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Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil

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Abstract

Six Atlantic forest reserves, two large (c. 20,000 ha each), two medium-sized (c. 2,000 ha each) and two small (c. 200 ha each), located in northern Espírito Santo, south-eastern Brazil were censused for mammals from October 1994 to April 1996. Diurnal and nocturnal line-transect sampling was used for censusing mammals >1 kg body weight, and the relative abundance of species in the six fragments was compared. The number of mammal species recorded in the reserves was strongly related to the forest area, the richest community being recorded in the two large reserves and the poorest in the two small reserves. The large reserves had a structurally more complex community, with top predators, large, terrestrial frugivores and large myrmecophages. The mammal community of the small and the medium-sized reserves was impoverished and less complex. Frugivores were numerically predominant in both large and medium-sized reserves, whereas herbivores dominated the mammal community of the small reserves, mainly through the absence of agoutis *Dasyprocta leporina* and the high density of maned sloth *Bradypus torquatus* in the two small reserves. The lack of predators and the proliferation of secondary vegetation and lianas throughout the small reserves are probably the main causes for the success of arboreal folivores there. Illegal hunting was found to reduce the encounter rates of mostly large, terrestrial frugivores such as agoutis, pacas *Agouti paca*, peccaries *Pecari tajacu* and *Tayassu pecari* and deer *Mazama* spp., and is contributing to keep the population of the surviving species low. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Atlantic forest; Brazil; Forest fragmentation; Mammal community

1. Introduction

When a formerly continuous forest is isolated, the number of species will shift from its original equilibrium, mainly because of the effects of area reduction and distance to continuous forest or between forest patches. With time, the diversity will decline, eventually reaching a new, less diverse steady state (MacArthur and Wilson, 1967; Harris, 1984). The number of species a habitat can be expected to hold after a period of isolation is strongly area-dependent. The larger the forest island the higher the original number of species included and the lower is the rate of subsequent extinctions (Terborgh and Winter, 1980). Willis (1979), for example, comparing the bird community of three Atlantic forest fragments of differing sizes (1400, 250 and 21 ha) found 202, 146 and 93 bird species, respectively. Similar results were found for the community of small mammals in temperate forests (Matthiae and Stearns, 1981) and for arboreal marsupials in forest isolates of tropical Australia (Laurance, 1990). There are some conflicting results, however, and the relationship between mammalian species richness and forest size is not always clear-cut (Mathiae and Stearns, 1981). Generally, the disappearance of species fits a pattern of early loss of large specialised species, a pattern known as "ecological truncation", probably mainly due to the fact that most such species occur at very low densities, require large areas, or both (Wilson and Willis, 1975). The disappearance of ant-following birds of Barro Colorado Island is a clear example of this phenomenon.

In this paper I present a detailed analysis of the community of large and medium-sized mammals currently present in six remnants of the lowland Atlantic forest. Originally this forest extended almost continuously from the state of Rio Grande do Norte, in north-east Brazil, to the Rio Grande do Sul, the southernmost state of the country, stretching over an area of 1,200,000 km^2 or ca. 12% of the country (Brown and Brown, 1992). As this region coincides with the highest density of urban settlements, it has been cleared, disturbed, or

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burnt almost continuously since the arrival of the first Europeans in the early 1500s (Fonseca, 1985; Dean, 1995). Currently, 43% of the Brazilian population is concentrated in this region (Fonseca, 1985), and consequently, only about 5–12% of the original forest remains (Brown and Brown, 1992) as isolated forest remnants, scattered throughout a landscape dominated mainly by pasturelands and agricultural fields.

The main objectives of this paper were: (1) to identify the mammal species richness and the relative abundance of individuals surviving in each reserve, and (2) to analyse changes in the structure of the mammal community contrasting the relative abundances of orders and dietary categories between reserves of differing sizes. Given that community studies with large mammals of the Atlantic forest are lacking, the results reported here are compared mainly to both small and large mammals studied elsewhere in the tropics.

2. Methods

2.1. Study areas

Data were collected in six Atlantic Forest reserves, varying in size from 210 to 24,250 ha, located in northern Espírito Santo state in south-eastern Brazil (18°12′–19°48′S; 39°50′–40°15′W; Fig. 1). This region has been disturbed since the early 1500s, but forest destruction increased greatly during the early 20th century (Aguirre,

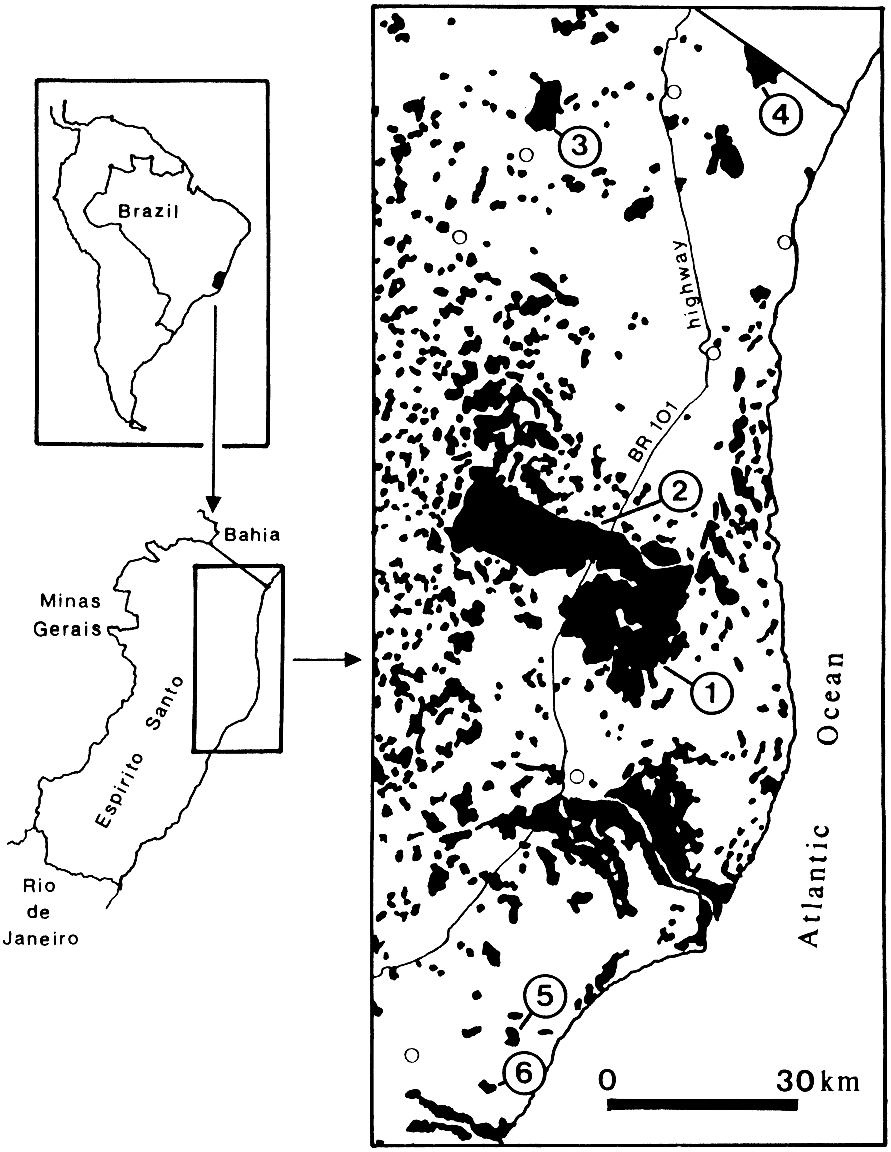


Fig. 1. Detail of Northern Espírito Santo state, in south-eastern Brazil, showing the patches of native forests (dark areas) remaining in 1995, urban areas (open circles), and the study sites (1–6) (based on satellite images from SOS Mata Atlântica and INPE, 1997). Large reserves: LFR (1) and SBR (2); medium-sized reserves: CVBR (3) and CGBR (4), and small reserves: M7/317 (5) and Putiri (6).

1951). The principal cause of deforestation was logging (Heinsdijk et al., 1965), which is still taking place in the region, as satellite images indicated that 5.5% of the state's area was cleared of forests between 1990 and 1995 (SOS Mata Atlântica et al., 1998). The most recent estimate available (1995) revealed that < 9% of the state area is still covered with native forests, and the majority of the remnants are small and isolated forest patches of < 1000 ha of area (SOS Mata Atlântica et al., 1998; Fig. 1).

Three of the study areas are privately owned reserves (LFR, M7/317 and Putiri) and the other three (SBR, CVBR and CGBR) are biological reserves administered by the Brazilian Environmental Agency (IBAMA). All reserves exhibit signs of past human disturbance, including illegal hunting, intrusion of fires from adjacent pasturelands, and logging, but large tracts of predominantly primary forest are still found in the two larger reserves (Table 1). The extreme north of LFR is contiguous with the other large reserve (SBR) but the latter is crossed in its eastern part by a highway (Fig. 1). The remaining study areas are isolated from each other and from other forest fragments. The landscape matrix in which the large and medium-sized reserves are immersed is composed predominantly of pasturelands and agricultural fields (mainly coffee and sugar cane), whereas extensive plantations of *Eucalyptus* spp. for the production of cellulose, surround the two small reserves (M7/315 and Putiri).

The reserves have similar climatic, edaphic, topographic and physiognomic conditions, and, therefore, their fauna and flora were assumed to be composed originally of similar sets of species. The predominant vegetation in all reserves is the tropical rain forest of the Tertiary tablelands ("Mata de Tabuleiros"), which is a semi-deciduous, mesophytic forest formation of the Atlantic forest domain (Rizzini, 1963). The soils of this region are predominantly acidic Tertiary sediments (Hiensdijk et al., 1965) with poor to average fertility (Moraes, 1974), and the topography is flat with altitudes of 30–90 m (Moraes, 1974). The predominant climate is the *Aw* of Koppen: hot and humid with a dry season during autumn–winter (April–September) and a wet season during spring–summer (October–March). The climate is similar for the six study areas, with average temperatures of 23–25°C and annual rainfall of 1050–1420 mm (unpublished data from weather stations of Companhia Vale do Rio Doce SA and Aracruz Celulose SA).

2.2. Data collection

The sampling protocol in all study areas consisted of line transect sampling sensu Buckland et al. (1993). All mammal species seen during censusing, both during the day and at night, were included in the analysis, except bats and small mammals such as rodents and marsupials, which require specific sampling methods beyond the scope of this study. The only exceptions were the common opossum *Didelphis aurita* and the bare-tailed woolly opossum *Caluromys philander*, seen frequently during transect sampling.

Straight trails of 1500–2000 m of length and 1.5 m wide were cut in each study site in locations selected to include all forest types present in the reserve or fragment in question. Non-forested areas such a native open fields and marsh areas were not sampled, but some parts of the forest edges were used. Trails were allowed to "rest" for a month before the beginning of sampling and were not censused on consecutive sampling days. Diurnal censuses started before sunrise and were terminated after 3–4 h. The nocturnal censuses started after sunset and were finished, on average, after 3–4 h. Effort was made to keep the walking speed as constant as possible at ca. 1 km/h. About 30 censuses were carried out in each reserve, totalling 175 censuses in the six

Table 1
Area, approximate time elapsed since isolation, disturbance level, predominant forest type, and hunting pressure of the six reserves included in this study

Study area	Area (ha)	Years since isolation	Disturbance level[a]	Predominant forest type[b]	Hunting pressure
Large reserves					
Linhares Forest Reserve (LFR)	21,800	± 30	Light	Primary	Low
Sooretama Biological Reserve (SBR)	24,250	± 30	Light	Primary	High
Medium-sized reserves					
Córrego do Veado Biological Reserve (CVBR)	2400	± 30	High	Secondary	Moderate
Córrego Grande Biological Reserve (CGBR)	1504	10–15	Moderate	Secondary	Moderate
Small reserves					
M7/317	260	25	Moderate	Secondary	Moderate
Putiri	210	23	Moderate	Secondary	Moderate

[a] Forest disturbance caused by accidental intrusion of fires, clearings, and selective logging in the past.

[b] Type of forest currently covering more than half of the reserve's area.

Table 2
Number and length (km) of diurnal and nocturnal censuses of mammals in the six study areas

	Diurnal		Nocturnal		Total	
Area	No.	Length	No.	Length	No.	Length
LFR	21	64.9	9	15.2	30	80.1
SBR	21	66.1	11	17.5	32	83.6
CVBR	19	66.4	13	18.9	32	85.3
CGBR	18	66.9	11	21.0	29	87.9
M7/317	17	45.6	10	17.3	27	62.9
Putiri	16	48.9	9	10.0	25	59.0
Total	112	358.9	63	99.9	175	458.8

study areas, 465.9 h of sampling and a total transect length of 458.8 km (Table 2). Unfortunately, time and logistic limitations prevented an equal amount of effort allocated to nocturnal and diurnal sampling, but the time allocated to nocturnal and diurnal sampling was similar between reserves (Table 2).

Here the term "visual encounter" refers to those occasions in which data such as species, group size and composition (if social) could be collected for the specimen in question. Binoculars (8 × 42) were used during all observations. For the nocturnal censuses, a 55-watt hand-held spotlight was used. Data on calls, footprints, faeces, and carcasses found in the reserves during the study were also recorded as additional evidence of a species' presence there. Interviews were conducted with some local woodsmen, former hunters and the staff of all reserves, in order to collect additional information on mammal species not seen during the study.

2.3. Data analysis

Encounter rates were used to compare the relative abundance of mammal species between reserves (Janson and Emmons, 1990). This method was chosen because, for most species, the number of encounters was not large enough to estimate their true densities without incurring serious bias. Encounter rates were calculated taking into account the species' period of activity. For all species, the total transect length was calculated as the summation of the lengths of all individual trails censused. For those species active both during the day and at night, for example, armadillos, tamanduas and peccaries, the total transect length included both diurnal and nocturnal sampling. Encounter rates were calculated as the total number of encounters/10 km for all mammal species seen during transect sampling, and these data were used in a Hierarchical Cluster Analysis in order to arrange reserves into groups (Dillon and Goldstein, 1984). Following Kent and Coker (1996), the Ward's minimum variance was chosen as the preferred method of similarity analysis and the squared Euclidean distance was used as a measure of dissimilarity. Data on encounter rates were grouped by orders following the classification of Wilson and Reeder (1993) and by dietary categories following the scheme originally proposed by Eisenberg (1981) and latter modified by Robinson and Redford (1986).

Multiple regression analysis was used to assess the influence that habitat variables, such as fragment size, time since isolation, disturbance level and hunting pressure, have on species richness and abundance (encounter rate). The two categorical variables, disturbance level and hunting pressure, were coded, from lowest to highest, as follows: disturbance level = 1 (LFR and SBR), 2 (CGBR, M7/317 and Putiri) and 3 (CVBR); hunting pressure = 1(LFR); 2 (CVBR, CGBR, M7/317 and Putiri), and 3 (SBR). The disturbance degree of each reserve was ranked taking into account the proportion of area covered by secondary vegetation, including cleared and burnt areas, and by signs of past logging activities (Chiarello, 1997). Hunting pressure was assessed by the number of occasions shots were heard during censuses, by the number of hunter trails found, and by the frequency of encounters with hunters or their dogs during censusing (Chiarello, 1997). After several experimental runs, a stepwise method was chosen in which these four habitat variables were included or excluded from the regression equation after passing a significant test, with a significance of 0.10 for inclusion (p in) and 0.20 for exclusion (p out). All statistical analyses were carried out in IBM-compatible computers with the SPSS software package (Norusis, 1993), and all probabilities reported here are 2-tailed.

3. Results

3.1. Species richness

Table 3 lists the 37 mammal species recorded in the area of the six reserves and fragments during the present study. The number of species not recorded in the two small reserves (M7/317 and Putiri) was about twice the figure observed for the medium-sized reserves (CVBR and CGBR), but only one species found in smaller reserves, the maned sloth *Bradypus torquatus* was not recorded in the two large reserves. The number of species in each reserve showed a positive relationship with forest area, i.e. the larger the reserve's area the higher the number of species recorded in it (multiple regression analysis; $R^2 = 0.960$; $F = 96.801$; $p = 0.006$). Fragment size was the only independent variable selected by the stepwise method in this analysis (regression coefficient or $Beta = 0.980$; $p < 0.001$); time since isolation, disturbance level and hunting pressure were excluded from the final equation. Conversely, the number of species extinct or otherwise not recorded in the reserves was

Table 3
Mammal species seen, heard, reported by local people, or whose footprints or faeces where found in the six reserves during the present study[c]

		Large		Medium-sized		Small	
Common name[a]	Scientific name[b]	LFR	SBR	CVBR	CGBR	M7/317	Putiri
1 Bare-tailed wooly opossum	*Caluromys philander*	?	v	?	v	–	–
2 Southeastern common opossum	*Didelphis aurita*	v	v	v	r	r	v
3 Maned sloth	*Bradypus torquatus*	–	–	–	r	v	v
4 Brown-throated three-toed sloth	*Bradypus variegatus*	v	r	r	–	–	–
5 Southern naked-tailed armadillo	*Cabassous unicinctus*	v	?	r	?	–	–
6 Nine-banded long-nosed armadillo	*Dasypus novemcinctus*	v	v	v	r	v	v
7 Giant armadillo	*Priodontes maximus*	r	r	–	–	–	–
8 Southern tamandua	*Tamandua tetradactyla*	r	r	c	v	v	?
9 Giant anteater	*Myrmecophaga tridactyla*	?	?	?	?	–	–
10 Tufted-ear marmoset	*Callithrix geoffroyi*	v	v	v	v	r	v
11 Masked titi monkey	*Callicebus personatus*	v	v	a	–	v	v
12 Brown capuchin monkey	*Cebus apella*	v	v	v	v	v	v
13 Brown howler monkey	*Alouatta fusca*	v	a,fa	–	?	v	–
14 Crab-eating fox	*Cerdocyon thous*	v	fa	v	v	v	v
15 Jaguarundi	*Herpailurus yaguarondi*	v	r	r	r	v	?
16 Ocelot	*Leopardus pardalis*	r	r	?	?	–	–
17 Oncilla	*Leopardus tigrinus*	r	v	r	?	r	?
18 Margay	*Leopardus wiedii*	r	?	r	v	r	?
19 Puma	*Puma concolor*	r,fo	r,fa	–	fa,r	–	–
20 Jaguar	*Panthera onca*	v	r	–	–	–	–
21 Tayra	*Eira barbara*	r	r	r	v	v	?
22 Grison	*Galictis vittata*	r	r	r	?	?	?
23 South American coati	*Nasua nasua*	v	v	v	v	v	v
24 Crab-eating raccoon	*Procyon cancrivorus*	v	fo	r	fo	fo	?
25 Kinkajou	*Potos flavus*	v	r	v	v	–	–
26 Brazilian tapir	*Tapirus terrestris*	v	r	v	fo,a	–	–
27 Collared peccary	*Pecari tajacu*	v	r	–	v	–	–
28 White-lipped peccary	*Tayassu pecari*	v	r	v	–	–	–
29 Gray brocket deer	*Mazama gouazoupira*	v	v	–	–	–	–
30 Red brocket deer	*Mazama americana*	r	r	r	?	v	v
31 Guianan squirrel	*Sciurus aestuans*	v	v	v	v	v	v
32 Bahia hairy dwarf porcupine	*Sphiggurus insidiosus*	r	v	v	?	?	v
33 Capybara	*Hydrochaeris hydrochaeris*	fo,fa	r	?	?	?	?
34 Red-humped agouti	*Dasyprocta leporina*	v	v	v	v	–	–
35 Paca	*Agouti paca*	v	fo	v	v	r	r
36 Bristle-spined porcupine	*Chaetomys subspinosus*	?	?	?	?	r	v
37 Tapiti	*Sylvilagus brasiliensis*	v	v	v	r	v	?
Presence confirmed (1)		33	32	25	21	20	13
Presence probable (2)		3	4	5	10	3	9
Total surviving (1) + (2)		36	36	30	31	23	22
Extinct or absent		1	1	7	6	14	15

[a] Common names from Emmons and Feer (1997).

[b] Scientific names from Wilson and Reeder (1993).

[c] Abbreviations: (a) auditory evidence (calls or noise when flushed); (c) carcass found; (fa) faeces found; (fo) footprints; (r) reported by other researchers or local people; (v) visual encounter; (?) presence probable but not confirmed during study; (–) extinct or absent (i.e. never cited for the location).

negatively related to reserve area ($R^2 = 0.961$; $F = 98.996$; $p < 0.001$), and again fragment size was included in the final regression with a significant coefficient ($Beta = -0.980$; $p < 0.001$).

The two large reserves (LFR and SBR) presented the richest fauna and virtually the same composition of species, which included three species found exclusively there: the giant armadillo *Priodontes maximus*, the jaguar *Panthera onca* and the gray brocket deer *Mazama gouazoupira*. The presence of other large-bodied species such as tapirs *Tapirus terrestris* and two peccaries, *Pecari tajacu* and *Tayassu pecari*, were also confirmed there. These two large reserves had the most diverse fauna of predators, composed by a total of 10 species, eight of which potentially capable of taking mammals $\geqslant 1$ kg of body weight, namely two big cats, the jaguar and puma *Puma concolor*, the ocelot *Leopardus pardalis*, three small cats *Herpailurus yaguarondi*, *Leopardus wiedii*, *L. tigrinus*, the tayra *Eira barbara* and the crab-eating fox *Cerdocyon thous*. The two medium-sized reserves (CVBR and CGBR) presented a slightly less diverse fauna but interesting differences were found between them. While the jaguar was not recorded in either the medium-sized reserves, evidence of the presence of the other large cat (puma), was found in the CGBR. The tapir was recorded in both reserves, but only the collared peccary *P. tajacu* was observed in CGBR and the white-lipped peccary *T. pecari* in the CVBR. The most striking difference between study areas was the total absence of terrestrial, large-bodied species such as tapirs, peccaries, giant armadillos, and predators such as jaguars and pumas in the two small fragments (M7/317 and Putiri). Another notable absence in these fragments was the agouti *Dasyprocta*

Table 4
Number of visual encounters with mammals/10 km of transect sampling for the six study areas

			Large		Medium-sized		Small		
Species/order[a]	Dietary category[c]	Habit[d]	LFR	SBR	CVBR	CGBR	M7/317	Putiri	Mean
Didelphimorphia									
1 *Caluromys philander*	Fr/om	Arb	0	0.57	0	0.95	0	0	0.25
2 *Didelphis aurita*	Fr/om	Sca	0.66	1.14	2.65	0	0	1.00	0.91
Xenarthra									
3 *Bradypus torquatus*	He/br	Arb	0	0	0	0	5.70	4.70	1.73
4 *Dasypus novemcinctus*	In/om	Ter	0.12	0.12	0.23	0	0.16	0.17	0.13
5 *Tamandua tetradactyla*	Myr	Sca	0	0	0	0.34	0.16	0	0.08
Primates									
6 *Callithrix geoffroyi*[b]	Fr/om	Arb	2.16	1.81	1.05	0.15	0	0.20	0.90
7 *Callicebus personatus*[b]	Fr/he	Arb	1.23	1.66	0	0	0.22	1.02	0.69
8 *Cebus apella*[b]	Fr/om	Arb	2.47	1.51	1.05	0.60	2.19	1.23	1.51
9 *Alouatta fusca*[b]	Fr/he	Arb	0.15	0	0	0	0.22	0	0.06
Carnivora									
10 *Cerdocyon thous*	Fr/om	Ter	0	0	0	0.48	0	0	0.08
11 *Leopardus tigrinus*	Car	Ter	0	0.12	0	0	0	0	0.02
12 *Herpailurus yaguarondi*	Car	Ter	0.12	0	0	0	0	0	0.02
13 *Eira barbara*	Fr/om	Sca	0	0	0	0.15	0.22	0	0.06
14 *Potos flavus*	Fr/om	Arb	0	0	1.06	2.38	0	0	0.57
15 *Nasua nasua*[b]	Fr/om	Sca	0.15	0.30	0.60	0.60	0.22	0.20	0.35
Perissodactyla									
16 *Tapirus terrestris*	Fr/he	Ter	0.12	0	0.23	0	0	0	0.06
Artiodactyla									
17 *Pecari tajacu*[b]	Fr/he	Ter	0	0	0	1.02	0	0	0.17
18 *Tayassu pecari*[b]	Fr/he	Ter	0	0	0.12	0	0	0	0.02
19 *Mazama* spp.	Fr/he	Ter	2.50	0.60	0	0	0.95	0.34	0.73
Rodentia									
20 *Sciurus aestuans*	Fr/gr	Arb	7.55	6.80	10.54	8.22	2.85	3.68	6.61
21 *Sphiggurus insidiosus*	Fr/gr	Arb	0	0	0.23	0	0	0.17	0.07
22 *Dasyprocta leporina*	Fr/gr	Ter	6.01	1.97	3.46	0.30	0	0	1.96
23 *Agouti paca*	Fr/gr	Ter	1.32	0	1.06	0.48	0	0	0.48
24 *Chaetomys subspinosus*	He/br	Arb	0	0	0	0	0	0.34	0.06
Lagomorpha									
25 *Sylvilagus brasiliensis*	He/gz	Ter	1.98	0.57	0.53	0	1.16	0	0.71
Mean			19.6	12.4	15.0	10.0	10.2	10.3	13.1

[a] Following Wilson and Reeder (1993).

[b] Species whose encounter rates are given in groups/10 km.

[c] Dietary categories from Eisenberg (1981) and Robinson and Redford (1986): He/gz (herbivore–grazer), He/br (herbivore–browser), Fr/he (frugivore–herbivore), Fr/gr (frugivore–granivore), Fr/om (frugivore–omnivore), In/om (insectivore–omnivore), Myr (myrmecophage), and Car (carnivore).

[d] Habits: Ter (terrestrial), Sca (scansorial), Arb (arboreal).

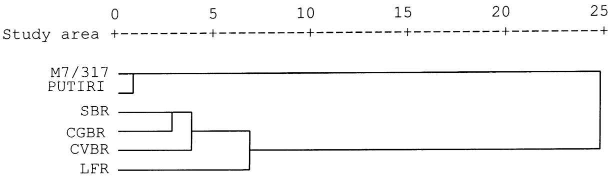


Fig. 2. Dendrogram produced by the Hierarchical Cluster Analysis of encounter rates with 25 mammal species during transect sampling in the six study sites. The scale (0–25) is a measure of distance between clusters. Large reserves (LFR and SBR), medium-sized reserves (CVBR and CGBR), small reserves (M7/317 and Putiri).

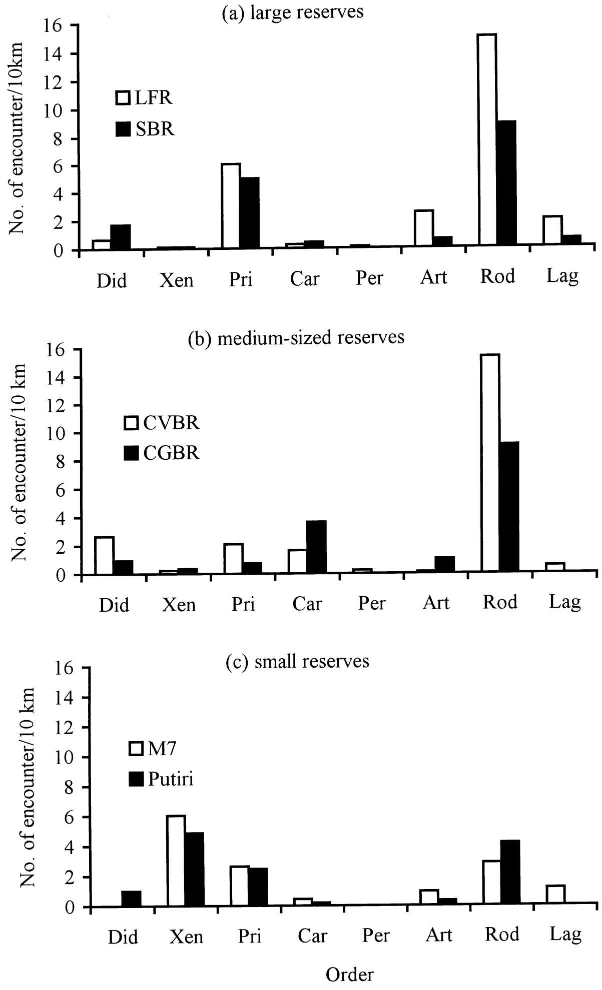


Fig. 3. Number of encounter/10 km of transect sampling for mammalian orders in the six study sites. (a) Large reserves (LFR and SBR); (b) medium-sized reserves (CVBR and CGBR), and (c) small reserves (M7/317 and Putiri). Orders: Did (Didelphimorphia), Xen (Xenarthra), Pri (Primates), Car (Carnivora), Per (Perissodactyla), Art (Artiodactyla), Rod (Rodentia), and Lag (Lagomorpha).

leporina. The mammalian faunas of the two small fragments (M7/317 and Putiri), although depleted in terms of species number, were very similar.

3.2. Species abundance

The rate of encounter/10 km of census walked is presented in Table 4 for the 25 mammal species seen during transect sampling, representing 68% of the mammal fauna known to occur in the six study areas. This species list resulted from 602 encounters with mammals (509 encounters if individuals flushed during censuses are not taken into account). A significant relationship (Multiple regression analysis; $R^2 = 0.925$; $F = 18.512$; $p = 0.021$) was found between encounter rate, the dependent variable, and two independent variables: fragment size ($Beta = 0.708$; $p = 0.045$) and hunting pressure ($Beta = -0.610$; $p = 0.066$). The stepwise method did not include time since isolation and disturbance level in the final regression equation of this analysis.

The average figure for the six reserves and for all mammal species was 13.1 encounters/10 km, but significant differences were observed between study areas. On average, mammals were about twice as abundant in one large reserve (LFR), as in the two small reserves (M7/317 and Putiri) and the medium-sized CGBR. The other medium reserve (CVBR) presented the second highest abundance of mammals, and the third figure was recorded for the large SBR. The Guianan squirrel *Sciurus aestuans* and the agouti were, respectively, the first and second most commonly seen species in LFR, SBR and CVBR. On the other hand, the maned sloth was the most abundant mammal encountered in the two small fragments.

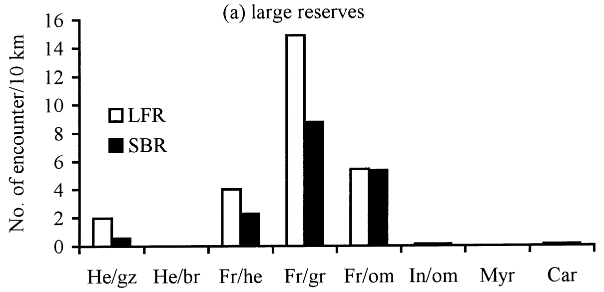
3.2.1. Encounter rates

The two small fragments (M7/317 and Putiri) were very similar in terms of encounter rates, with mammal species forming an external cluster unlike the other four study areas (Fig. 2). The other four reserves formed a separate group of which LFR was the most divergent. Considering data from all six reserves together, the top three orders in relative abundance were rodents, primates and xenarthrans, respectively (Fig. 3), but two distinct patterns emerged among the study areas. First, similar-sized reserves had similar faunas. Secondly, large and medium-sized reserves had similar abundances of orders, with a clear dominance of rodents (Fig. 3a and b), unlike the two small reserves (Fig. 3c). Large and medium-sized reserves differed slightly, however, in the abundance of primates, which were more abundant in the two largest areas ($\chi^2 = 4.788$; *d.f.* = 1; $p < 0.05$; Fig. 3a). In the small reserves, xenarthrans were as abundant as rodents ($\chi^2 = 0.827$; *d.f.* = 1; $p > 0.50$; Fig. 3c).

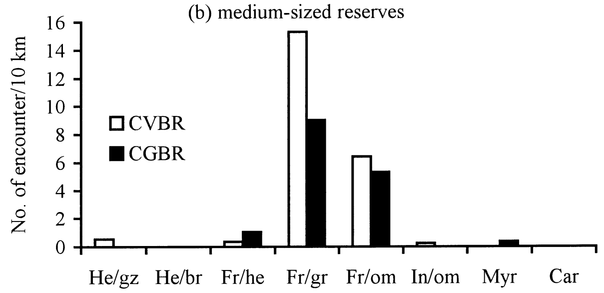
3.2.2. Dietary categories

While frugivores were the dominant category in the four larger reserves (Fig. 4a and b), herbivores had the highest abundance in the two small-sized reserves (Fig. 4c).

(a) large reserves



(b) medium-sized reserves



(c) small reserves

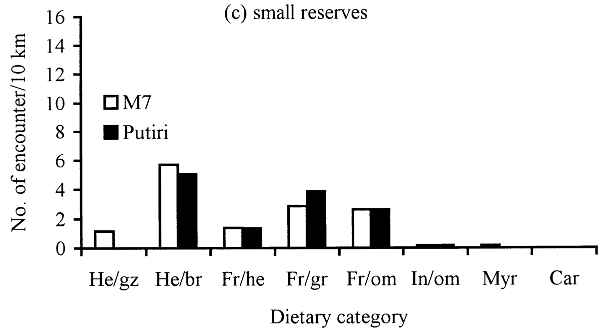


Fig. 4. Number of encounter/10 km of transect sampling for dietary categories in the six study sites. (a) Large reserves (LFR and SBR); (b) medium-sized reserves (CVBR and CGBR), and (c) small reserves (M7/317 and Putiri). Dietary categories: He/gz (herbivore–grazer), He/br (herbivore–browser), Fr/he (frugivore–herbivore), Fr/gr (frugivore–granivore), Fr/om (frugivore–omnivore), In/om (insectivore–omnivore), Myr (myrmecophage), and Car (carnivore).

This difference was due to the complete absence of agoutis and to the lower abundance of squirrels in both M7/317 and Putiri (Table 4). Within herbivores, herbivore-browsers, represented by sloths *Bradypus* spp. and by the bristle-spined porcupine *Chaetomys subspinosus*, was the category that exhibited major differences in density among study sites.

3.2.3. Habit and hunting

Major differences between study areas occurred in density of terrestrial and, to a lesser extent, scansorial species (Fig. 5). Terrestrial species were more abundant in large and medium-sized reserves (LFR, CVBR and SBR), and the lowest densities were found in the small fragments, but notably in Putiri, where only one terrestrial mammal was encountered, on average, in each 20 km of censusing (0.5 encounter/10 km). The two large reserves had contrasting abundances of terrestrial mammals as a much lower density was found in SBR than in LFR (Fig. 5). Since these two reserves had contrasting hunting pressures, the Chi-square test was used to check if hunting could account for this difference, comparing the encounter rates of hunted and non-hunted species between these two reserves. For hunted species (tapirs, peccaries, brocket deer, agoutis, pacas *Agouti paca*, tapitis *Sylvilagus brasiliensis* and armadillos *Dasypus novemcinctus*) the encounter rate was significantly higher in LFR (12.05 encounter/10 km) than in SBR (3.26 encounter/10 km) ($\chi^2 = 5.048$; $d.f. = 1$; $p < 0.025$), but no statistical difference was found for non-hunted species (all other species; LFR = 14.49 encounter/10 km; SBR = 13.91 encounter/10 km; $\chi^2 = 0.012$; $d.f. = 1$; $p > 0.90$).

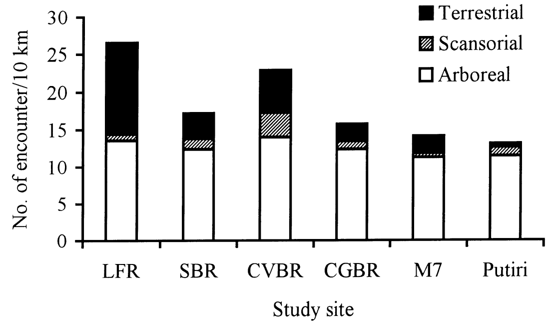


Fig. 5. Number of encounters/10 km of transect sampling for arboreal, scansorial and terrestrial species in the six study areas.

4. Discussion

4.1. Species richness

The number of mammal species recorded in the study areas was highest in the large reserves, intermediate in the medium-sized reserves and lowest in the two small fragments, as classically predicted by the island biogeography theory (MacArthur and Wilson, 1967). Extinction becomes the predominant phenomenon that accounts for this process of species loss in forest fragments because, being isolated by non-forest vegetation, they lack the sources of potential new migrants. In agreement with the nested subset hypothesis of Patterson (1987), the mammalian faunas recorded here for the small and medium-sized fragments were, indeed, subsets of those in larger reserves. This was because extinction-prone species were progressively lost from fragments over time, with smaller fragments exhibiting the greatest losses. Several studies on forest fragmentation have demonstrated that larger fragments support higher species richness than smaller fragments (Matthiae and Stearns, 1981; Fonseca and Robinson, 1990; Laurance, 1990). A number of factors may contribute to this, the most obvious one being the fact that, as the forest area is fragmented and reduced, some species, especially those with the largest spatial requirements, can not find sufficient food or other vital resources to survive in the long term in a smaller area (McNab, 1963; Redford and Robinson, 1991). Thus large cats, tapirs, peccaries, giant armadillos and the giant anteater *Myrmecophaga tridactyla* were not recorded in the smaller fragments. For these species, forest areas of c. 200 ha are probably not large enough, while the jaguar and the giant armadillo, for example, were not recorded even in the medium-sized reserves of 2000 ha, where only one peccary species and only one deer species were recorded. The only species not recorded in the large reserve was the maned sloth, but this is almost certainly not a case of extinction, since the species has never been reported to occur there or in other forest patches of northern Espírito Santo, where, instead, the three-toed sloth *B. variegatus* is believed to occur (Oliver and Santos, 1991; pers. obs.).

In a fragmented forest, top predators, such as jaguars and pumas, are clearly among the most vulnerable species as they occur at low densities and occupy very large home ranges. Apart from the two large reserves, the presence of puma was confirmed only in the mid-sized CGBR, where a scat was found, although it is probably just a temporary visitor there, because fresh scats and footprints were not found there during the study. Similarly, the jaguars and pumas that once inhabited the 1500 ha Barro Colorado Island in the Panama Canal Zone, disappeared from there after that reserve became an island isolated by the rising waters of Gatun Lake when a dam was built to form the Panama Chanel (Glanz, 1990).

Although faunal inventories were not carried out in the study areas before the advent of fragmentation, the available evidence suggests that those species not recorded in both medium- and small-sized reserves during the present study were originally present there. Based on reports of early naturalists that travelled through the area in early 1800s (Wied-Neuwied, 1820; Saint-Hilaire, 1833), all the region to the north of present-day Aracruz was originally covered by an immense, unbroken forest. At that time, Wied-Neuwied (1820) listed for this region all six cat species, today found only in the two large reserves, as well as tapirs, two species of peccaries, two species of brocket deer and the giant anteater. The contemporaneous (1818) observations of Saint-Hilaire (1833) added to this list the elusive giant armadillo. Most of those species were relatively common in the past and were reported by local residents, or by former woodcutters, to occur in the study areas until the 1960s or early 1970s. Additionally, the faunal inventories carried out by Ruschi (1978) in the region of the small fragments, listed all 15 species not recorded there during the present study.

4.2. Species abundance

The relative abundance of individual mammal species varied between study areas, but no noticeable increase in encounter rates or absolute densities was found in small and medium-sized reserves in comparison with the large areas. This has been reported for small mammal communities in the fragments of Manaus (Malcolm, 1988), but they are not comparable to those studied here, because they are both near to and not completely isolated from the continuous forest. One cannot say that migration of large mammals never takes place between forest remnants, given that several fragments of native vegetation still exist in northern Espírito Santo. As mentioned above, the puma may roam between fragments, and species that can forage in several habitat types, such as the crab-eating fox, the crab-eating racoon *Procyon cancrivorous* and brocket deer, might easily cross through non-forest areas. But the potential for migration is certainly reduced there, as the fragments are small and widely separated. Moreover, most of them are probably overhunted and the majority have been highly degraded by edge effects or anthropogenic activities such as logging and fires. Fragmentation thus prevents a hunted population from being replenished through immigration and limits their movements across the landscape (Robinson, 1996).

Analysis of relative abundances showed that both large and medium-sized reserves had a marked predominance of rodents over any other mammalian order, and frugivores were more abundant there than herbivores. On the other hand, xenarthrans were the most abundant order in the two small reserves, and herbivores were encountered there more frequently than any other dietary category, including frugivores. Two main groups of factors may account for these differences. First, frugivores need larger home ranges than herbivores because fruit, compared to leaves or herbs, have a patchier distribution both in space and time (Milton and May, 1976), as fruiting trees are generally not distributed uniformly throughout the forest and seasons differ enormously in the amount and quality of fruit sources available to consumers (Gentry and Emmons, 1987). In the Brazilian Amazon, for example, the white-lipped peccary and the strictly frugivorous bearded saki *Chiropotes satanas* were among the first species to abandon a small forest fragment shortly after its isolation from the continuous forest (Lovejoy et al., 1986).

Secondly, the forests of M7/317 and Putiri, in comparison to the other areas, present an intensified damage due to a greater exposure to winds and hot-air curents. The combination of elevated tree mortality and the consequent proliferation of secondary vegetation, including lianas and vines, observed in the small fragments (Chiarello, 1997) are certainly detrimental to frugivores but, on the other hand, can aid arboreal folivores, like the maned sloth, the brown howler monkey *Alouatta fusca* and perhaps the bristle-spined porcupine. It is known that these three folivores can survive well in small patches of degraded forests, because of their ability to include secondary vegetation in the diet (Chiarello, 1994; Chiarello et al., 1997; Chiarello, 1998). Apart from the increased availability of food source (leaves), these arboreal folivores were greatly benefited in the small fragments from the total absence of predators such as large cats and harpy eagles *Harpia harpyja*.

It has been suggested that, in the absence of predators, local species richness would diminish because strong competitors among prey species would ultimately dominate the community (Paine, 1966). Fonseca and Robinson (1990), for example, noticed that some small forest patches of the Atlantic forest were dominated by the common opossum, a generalist species that, in the absence of predators, outcompeted other species of small mammals. It would be expected, therefore, that some prey species of the small reserves would achieve higher densities there than in the large areas, which have a full complement of both avian and mammalian predators. However, an increase in relative density was observed in small and medium-sized reserves for only a very few species and only those not normally taken by hunters (see below). The only species which showed very high densities in the small fragments (M7/317 and Putiri) was the maned-sloth, which has benefited from the absence of predators and abundance of food (leaves) there. All other mammal species found in the two fragments exhibited relative densities equal to or, in most cases, lower, than that recorded for the other areas.

The impoverishment of animal communities in small forest fragments may have important consequences for the recruitment of tree species that depend directly or indirectly on them as pollinators, or for seed dispersal and predation. It is hypothesised, for example, that certain tree species such as *Hymenaea courbaril* (Leguminosae) are wholly dependent on agoutis for dispersal (Hallwachs, 1986), while Dirzo and Miranda (1990) point out that the extirpation of herbivorous and granivorous mammals has profound effects on forest regeneration. Putz et al. (1990) found that only one or two tree species dominate the tiny islets (ca. 1 ha) formed 80 years ago in the Panama Canal Zone during the damming of the River Chagres as they are too small to harbour terrestrial species of frugivorous mammals.

4.3. Impact of hunting

Evidence of "recreational" or even commercial hunting were found in all study areas (Chiarello, 1997) but the hunting pressure seems to be lowest in LFR as this reserve has an active system of vigilance against poachers (pers. obs.), and is higher in all other areas, particularly in SBR, which is under the greatest hunting pressure of all study sites. The faunal comparison between SBR and the contiguous LFR revealed a much lower abundance of game species in SBR, notably pacas, agoutis and brocket deer. If the impact of hunting is severe in extensive areas of "pristine" forests (Redford, 1992), the consequences for isolated forest fragments can be disastrous, as hunters have greater access to forests in a fragmented landscape (Robinson, 1996) and most fragments lack the sources of potential new migrants to replenish hunted populations. Strict frugivores taken by hunters are especially vulnerable in small reserves. For example, the agouti is among the most procured prey by hunters in several localities in the Neotropics (Redford and Robinson, 1987), and this may explain why it is completely absent from M7/317 and Putiri, as well as from other reserves of similar or smaller size (pers. obs.).

The absence in these small fragments of tapir, two species of peccaries, the gray brocket deer and the agouti would be, theoretically, beneficial to the proliferation of the two species of terrestrial frugivores surviving there, that is, the paca and the red brocket deer *M. americana*, but these two species were not encountered there more frequently than in large and medium-sized reserves, most probably because their population are being kept low by hunting. Similarly, in medium-sized reserves, apart from the collared peccary, only those species not subjected to hunting exhibited higher densities. The evidence found here suggests, therefore, that hunting in isolated forest fragments is an "external" force that counteracts the influence of biological processes, such as competition and predation (MacArthur et al., 1972).

The results presented here show that isolated Atlantic forest fragments of 200 ha or less were too small and disturbed to maintain intact assemblages of mammals. Smaller fragments not only had an impoverished assemblage of species, but also, the few mammal species surviving in them have very small population sizes, most of which are less then 50 individuals/reserve (Chiarello, 1997). Such small populations are highly susceptible to stochastic factors, both demographic and environmental, and to genetic deterioration due to inbreeding and loss of allelic diversity (Frankham, 1998; Franklin and Frankham, 1998). Consequently, their chances of survival in the long term are very limited. After 20–30 years of isolation, only reserves with ca. 20,000 ha or more still harbour a practically intact mammalian fauna, from herbivores to top predators. The main implication is that, in the long term, large mammals of the Atlantic forest have good chances of survival only in a small number of reserves, as the great majority of forest remnants in this biome are disturbed, isolated, and have $<$ 1000 ha of area (SOS Mata Atlântica et al., 1998). The loss of an important component of this biodiversity hotspot (Mittermeier et al., 1998) is, therefore, already well underway and will tend to increase in the next few decades.

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