	
Guarea guidonia (L.) Sleumer (Meliaceae)	CL	4.58	0.343	40	41.7
Cecropia glaziovii Snethl. (Cecropiaceae)	PI	4.58	0.15	40	13.9
Dialium guianense (Aubl.) Sandwith (Leg. Caesalpinioideae)	LS	3.33	0.595	50	27.8
Erythrina fusca Lour. (Leg. Faboideae)*	PI	3.13	0.956	25	138.9
Rollinia laurifolia Schltdl. (Annonaceae)	ES	2.5	0.161	40	
<i>Micropholis</i> sp. (Sapotaceae)	LS.	2.29	1.448	30	4458.3
Croton floribundus Spreng. (Euphorbiaceae)	PI	2.29	0.067	5	55.6
Spondias venulosa Mart. ex Engl. (Anacardiaceae)	ES	2.08	0.511	25	180.6
Tapirira guianensis Aubl. (Anacardiaceae)	PI	1.88	0.311	30	27.8
Cedrela odorata L. (Meliaceae)	ES	1.67	0.361	30	750.0
Pterocarpus rohrii Vahl (Leg. Faboideae)	ES	1.67	0.613	30	736.1
Acosmium tenuifolium (Vog.) Yakovl. (Leg. Faboideae)	ES	1.46	0.091	20	27.8
Cecropia pachystachya Trecul. (Cecropiaceae)	PI	1.46	0.021	30	
Artocarpus heterophylla Lam. (Moraceae)*	ES	1.25	0.17	20	861.1
Pseudobombax grandiflorum (Cav.) A. Robyns (Bombacaceae)	ES	1.25	0.546	25	125.0
Genipa americana L. (Rubiaceae)	LS	1.25	0.032	30	13.9
Inga subnuda subsp. subnuda T. D. Penn. (Leg. Mimosoideae)	LS	1.25	0.075	20	
Jacaranda puberula Cham. (Bignoniaceae)	ES	1.25	0.101	20	
Dead trees		1.25	0.34	20	
Ocotea aciphylla (Nees) Mez (Lauraceae)	LS	1.25	0.136	20	
Pterygota brasiliensis Fr. All. (Sterculiaceae)	LS	1.25	0.767	15	
Eriotheca macrophylla (K. Schum.) A. Robyns (Bombacaceae)	ES	1.04	0.293	15	
Leucaena leucocephala (Lam.) D. Wit. (Leg. Caesalpinioideae)*	PI	0.83	0.045	10	972.2
Cryptocarya aschersoniana Mez. (Lauraceae)	ES	0.83	0.237	15	875.0
Ocotea aff. cernua (Nees) Mez Vell. (Lauraceae)	ES	0.83	0.054	15	847.2
Chrysophyllum sp. (Sapotaceae)		CL 0.83	0.185	20	347.2
Lecythis pisonis Cambess. (Lecythidaceae)		CL 0.83	0.421	20	111.1
Sloanea eichleri K. Schum. (Elaeocarpaceae)		CL 0.83	0.241	15	27.8
Cariniana legalis (Mart.) Kuntze. (Lecythidaceae)	${\rm LS}$	0.83	0.595	20	13.9
Crataeva tapia L. (Capparidaceae)	ES	0.83	0.045	15	13.9
Brosimum lactescens (S. Moore) C.C. Berg (Moraceae)	CL	0.83	0.12	5	
Carpotroche brasiliensis (Raddi.) A. Gray (Flacourtiaceae)	CL	0.83	0.009	5	
Citharexylum aff. laetum Hiern. (Verbenaceae)	LS	0.83	0.212	20	
Jacaratia spinosa (Aubl.) A. DC. (Caricaceae)	PI	0.83	0.227	15	
Simarouba amara Aubl. (Simaroubaceae)	ES	0.83	0.255	15	
Trichilia quadrijuga Kunth. (Meliaceae)	ES	0.83	0.059	10	
Inga sp. (Leg. Mimosoideae)	PI	0.63	0.04	10	69.4
Cryptocarya saligna Mez. (Lauraceae)	CL	0.63	0.05	10	13.9
Inga striata Benth. (Leg. Mimosoideae)	ES	0.63	0.008	10	13.9
Andira ormosioides Benth. (Leg. Faboideae)	LS.	0.63	0.06	15	
Andradaea floribunda Allemao (Nyctaginaceae)	CL	0.63	0.382	15	
Astronium graveolens Jacq. (Anacardiaceae)	ES	0.63	0.071	15	

Table 1. (continued)

Species/family		EG DBH ≥ 5			DBH < 5	
		$n ha^{-1}$	$\mathrm{m}^2\,\mathrm{ha}^{-1}$ $F\%$ $\,$ $\mathrm{n}\,\mathrm{ha}^{-1}$			
Chorisia glaziovii (Kuntze) E. Santos (Bombacaceae)	ES.	0.63	0.343	15		
Ficus adhatodifolia Schott (Moraceae)	ES	0.63	0.383	15		
<i>Ficus gomelleira</i> Klunth and Bouche (Moraceae)	ES	0.63	0.387	15		
Glycydendron amazonicum Ducke (Euphorbiaceae)		ES 0.63	0.047	10		
Margaritaria nobilis L. f. (Euphorbiaceae)		ES 0.63	0.031	15		
Polyandrococos caudescens (Mart.) Barb. Rodr. (Arecaceae)		ES 0.63	0.006	5		
Symphonia globulifera L. (Clusiaceae)		LS 0.63	0.027	5		
Cabralea canjerana (Vell.) Mart. (Meliaceae)		CL 0.42	0.004	5	41.7	
<i>Tachigalia paratyensis</i> (Vell.) Lima (Leg. Caesalpinioideae)		ES 0.42	0.145	10	41.7	
Machaerium hirtum (Vell.) Stellfeld (Leg. Faboideae)		ES 0.42	0.008	10	27.8	
Campomanesia guavirova (DC.) Kiaersk. (Myrtaceae)		CL 0.42	0.072	10	13.9	
Cariniana estrellensis (Raddi.) Kuntze. (Lecythidaceae)		LS 0.42	0.165	10	13.9	
Coussapoa microcarpa (Schott) Rizzini (Cecropiaceae)		LS 0.42	0.008	5		
<i>Hydrogaster trinervis</i> Kuhlm. (Tiliaceae)		ES 0.42	0.382	10		
Schoepfia brasiliensis A. DC. (Olacaceae)		ES 0.42	0.037	5		
Tabernaemontana catharinensis A.DC. (Apocynaceae)		ES 0.42	0.015	5		
Cupania cf. vernalis Camb. (Sapindaceae)		ES 0.21	0.052	5	27.8	
Trema micrantha (L.) Blume (Ulmaceae)	PI	0.21	0.004	5	27.8	
Virola gardneri (A.DC.) Warb. (Myristicaceae)		CL 0.21	0.024	5	27.8	
Zollernia modesta A. M. Carvalho and Barneby (Leg. Faboideae) CL 0.21			0.056	5	13.9	
Albizzia falcataria (L.) Fosberg. (Leg. Mimosoideae)*		ES 0.21	0.001	5		
Aspidosperma pyricollum Müll. Arg. (Apocynaceae)		LS 0.21	0.054	5		
Astrocaryum aculeatissimum (Schott) Burret (Arecaceae)		CL 0.21	0.002	5		
Campomanesia guazumifolia (Camb.) Berg (Myrtaceae)		ES 0.21	0.023	5		
Casearia decandra Jacq. (Flacourtiaceae)		ES 0.21	0.001	5		
Casearia sp. (Flacourtiaceae)		ES 0.21	0.001	5		
Chrysophyllum splendens Spreng. (Sapotaceae)		CL 0.21	0.021	5		
Cordia sellowiana Cham. (Boraginaceae)	PI	0.21	0.014	5		
Cupania cf. scrobiculata L.C. Rich. (Sapindaceae)		CL 0.21	0.011	5		
Dalbergia nigra (Vell.) Fr. All. ex Benth. (Leg. Faboideae)		ES 0.21	0.003	5		
<i>Ephedranthus</i> sp. nov. (Annonaceae)		CL 0.21	0.013	5		
Eschweilera cf. ovata (Cambess.) Miers. (Lecythidaceae)		LS 0.21	0.004	5		
Eugenia brasiliensis Lam. (Myrtaceae)		CL 0.21	0.004	5		
Ficus clusiifolia Schott (Moraceae)		ES 0.21	0.108	5		
Guapira noxia (Netto) Lundell (Nyctaginaceae)		ES 0.21	0.004	5		
Hirtella hebeclada Moric. ex A. P. DC. (Chrysobalanaceae)		CL 0.21	0.005	5		
<i>Marlierea acuminatissima</i> (Berg) Legrand (Myrtaceae)		LS 0.21	0.009	5		
M. sylvatica (Gardner) Kiaersk. (Myrtaceae)		LS 0.21	0.014	5		
<i>Myrcia falax</i> (Richard) DC. (Myrtaceae)		CL 0.21	0.002	5		
Ocotea conferta Coe-Teixeira (Lauraceae)		LS 0.21	0.001	5		
O. aff. macrocalyx (Meisn.) Mez Vell. (Lauraceae)		ES 0.21	0.002	5		
Plinia strigipes (Berg) Sobral (Myrtaceae)		ES 0.21	0.005	5		
Pourouma guianensis Aubl. ssp. guianensis (Cecropiaceae)		CL 0.21	0.01	5		
Pouteria coelomatica Rizzini (Sapotaceae)		LS 0.21	0.081	5		
<i>Protium heptaphyllum</i> (Aubl.) Marchand. (Burseraceae)		ES 0.21	0.06	5		
Qualea jundiahy Warm. (Vochysiaceae)		LS 0.21	0.012	5		
Rhamnidium glabrum Reissek (Rhamnaceae)	ES	0.21	0.008	5		
Sapium glandulatum (Vell.) Pax. (Euphorbiaceae)		ES 0.21	0.004	5		

Table 1. (continued)

Species/family		EG DBH >5			DBH < 5
			$n \, \text{ha}^{-1}$ m ² ha ⁻¹ $F\%$ n ha ⁻¹		
Schoepfia oblongifolia Turez (Olacaceae)	CL	0.21	0.006	5	
Simaba subcymosa A. St. Hil. and Tul. (Simaroubaceae)	ES	0.21	0.004	5	
Sorocea guilleminiana Gaudich. (Moraceae)	CL	0.21	0.01	5	
Sparattosperma leucanthum (Vell.) K. Schum. (Bignoniaceae)	PI	0.21	0.01	5	
Spondias cf. macrocarpa Engl. (Anacardiaceae)	ES	0.21	0.002	5	
Stephanopodium blanchetianum Baill. (Dichapetalaceae)	CL	0.21	0.008	5	
Tabebuia roseo-alba (Ridley) Sandwith (Bignoniaceae)	ES	0.21	0.026	5	
Talisia intermedia Radlk. (Sapindaceae)	CL	0.21	0.052	5	
Tovomita brevistaminea Engl. (Clusiaceae)	CL	0.21	0.01	5	
<i>Trichilia</i> sp. (Meliaceae)	ES	0.21	0.013	5	
Virola oleifera (Schott) A. C. Smith (Myristicaceae)	CL	0.21	0.041	5	
Aegiphila sellowiana Cham. (Verbenaceae)	PI				27.8
Randia armata D.C. (Rubiaceae)	ES				27.8
<i>Allophylus petiolulatus Radlk. (Sapindaceae)</i>	CL				13.9
Tabebuia serratifolia (Vahl) Nichols. (Bignoniaceae)	ES				13.9
Vernonanthura phosphorica (Vell. Conc.) H. Rob. (Asteraceae)	PI				13.9
Total		105.6	24.2		11,597

*Non-native species.

Table 2. Species richness (S), density (n ha⁻¹) and basal area (m² ha⁻¹) for ecological groups recorded from 4.8 ha of cocoa agroforestry systems in Rio Doce, Brazil.

Ecological groups	S(%)	$n \, \text{ha}^{-1}$ (%)	m^2 ha ⁻¹ (%)		
Pioneer	13 (12.4)	32.3(30.6)	3.8(15.7)		
Early secondary	46(43.8)	42.1 (39.8)	13.7(56.5)		
Late secondary	19(18.1)	15.8(15.0)	4.3(17.7)		
Climax	26(24.8)	14.2 (13.4)	2.1(8.7)		
Dead trees	5	1.3(1.2)	0.3(1.4)		
Total	105 (100%)	105.6 (100%)	24.2 (100.0%)		

A. heterophylla, Ocotea cernua, Cedrela odorata, Pterocarpus rohrii, J. princeps and Chrysophyllum sp. The total number of species recorded in these subplots was 42. Five species and one family (Asteraceae) sampled in the regeneration subplots were not recorded among the trees with DBH >5 cm: Vernonanthura phosphorica (PI), Allophylus petiolulatus (CL), Tabebuia serratifolia (ES), Aegiphila sellowiana (PI) and Randia armata (ES). As observed for trees of larger DBH classes, pioneers and early secondary trees were also the dominant successional phases in the regeneration plots (<5 cm DBH), both in terms of number of trees (55.3%) and species richness (64.3%).

Figure 2. Distribution of tree DBH for cocoa agroforestry in Rio Doce, Linhares, Brazil. DBH classes are in increments of 10 cm, (7.5) 5–10, (15) 10–20, and so on. Ecological groups are: pioneer (PI), early secondary (ES), late secondary (LS) and climax (CL).

Discussion

Soil cover, as measured by the basal area value of the sampled native trees, can be considered as satisfactory in the current cabruca system $(24.2 \text{ m}^2/\text{ha})$, and if the cover promoted by the cocoa trees (ca. $2-5 \text{ m}^2/\text{ha}$) are included, the figure increases to ca. 26–30 m²/ha. The density of native trees is low (105.6 \pm 28.5 trees/ ha), however. This low density value is a characteristic intrinsic to the current cabruca system because, without the thinning, the cocoa plantation, which is cultivated at ca. 500 trees/ha, is said to be not viable economically. The observed richness of species (105 species for trees with DBH \geq 5 cm in a sampled area of 4.8 ha) is much lower when compared to less disturbed forests of the region. In the Vale do Rio Doce Forest Reserve, located 30 km to the north of the study sites, Peixoto and Gentry (1990), for example, recorded 99 tree species (DBH $>$ 10 cm) in a sampled area of just 0.1 ha, while Rolim and Nascimento (1997) estimated, for this same reserve, a value of 169 species/ha for trees of this DBH class. Although species were not exactly equivalent (Simberloff 1978), rarefaction curves indicate that cocoa agroforestry supports relatively lower species richness than a floristically and climatically similar site of primary Atlantic forest (Figure 3). Other studies carried out in cabrucas of the Ilhéus region, state of Bahia, present tree densities about half that observed in the present study, and tree species richness is also lower than the value observed for the cabruca of the Rio Doce region (ES) (Alves 1990; Hummel 1995; Sambuichi 2002).

Figure 3. Expected number of species in cocoa agroforestry in Rio Doce and in primary forest (Vale do Rio Doce Forest Reserve, see Figure 1). Individual rarefaction curves (solid lines curve) and confidence intervals computed with 95% (broken lines curve).

In all those areas, it is very likely that the original species richness was much higher in the beginning of the cocoa establishment, when farmers had rather variable cultivation protocols (Alvim 1966) and the natural death of native trees created gaps for growth of new tree recruitment, allowing better regeneration of the forest. This regeneration does no longer happen, however. Currently, what one observes is the proliferation of pioneer or early secondary trees and poor conditions for the establishment of late secondary and climax species, resulting, consequently, in a lowering of tree diversity. This is better understood in the light of the current management practices, especially where undergrowth is cleared out twice annually. Such clearings are not selective, that is, all regenerating trees are eliminated and only a few arboreal plants happen to escape the cutting occasionally. The absence of tree regeneration in the class of 2.5–5 cm DBH in the sampled subplots further demonstrates the difficulty of tree establishment.

The proliferation of pioneers also occurs in some abandoned cocoa tracts, where dead cocoa trees are not replaced (personal observation). Abandoned tracts are more common when the cocoa market prices are low, but dead cocoa trees are renewed when the opposite is observed. Another fact that leads to an increase of pioneers is their intentional plantation, mainly of E. fusca and Albizzia falcataria (non-native species) or J. princeps (native species), that is also actively kept by the farmers, and by the invasion or intentional plantation of L. leucocephala, a non-native species with high potential of biotic invasion. These trees are preferred because of their rapid growth, which, in turn, promotes quick shading of the cocoa trees. Some areas in Ilhéus, in southern Bahia, present even higher densities of exotic tree species than that observed in the region of the present study (Alves 1990; Hummel 1995; Sambuichi 2002).

This is the main problem with the cabruca system: the dying of the forest. The deficient regeneration process can be easily seen in Figure 2. Frequency distribution data from two less disturbed forest reserves of the region (Chiarello 1997; Rizzini et al. 1997) and from other tropical forest sites as well (Manokaran and Kochummen 1987; Swaine et al. 1987; Carey et al. 1994) indicate that native trees of 10–20 cm DBH are at least 10–20 times more abundant than in the study site, and much more so for trees of 5–10 cm DBH (Rizzini et al. 1997). Further, regenerating trees are composed mainly of pioneer species (Figure 2). A similar pattern of distribution, with a high disproportion between regeneration and adult trees, was also observed by Hummel (1995) and Sambuichi (2002).

These results indicate that the forest existing 50 or 100 years ago, when most cocoa plantations were first established in the estuary region of Rio Doce (personal communication from owners of the farms visited), is aging very rapidly and the observed regeneration does not seem to be satisfactory. Both natural succession and gap dynamics are being impaired and the maintenance of diversity is certainly jeopardized. That species are replaced in space and time, changing the floristic composition, is a well known characteristic of tropical forests under natural conditions (Lieberman et al. 1985; Reice 1994; Rolim et al. 2001), but what will be the structure and species composition of the cabruca forests in the next 50 years under the current management practices? Will the exotic species mentioned above increase in density? Will the climax and late secondary trees have even lower importance in the forest structure? Unfortunately, data from this paper, together with the general opinion of cabruca owners, which are not keen to implement management that might reduce the short term profit of their farms, lead one to believe so.

Apart from the floristic impoverishment, the cabruca forest is also suffering from other kinds of disturbance, such as the deleterious effect of the undergrowth removal and decades of insecticide utilization that, although not yet studied, might be negatively affecting the fauna (Delabie 1988). Studies carried out in several farms located along both margins of the Rio Doce between the municipality of Linhares and the mouth of this river indicate the absence or great reduction in density of medium- to large-size mammals $($ >1 kg of body weight) when compared with less disturbed nearby forests. The average encounter rate (a measure of relative abundance) with mammals observed in the cabruca farms was 1.68 encounters $/10$ km of line transect sampling (A.G. Chiarello, unpublished data), while in two less disturbed forest reserves located 30 km to the north of the study sites (Sooretama Biological Reserve and Vale do Rio Doce Forest Reserve), the corresponding encounter rates were 9.81 and 14.23 encounters/10 km, respectively (Chiarello 1999). Both terrestrial and arboreal species were affected; some have become locally extinct (peccaries, tapirs and agoutis), while others have drastically reduced population densities (primates, sloths, brocket deer and pacas) (A.G. Chiarello, unpublished data). Although illegal hunting is contributing to the overall reduction

of mammal abundance there (Chiarello 2000a, b), it is likely that the altered forest structure and dynamics of the cabruca forest, which has a lower availability of food resources (fruits, flowers and leaves of native tree and liana species) and a highly broken canopy that hampers the movements of arboreal species, are causing negative impacts on those species.

Additionally, as primates (Cebus robustus, Alouatta guariba, Callicebus personatus and Callithrix geoffroyi), squirrels (Sciurus aestuans) and some terrestrial species like tapirs (Tapirus brasiliensis), peccaries (Tayassu pecari and Pecari tajacu), pacas (Agouti paca) and agoutis (Dasyprocta aguti) are important seed dispersers (Bodmer 1991; Julliot 1994; Tabarelli and Mantovani 1996), the local extinction or reduced population densities of these species in the cabruca forests can be considered as an additional factor contributing to the reduction of reproductive success of several species of native trees.

The cocoa agroforestry systems can be subjected to differing management strategies (Greenberg 1998; Sambuichi 2002), preventing the comparison between central America, Africa and Brazil. There are data from other cocoa agroforests, however, that do not indicate such a bad ecological scenario. Results from Parrish et al. (1998), for example, from a study in Talamanca, Costa Rica, show that cocoa forests can have a high diversity of birds, equivalent to that of nearby undisturbed forests. Power and Flecker (1998) presented a case from the Dominican Republic in which bird and lizard diversities were as high in the cocoa plantations as in primary forests. Other studies also stressed the important conservation role of cocoa in the Brazilian Atlantic forest (Alves 1990; Hummel 1995; Alger 1998; Johns 1999; Moura 1999; Pardini 2001; Sambuichi 2002), and in central America and Africa (Duguma et al. 1998; Greenberg 1998).

Also, agroforestry systems have served, in general, as faunal refuges (Griffith 2000) and the cocoa agroforestry is, without doubt, a better alternative for conservation of biodiversity than traditional intensive agriculture. Nevertheless, we are convinced that the current management practices used in the cocoa agroforestry of the Rio Doce region are dooming the long term survival of native forest. Its role in the conservation of biodiversity is, therefore, questioned. It is probable that the same scenario is taking place in other regions where cocoa is cultivated under the shade of native trees after the thinning of the understorey. We believe that the cocoa agroforestry does have great potential for biodiversity conservation, since its structure provides resources and niches for a variety of native species of fauna and flora.

After all, as stated by Phillips (1997) "... all biologists would probably agree that even a degraded forest is better than no forest at all''. Nevertheless, we stress that management practices must be improved to justify the role of conservation normally attributed to those agroforestry systems, especially when the long-term conservation of biodiversity is the goal. Some practices for improvement of cocoa might be advanced, such as, for example, the eradication of non-native species and permanence of saplings of native species, that should be allowed to grow to ultimately replace mature or over-mature canopy trees. A mosaic of cocoa agroforestry and natural Atlantic forest is probably also more viable for conservation of biodiversity than a homogeneous landscape composed solely of cocoa agroforestry (Ewel 1986; Myers 1986).

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References

- Alger K. 1998. The Reproduction of the Cocoa Industry and Biodiversity in Southern Bahia, Brazil. Proc. 1st Int. Workshop on Sustainable Cocoa Growing, Panama, $3/30-4/2$, 1998, Smithsonian Migratory Bird Center, Panama (http://www.nationalzoo.si.edu/smbc/Research/Cacao/cacao.asp).
- Alves M.C. 1990. The role of cocoa plantations in the conservation of the Atlantic forest of Southern Bahia, Brazil. M.S. Thesis, University of Florida, Gainesville, Florida.
- Alvim P.T. 1966. O problema do sombreamento do cacaueiro. Cacau Atualidades 3: 2–5.
- Alvim R. and Nair P.K.R. 1986. Combination of cacao and eight other plantation crops: An agroforestry system in Southeast Bahia, Brazil. Agroforestry Systems 4: 3–15.
- Alvim P.T. and Pereira C.P. 1965. Sombra e espaçamento nas plantações de cacau no estado da Bahia e Centro de Pesquisas do Cacau, Relatório Anual 1964, CEPLAC/CEPEC, Ilhéus, pp. 18–19.
- Batista L.P. and Alvim R. 1981. Efeitos da intensidade luminosa e do fenótipo sobre o crescimento em altura do fuste do cacaueiro. Revista Theobroma 11: 61–76.
- Bodmer R.E. 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. Biotropica 23: 255–261.
- Budowski G. 1965. Distribution of tropical American rain forest species in the light of sucessional processes. Turrialba 15: 40–42.
- Carey E.V., Brown S., Gillespie A.J.R. and Lugo A.E. 1994. Tree mortality in mature lowland tropical moist and tropical lower montane moist forests of Venezuela. Biotropica 26: 255–265.
- Chiarello A.G. 1997. Mammalian community and vegetation structure of Atlantic forest fragments in south-eastern Brazil. Ph.D Thesis, University of Cambridge, Cambridge, UK.
- Chiarello A.G. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in southeastern Brazil. Biological Conservation 89: 71–82.
- Chiarello A.G. 2000a. Influência da caça ilegal sobre mamíferos e aves das matas de tabuleiro do norte do estado do Espírito Santo. Boletim do Museu de Biologia Mello Leitão (Nova Série) 11/12: 229–247.
- Chiarello A.G. 2000b. Density and population size of mammals in remnants of Brazilian Atlantic forest. Conservation Biology 14: 1649–1657.
- Cochran W.G. 1977. Sampling Techniques. John Wiley and Sons, New York.
- Constanza R., D'Arge R., Groot R., Farber S., Grasso M., Hannon B. et al. 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253–260.
- Constanza R., D'Arge R., Groot R., Farber S., Grasso M., Hannon B. et al. 1998. The value of ecosystem services: putting the issues in perspective. Ecological Economics 25: 67–72.
- Cullen Jr. L., Bodmer R.E. and Pa´dua C.V. 2000. Effects of hunting in habitat fragments of the Atlantic forests, Brazil. Biological Conservation 95: 49–56.
- Cunningham R.K. and Burridge J.C. 1960. The growth of cacao (Theobroma cacao L.) with and without shade. Annals of Botany 24: 458–462.

Delabie J.H.C. 1988. Ocorrência de Wasmannia auropunctata (Roger, 1863) (Hymenoptera, Formicidae, Myrmicinae) em cacauais na Bahia, Brasil. Revista Theobroma 18: 29–37.

- Duguma B., Gockowski J. and Bakala J. 1998. Smallholder cocoa (Theobroma cacao) cultivation in agroforestry systems of west and central Africa: challenges and opportunities. Proc. 1st Int. Workshop on Sustainable Cocoa Growing, Panama, 3/30-4/2, 1998, Smithsonian Migratory Bird Center, Panama (http://www.nationalzoo.si.edu/smbc/Research/Cacao/cacao.asp).
- Ewel J.J. 1986. Designing agricultural ecosystems for the humid tropics. Annual Review of Ecology and Systematic 17: 245–271.
- Fassbender H. 1993. Modelos edafológicos de sistemas agroforestales. Turrialba, CATIE, Costa Rica.
- Fernandes E.N. and Vinha S.G. 1984. Recomposição florística do Parque Zoobotânico do Centro de Pesquisas do Cacau. Revista Theobroma 14: 1–25.
- Gotelli N.J. and Colwell R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.
- Gotelli N.J. and Entsminger G.L. 2003. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. and Kesey-Bear, Burlington, Vermont (http://homepages.together.net/ \sim g entsmin/ecosim.htm).
- Greenberg R. 1998. Biodiversity in the Cacao Agroecosystem: Shade Management and Landscape Considerations. Proc. 1st Int. Workshop on Sustainable Cocoa Growing, Panama, $3/30-4/2$, 1998, Smithsonian Migratory Bird Center, Panama (http://www.nationalzoo.si.edu/smbc/Research/ Cacao/cacao.asp).
- Griffith D.M. 2000. Agroforestry: a refuge for tropical biodiversity after fire. Conservation Biology 14: 325–326.
- Hummel M. 1995. Botanical analysis of the shade tree population in two cabruca cocoa plantations in southern Bahia, Brazil. Dissertation in Agricultural Biology, University of Stuttgart, Stuttgart, Germany.

Johns N.D. 1999. Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. Environmental Management 23: 31–47.

- Julliot C. 1994. Frugivory and seed dispersal by red howler monkeys: evolutionary aspect. Revue d'Ecologie (Terre Vie) 49: 331–341.
- Kinzey W.G. 1982. Distribution of primates and forest refuges. In: Prance G.T. (ed) Biological Diversification in the Tropics. Columbia University Press, New York, pp. 455–482.
- Laurance W.F., Vasconcelos H.L. and Lovejoy T.E. 2000. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. Oryx 34: 39–45.
- Lieberman M., Lieberman D., Hartshorn G.S. and Peralta R. 1985. Small-scale altitudinal variation in lowland wet tropical forest vegetation. Journal of Ecology 73: 505–516.
- Manokaram N. and Kochummen K.M. 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. Journal of Tropical Ecology 3: 315–330.
- Montagnini F. 1992. Sistemas agroforestales: principios y aplicaciones en los trópicos. Organización para Estudios Tropicales (OET), San José, Costa Rica.
- Mori S.A., Boom B.M., Carvalho A.M. and Santos T.S. 1983. Southern Bahian moist forests. The Botanical Review 49: 155–232.
- Moura R.T. 1999. Análise Comparativa da Estrutura da Comunidade de Pequenos Mamíferos em Remanescentes da Mata Atlântica e Plantio de Cacau em Sistema de Cabruca no Sul da Bahia. M.Sc. Thesis, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.
- Mueller-Dombois D. and Ellenberg H. 1974. Aims and Methods of Vegetation Ecology. John Wiley, New York.
- Myers N. 1986. Forestland farming in western Amazonia: stable and sustainable. Forest Ecology and Management 15: 81–93.
- Myers N. 1989. Deforestation Rates in Tropical Forests and their Climate Implications. Friends of the Earth, London.
- Nair P.K.R. (ed) 1989. Agroforestry Systems in the Tropics. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Pardini R. 2001. Pequenos mamíferos e a fragmentação da Mata Atlântica de Una, sul da Bahia processos e conservação. Ph.D. Thesis, Universidade de São Paulo, São Paulo, Brazil.
- Parrish J., Reitsma R. and Greenberg G. 1998. Cacao as crop and conservation tool. Lessons from the Talamanca region of Costa Rica. Proc. 1st International Workshop on Sustainable Cocoa Growing, Panama, 3/30–4/2, 1998, Smithsonian Migratory Bird Center, Panama (http://www.nationalzoo. si.edu/smbc/Research/Cacao/cacao.asp).
- Peixoto A.L. and Gentry A. 1990. Diversidade e composição florística da Mata de Tabuleiro na reserva florestal de Linhares (Espírito Santo, Brasil). Revista Brasileira de Botânica 13: 19–25.
- Peixoto A.L. and Silva I.M. 1997. Tabuleiro forests of northern Espírito Santo, southeastern Brazil. In: Davis S.D., Heywood V.H., Herrera-Macbryde O., Villa-Lobos J. and Hamilton A.C. (eds) Centres of Plant Diversity: A Guide and Strategy for their Conservation. The Americas, WWF and IUCN, London, pp. 369–372.
- Peres C.A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forest. Conservation Biology 14: 240–253.
- Phillips O.L. 1997. The changing ecology of tropical forests. Biodiversity and Conservation 6: 291–311.
- Power A.G. and Flecker A.S. 1998. Agroecosystems and biodiversity. Proc. 1st Int. Workshop on Sustainable Cocoa Growing, Panama, $3/30-4/2$, 1998, Smithsonian Migratory Bird Center, Panama (http://www.nationalzoo.si.edu/smbc/Research/Cacao/cacao.asp).
- Prance G.T. 1987. Biogeography of neotropical plants. In: Whitmore T.C. and Prance G.T. (eds) Biogeography and Quaternary History in Tropical America. Clarendon Press, Oxford, UK, pp. 46–65. Redford K.H. 1992. The empty forest. Bioscience 42: 412–422.
- Reice S.R. 1994. Nonequilibrium determinants of biological community structure. American Scientist 82: 424–435.
- Rizzini C.M., Aduan R.E., Jesus R.M. and Garay I. 1997. Floresta pluvial de tabuleiro, Linhares, ES, Brasil, sistemas primários e secundários. Leandra 12: 54–76.
- Rolim S.G. and Nascimento H.E.M. 1997. Richness, diversity and species-abundance relationships of a tropical tree community in different samplings. Scientia Forestalis 52: 7–16.
- Rolim S.G., Couto H.T.Z. and Jesus R.M. 2001. Fluctuaciones temporales en la composición florística del bosque tropical atla´ntico. Biotropica 33: 12–22.
- Saatchi S., Agosti D., Alger K., Delabie J. and Musinski J. 2001. Examining fragmentation and loss of primary forest in the southern Bahian Atlantic forest of Brazil with radar imagery. Conservation Biology 15: 867–875.
- Sambuichi R.H.R. 2002. Fitossociologia e diversidade de espécies arbóreas em cabruca (mata atlântica raleada sobre plantação de cacau) na região sul da Bahia, Brasil. Acta Botânica Brasilica 16: 89–101.
- Sena Gomes A.R. 1992. Agrosilvicultural systems in southeastern Bahia. In: Anais do II Encontro Brasileiro de Economia e Planejamento Florestal, 30/09 a 04/10/1991. EMBRAPA/CNP Floresta. Curitiba, Paraná, pp. 109-122.
- Silva J.M.C. and Tabarelli M. 2000. Tree species impoverishment and the future flora of the Atlantic forest northeast Brazil. Nature 404: 72–74.
- Simberloff D. 1978. Use of rarefaction and related methods in ecology. In: Dickson K.L., Cairns Jr. J. and Livingston R.J. (eds) Biological Data in Water Pollution Assessment: Quantitative and Statistical Analyses, ASTM STP 652. American Society for Testing and Materials, Philadelphia, Pennsylvania, pp. 150–165.
- Suguio K., Martin L. and Dominguez J.L.M. 1982. Evolucão da planície costeira do Rio Doce (ES) durante o quaternário: Influência das flutuações do nível do mar. In: Suguio K., De Meis M.R.M. and Tessler M.G. (eds) Anais do IV Simpósio do Quaternário no Brasil. Rio de Janeiro, Brazil, pp. 93–116.
- Swaine M.D., Hall J.B. and Alexander I.J. 1987. Tree population dynamics at Kade, Ghana (1968–1982). Journal of Tropical Ecology 3: 331–345.
- Tabarelli M. and Mantovani W. 1996. Remoção de sementes de Bertholletia excelsa (Lecythidaceae) por animais em uma floresta de terra firme na Amazônia central, Brasil. Revista Brasileira de Biologia 56: 755–760.
- Terborgh J. 1992. Maintenance of diversity in tropical forest. Biotropica 24: 283–292.
- Thomas W.W. and Carvalho A.M.V. 1997. Atlantic moist forest of Southern Bahia, south-eastern Brazil. In: Davis S.D., Heywood V.H., Herrera-Macbryde O., Villa-Lobos J. and Hamilton A.C. (eds), Centres

of Plant Diversity: A Guide and Strategy for their Conservation, The Americas. WWF and IUCN, London, pp. 364–368.

- Thomas W.W., Carvalho A.M.V., Amorim A.M.A., Garrison J. and Arbeláez A.L. 1998. Plant endemism in two forests in southern Bahia, Brazil. Biodiversity and Conservation 7: 311–322.
- Vinha S.G., Silva L.A.M., Carvalho A.M., Pereira R.C. and Reyes-Zumeta H. 1983. Plantas Herbáceas, Epífitas, Arbustivas e Trepadeiras Associadas à Cultura do Cacaueiro. Centro de Pesquisas do Cacau, Itabuna, Ilhéus, Bahia, Brazil.
- Whitmore T.C. and Sayer J.A. 1992. Tropical Deforestation and Species Extinction. Chapman & Hall, London.