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# Priority areas for the conservation of Atlantic forest large mammals

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#### ABSTRACT

Large mammal faunas in tropical forest landscapes are widely affected by habitat fragmentation and hunting, yet the environmental determinants of their patterns of abundance remain poorly understood at large spatial scales. We analysed population abundance and biomass of 31 species of medium to large-bodied mammal species at 38 Atlantic forest sites (including three islands, 26 forest fragments and six continuous forest sites) as related to forest type, level of hunting pressure and forest fragment size using ANCOVAs. We also derived a novel measure of mammal conservation importance for each site based on a "Mammalian Conservation Priority index"  $(MP_1)$  which incorporates information on species richness, population abundance, body size distribution, conservation status, and forest patch area. Mammal abundance was affected by hunting pressure, whereas mammalian biomass of which was largely driven by ungulates, was significantly influenced by both forest type and hunting pressure. The  $MP_i$  index, when separated into its two main components (i.e. site forest area and species-based conservation index  $C_i$ ), ordered sites along a gradient of management priorities that balances species-focused and habitatfocused conservation actions. Areas with the highest conservation priority were located in semi-deciduous forest fragments, followed by lowland forests. Many of these fragments, which are often embedded within large private landholdings including biofuel and citrus or coffee crops, cattle ranches and pulpwood plantations, could be used not only to comply with environmental legislation, but also enhance the prospects for biodiversity conservation, and reduce edge effects and hunting.

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#### 1. Introduction

There is a wide consensus that setting aside large natural areas as reserves is one of the most effective way to maintain wildlife populations and their ecological roles (Bruner et al., 2001; Peres, 2005). In fact, the long-term survival of large-bodied vertebrates, such as top predators and large herbivores that may be intolerant of human persecution and habitat changes, will only be ensured if these reserves are effectively protected and well connected (Newmark, 1987; Marsden et al., 2005; Chetkiewicz et al., 2006).

The population density of tropical forest vertebrates largely depends on climatic factors (temperature, rainfall), elevation, floristic composition and net primary productivity. For large-bodied species, however, population density is primarily associated with both hunting pressure (Peres and Palacios, 2007) and habitat fragmenta-

tion (Chiarello, 2000a; Michalski and Peres, 2007). While some studies have attempted to elucidate the effects of climatic variables and habitat productivity on the abundance of tropical wildlife populations (e.g. Barnes and Lahm, 1997; Stevenson, 2001), the interaction between anthropogenic disturbance and baseline environmental variables remains poorly understood, especially in complex human-dominated biomes such as the Atlantic forest.

The Atlantic forest of eastern Brazil is an ideal region to examine how environmental and anthropogenic factors mediate wildlife population abundance. This forest biome once extended from 4° to 32° S, likely comprising the longest latitudinal gradient of tropical forests worldwide (Galindo-Leal and Câmara, 2003; Ribeiro et al. 2009). The Atlantic forest is a global conservation priority containing one of the world's highest plant and vertebrate diversity, and where many species are seriously threatened by anthropogenic pressure (Myers et al., 2000; Brooks et al., 2002; Galindo-Leal and Câmara, 2003; Orme et al., 2005; Ceballos and Ehrlich, 2006).

Wildlife surveys in most large remaining Atlantic forest patches are sparse and poorly documented, and few patches larger than 20,000 ha have been intensively censused in terms of the

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abundance of medium and large mammals (Cullen et al., 2000; Chiarello, 2000a). Large mammals can critically influence ecosystem dynamics by affecting either prey populations or the composition of the surrounding vegetation (Terborgh et al., 2001). In the neotropics, most medium to large-bodied mammals are important herbivores, seed dispersers and predators shaping patterns of plant distribution and diversity (Wright, 2003; Galetti et al., 2006; Stoner et al., 2007). Studies in both temperate and tropical terrestrial ecosystems have shown that the loss of large mammals often results in strong trophic cascades with profound consequences on both higher and lower trophic levels (Ripple and Beschta, 2006; Palmer et al., 2008). Therefore, the first step to understand the myriad consequences of the loss or decline of large mammals in tropical forests is to quantify their distribution and abundance.

Here, we present population abundance estimates for a range of medium and large sized mammal species in 11 Atlantic forest reserves within the State of São Paulo, Brazil, which retains the largest remaining forest cover of all eastern Brazilian states (Galindo-Leal and Câmara, 2003; Ribeiro et al., 2009). The information on these areas was then combined with data compiled from 27 additional Atlantic forest sites, amounting to 37 sites in Brazil and one in Paraguay (Fig. 1). In particular, we consider the effects of key environmental variables including forest type, forest patch size, and level of hunting pressure. This analysis is the first attempt to understand the major drivers of mammal abundance in a highly fragmented biome. We recognize that historical effects may also have had a profound impact on forest cover and mammal abundance (see Dean, 1996), but these are likely to be less important than those occurring more recently. Finally, we propose a "mammalian priority conservation index" to rank all survey sites in relation to their current mammal conservation value based on the species richness, size distribution, conservation status, and population sizes in an attempt to pinpoint urgent conservation efforts.

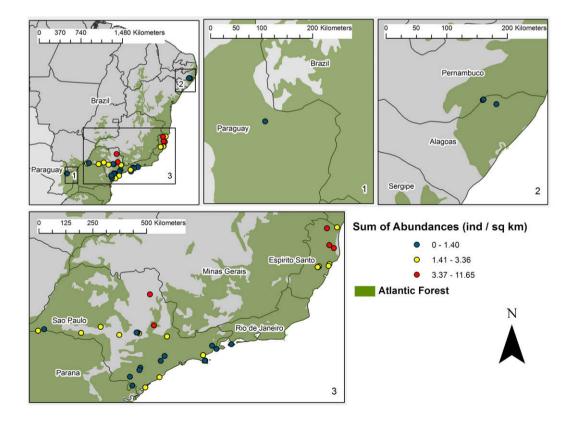
#### 2. Material and methods

#### 2.1. Species surveyed

We restricted our field surveys to a limited number of diurnal or crepuscular primary and secondary consumers which comprise the most common medium and large mammals larger than 1 kg in our study sites, including primates, ungulates, small carnivores, caviomorph rodents and armadillos. We also surveyed two groups of arboreal mammals smaller than 1 kg that were relatively common in these areas: squirrels (Sciurus spp.) and marmosets (Callithrix spp.). With the exception of squirrels and marmosets, the mammal species we censused are widely hunted throughout the Neotropics (Redford, 1992; Peres, 2000), but the choice of game species harvested depends on both prey availability and the cultural background of consumers (Jerozolimski and Peres, 2003). Ungulates, followed by large rodents and armadillos, are by far the most preferred groups of game species targeted by contemporary hunters in the Atlantic forest (Cullen et al., 2001, 2004), but primates are also hunted to a lesser extent (Lane, 1990).

### 2.2. Line-transect censuses and data compilation

As part of the BIOTA biodiversity sampling program (see http://www.biota.org.br/ and Acknowledgements), mammal abundance estimates for 11 protected Atlantic forest areas in São Paulo state were obtained from a standardized series of diurnal line-transect surveys (Table 1), using the census methods described by Peres



**Fig. 1.** Study sites where information on population abundance (individuals/10 km) of medium and large mammals in the Atlantic forest is available. Circle sizes are based on the overall abundance summed over allspecies. Green shaded area represents the original range of the Atlantic forest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**Study sites characteristics, number of species sampled, and mean (±SD) aggregate abundance and biomass of medium and large mammals sampled using line transects in the Atlantic forest, showing the Mammalian Priority index (MP<sub>i</sub>) and a classification of the overall importance of the site for mammal conservation based on this index.

Site <sup>a</sup>	Species sampled	Km sampled	Vegetation	Status	Mean abundance (ind/10 km)	Mean biomass (kg/10 km)	$MP_i$	Overal importance
Morro do Diabo, SP <sup>1</sup>	13	618	Semi-deciduous	PA	1.66 ± 2.78	26.42 ± 57.27	160.45	Higher
Res. Natural Vale, ES <sup>2</sup>	8	65	Lowland	PA	5.88 ± 5.36	11.06 ± 12.69	132.35	Higher
Carlos Botelho, SP <sup>3</sup>	9	237	Sub-Montane	PA	1.33 ± 1.79	12.30 ± 16.61	127.48	Higher
Caetetus, SP <sup>1</sup>	10	461	Semi-deciduous	PA	3.70 ± 6.33	46.76 ± 89.62	114.77	Higher
Ilha do Cardoso, SP <sup>3</sup>	15	273	Lowland	PA	1.77 ± 2.37	32.97 ± 65.73	108.85	Higher
Augusto Ruschi, ES <sup>2</sup>	9	36.7	Montane	PA	2.72 ± 2.49	12.63 ± 13.80	94.60	Higher
São Lourenço, ES <sup>2</sup>	8	35	Montane	PA	2.25 ± 2.32	$3.84 \pm 6.01$	92.94	Higher
Sooretama, ES <sup>2</sup>	7	66	Lowland	PA	5.04 ± 3.87	$7.08 \pm 7.79$	89.37	Higher
Mbaracayu, Paraguay <sup>4</sup>	5	693	Semi-deciduous	PA	1.68 ± 3.00	11.67 ± 12.66	82.19	Higher
Santa Lúcia, ES <sup>2</sup>	9	40	Montane	PA	1.95 ± 1.13	$5.70 \pm 6.71$	75.37	Higher
Fazenda Rio Claro, SP1	7	216	Semi-deciduous	NP	2.85 ± 3.19	21.21 ± 27.06	67.15	Higher
Viraeiro, SP <sup>5</sup>	11	131	Semi-deciduous	NP	2.03 ± 2.89	12.75 ± 22.04	56.86	Higher
Córrego Grande, ES <sup>2</sup>	11	67	Lowland	PA	$2.04 \pm 2.44$	8.93 ± 17.27	50.15	Higher
Mosquito, SP <sup>2</sup>	11	474	Semi-deciduous	NP	1.78 ± 2.86	12.15 ± 15.95	47.44	Medium
Monal, SP <sup>5</sup>	8	35	Semi-deciduous	NP	2.73 ± 2.58	18.91 ± 19.27	44.42	Medium
Cunha/Sta Virgínia, SP3	8	218	Sub-Montane	PA	0.99 ± 1.18	16.80 ± 38.92	43.37	Medium
Juréia, SP <sup>3</sup>	5	109	Lowland	PA	3.30 ± 4.73	26.16 ± 40.91	35.97	Medium
Intervales, SP <sup>3</sup>	7	236	Sub-Montane	PA	$0.60 \pm 0.81$	4.19 ± 8.15	35.07	Medium
Córrego do Veado, ES2	6	67	Lowland	PA	4.71 ± 3.60	14.18 ± 20.57	34.17	Medium
Morro Grande, SP <sup>6</sup>	5	241	Sub-Montane	PA	0.76 ± 0.29	2.43 ± 3.18	32.25	Medium
Cachoeira, AL <sup>7</sup>	6	216	Semi-deciduous	NP	$0.60 \pm 0.73$	6.88 ± 7.99	26.62	Medium
Petar, SP <sup>3</sup>	6	256	Sub-Montane	PA	$0.37 \pm 0.70$	2.71 ± 2.25	22.38	Medium
Ilha Grande, RJ <sup>8</sup>	8	404	Lowland	PA	$0.94 \pm 0.92$	2.99 ± 4.03	22.25	Medium
Capoeirão, AL <sup>7</sup>	6	216	Lowland	NP	$0.44 \pm 0.61$	2.86 ± 3.77	17.85	Medium
Sarã, SP <sup>5</sup>	8	68	Semi-deciduous	NP	1.77 ± 2.21	13.40 ± 19.02	17.76	Medium
São José, SP <sup>9</sup>	4	99	Semi-deciduous	NP	6.14 ± 6.26	9.75 ± 17.48	17.17	Medium
Ribeirão Cachoeira, SP10	8	271	Semi-deciduous	NP	2.14 ± 4.61	11.22 ± 29.96	13.76	Lower
M7, ES <sup>2</sup>	7	46	Lowland	NP	2.81 ± 4.93	6.88 ± 12.33	9.42	Lower
Tucano, ES1	7	357	Semi-deciduous	NP	1.81 ± 2.62	$7.93 \pm 9.93$	9.11	Lower
Picinguaba, SP <sup>3</sup>	4	202	Lowland	PA	$0.48 \pm 0.38$	8.08 ± 13.94	8.86	Lower
Putiri, ES <sup>2</sup>	5	49	Lowland	NP	3.46 ± 2.83	5.97 ± 7.81	8.72	Lower
Coimbra, AL <sup>7</sup>	7	216	Sub-Montane	NP	0.21 ± 0.19	1.12 ± 1.14	7.62	Lower
Jacupiranga, SP <sup>3</sup>	4	103	Sub-Montane	PA	$0.58 \pm 0.46$	2.99 ± 3.35	6.56	Lower
Caraguatatuba, SP <sup>3</sup>	3	137	Lowland	PA	1.84 ± 2.25	$6.00 \pm 5.46$	3.19	Lower
Água Sumida, SP <sup>5</sup>	2	40	Semi-deciduous	NP	2.80 ± 1.41	10.51 ± 1.43	1.44	Lower
Jurupará, SP <sup>3</sup>	4	251	Sub-Montane	PA	$0.16 \pm 0.12$	0.55 ± 0.45	1.17	Lower
Fazenda Serra, SP <sup>11</sup>	2	28	Semi-deciduous	NP	11.65 ± 6.35	19.09 ± 27.34	0.92	Lower
Ilhabela, SP <sup>3</sup>	2	268	Lowland	PA	0.97 ± 0.15	1.18 ± 1.38	0.68	Lower

a Based on 1. Cullen et al. (2000), 2. Chiarello (1999, 2003, unpub. data), 3. This study, 4. Hill et al. (2003), 5. Martins (2005, unpubl. data), 6. Negrão and Valladares-Padua (2006), 7. Fernandes (2003), 8. Pereira (2006), 9. Bernardo and Galetti (2004), 10. Gaspar (2005), 11. Chiarello (2000b). Area Status: PA=protected area, NP=non-protected.

(2000), which are widely used throughout the neotropics (see Peres and Palacios, 2007). Line-transect censuses at each site were conducted by previously trained observers who systematically walked three to six transects that varied from 2 to 8 km in length depending on local topography and forest patch size. Each area was sampled monthly for at least one year to avoid seasonal bias for semi-nomadic or wide-ranging species, such as white-lipped peccaries (*Tayassu pecari*) (Keuroghlian et al., 2004), resulting in an average of 208 km (range = 103–273 km) of census walks per site. This amounted to a cumulative total of 2290 km walked at all 11 sites.

The relative biomass of each species was calculated by multiplying its body weight (kg, following Fonseca et al., 1996) by its local abundance (individuals per 10 km walked). For social species (e.g. primates, coatis *Nasua nasua* and peccaries), whenever the abundance had been estimated in terms of groups per 10 km walked we simply multiplied this metric by the mean group size at each site to obtain the population abundance in terms of individuals per 10 km.

In addition to the 11 sites that we surveyed, we added to our analysis all wildlife surveys using line-transect techniques performed elsewhere in the Atlantic forest biome that reported data on population abundance of mammal species larger than 1.5 kg (Table 1). We identified appropriate studies through Web of Science and Google scholar searches, from our own knowledge of the literature, dissertations, theses, and our own unpublished data.

In our first compilation we uncovered 48 sites at which the local mammal assemblage had been surveyed, but we subsequently discarded nine of these sites with a census effort lower than 20 km of transect walks per site. Observers in all selected studies sampled the entire spectrum of medium and large mammal species, and we excluded studies focused on a single mammal order.

We failed to uncover community-wide studies targeting the medium and large mammal fauna in several important regions of the Atlantic forest, including the Brazilian states of Paraná, Santa Catarina, Rio Grande do Sul, Bahia, Minas Gerais and Rio de Janeiro (except for Ilha Grande), and the Argentinean state of Missiones (Fig. 1). We excluded information on Ilha Anchieta, a land-bridge island off the coast of São Paulo, because deliberate introductions of confiscated animals most likely resulted in abnormally hyperinflated population abundances of several mammal species (Bovendorp and Galetti, 2007).

#### 2.3. Explanatory variables

The level of hunting pressure imposed on the mammal community of each forest site was determined independently of biotic data collection. For all sites in our analysis we assigned a hunting pressure score based on information explicitly provided by the site-specific publication, personal communication with observers who carried out the surveys, park rangers, reserve managers or our own first-hand knowledge of the area. This estimate was based

on direct or indirect evidence of hunter activity encountered during censuses or reported in the papers, dissertations and reports, such as detection of shotgun blows within hearing range, spent shotgun cartridge, hunting trails, ambush "waiting" stations, hunter campsites, and direct encounters with hunters. Since all sites in the Atlantic forest were accessible to hunters and have some poaching pressure, we broke down levels of hunting pressure into only two levels:

- 1. Light-moderate. Forest sites located in areas with low to moderate densities of human residents and weak evidence of hunting. Usually, these sites were protected by rangers who regularly patrolled the sites.
- 2. Heavy. Forest sites occupied by large human populations (i.e. acculturated Indians, quilombolas and caicaras) and exhibiting considerable evidence of hunting. These protected areas were usually legally or illegally occupied by self-declared indigenous communities claiming ancestral rights to these parks (Olmos et al., 2004; Olmos and Galetti, 2004). Like in other parts of Brazil, these Indigenous communities are given legal permission to hunt within the parks, whereas all non-indigenous rural folk are not. In several protected parks (e.g. Jurupará and Juréia), hunting is also carried out by people from nearby cities, and villages.

We acknowledge that hunting pressure is, however, the most imprecise variable incorporated into our models, and more detailed studies on the impact of subsistence hunting within legally occupied protected areas are urgently needed (Peres and Nascimento, 2006), especially in the Atlantic forest (Nobre, 2007; Pinto et al. 2009).

The classification of forest types of all study sites where wildlife surveys were carried out was based on Oliveira and Fontes (2000). This classification scheme already takes into account a number of environmental gradients including soil types, floristic composition, rainfall and elevation. In the Atlantic forest, forest sites are generally classified as either evergreen or semi-deciduous, and then divided into four elevational classes, resulting in eight main forest domains. Areas north of 23° 20'S (tropical climates) or below 700 m above sea level (lowland climates) have been classified as evergreen forests in which the short dry season lasts 30 days or less. Semi-deciduous forests, on the other hand, are seasonally dry, with an extended dry season lasting 40-160 days. Areas located south of 23° 20'S and above 700 m (montane subtropical climates) were classified as either evergreen or semi-deciduous forests if their total annual rainfall was 2000-3600 mm or 1500-2000 mm, respectively. The elevational categories in the Oliveira and Fontes (2000) classification scheme are: lowland, <300 m; sub-montane, 300-700 m; lower montane, 700-1100 m; and upper montane, >1100 m. Among the eight possible forest domains, only four were represented by survey sites: (1) sub-montane semi-deciduous; (2) lowland evergreen forest; (3) sub-montane evergreen forest and (4) montane evergreen forest. Hereafter we refer to evergreen forests by their elevational category, and to sub-montane semi-deciduous forests as simply semi-deciduous.

## 2.4. Statistical analysis

Because mammal population density estimates were rarely available, abundance estimates at different sites, as derived from our own wildlife surveys and those conducted by other investigators, were expressed for each species as an encounter rate (individuals per 10 km of census effort). We also explicitly consider forest type, extent of forest patches (ha), and hunting pressure, which were entered as independent variables in a linear Analysis of Covariance model (ANCOVA).

Using ANCOVAs (Quinn and Keough, 2002), we examined spatial variation in mammal abundance and biomass as related to forest type (categorical), degree of hunting pressure (ordinal) and forest fragment area (ha) within which the surveys were carried out (continuous covariate). Some sites are embedded in 'continuous' forests (i.e. contiguous with vast tracts of remaining Atlantic forests of Serra do Mar-Paranapiacaba massif, see Ribeiro et al., 2009). For these sites, however, we attributed a conservative value for forest area that is equivalent to one order of magnitude greater than the size of the largest forest site (Mbaracayu, c. 60,000 ha) that could not be defined as continuous (hereafter, forest fragment) (see Ribeiro et al., 2009).

The linear model employed for each dependent variable included only the main effects. We could not test the interaction between categorical variables because some cell combinations were not supported by the data set. The interactions with forest area were included only in an initial trial, to verify the assumption of homogeneity of slopes. These were, however, excluded from further analysis because they were not significant.

We first examined the aggregate mammal abundance and biomass (summed over all species), and then repeated the same analyses separately for each major order of mammal species (Artiodactyla-Perisodactyla (grouped as Ungulates), Primates, Rodentia and Cingulata). For primates and rodents, we excluded the data for marmosets and squirrels, respectively, as these species are not usually hunted (Cullen et al. 2000). Another dependent variable was the mean body weight  $\overline{W_i}$  (kg) of each mammal assemblage, calculated for each site "i" as following:

$$\overline{W_i} = \sum_{k}^{S} W_k \cdot p_{k,i}$$
where  $p_{k,i} = \frac{a_{k,i}}{\sum_{k}^{S} a_{k,i}}$ . (1)

In Eq. (1), "k" represents each species, "S" is the species richness of that site,  $W_k$  is the typical weight of species "k" (kg),  $p_{k,i}$  is the relative abundance (from 0 to 1) of species "k" at the site "i", and " $a_{ki}$ " is the abundance (ind./10 km) of that species in that site. We expected that sites under high levels of hunting pressure should have a lower mean body weight, as large-bodied species are generally the most vulnerable and the most prone to local extinction at those sites (Peres, 2000). To avoid possible nonlinearities and homogenize variances, the response variables were log(x + 1) transformed, except for mean body weight, which was log(x) transformed.

To account for purely spatial influences and avoid spurious statistical results, we used spatial correlograms to verify if the residuals from linear models exhibited spatial autocorrelation (Diniz-Filho et al., 2003; Legendre and Legendre, 1998). We calculated the Moran's I index of autocorrelation for each one of a series of distance classes, and tested its significance using a permutation test employing 1000 permutations and proceeding with a progressive Bonferoni's correction for multiple testing (Legendre and Legendre, 1998). We accounted for significant autocorrelations in the residuals, whenever at least one was detected, by applying eigenvector filtering analysis (Diniz-Filho and Bini, 2005; Rangel et al., 2006) and including selected spatial filters as explanatory variables in the linear models. We selected the filters by sequentially adding them into the models until the elimination of significant spatial autocorrelation in the residuals. All spatial analyses were carried out using the software SAM 2.0 (Rangel et al., 2006). Geodesic distances were calculated among sites, based on their geographic coordinates, to account for the Earth's curvature. They were grouped into nine distance classes, according to Sturge's rule for a compromise between spatial resolution and statistical power (Legendre and Legendre, 1998). The classes were delimited in such a way to balance the number of pairs of sites within each class, thereby providing a similar power for the tests of significance of autocorrelation coefficients.

In most analyses, we detected deviations from assumptions of homocedasticity by means of Levene's tests. This occurred with total and large mammal abundances. Nevertheless, our main estimates remain well supported, as this assumption was not violated in the analyses using biomass estimates, which also showed significant effects in the same direction as those observed for abundances.

We also provide for each site a measure of importance of its conservation value for large-bodied mammal species. First, we propose an index that includes native species richness, species threat status (based on IUCN status), species uniqueness and body size. This species-based conservation importance for a given site "i"  $(C_i)$ , is calculated as following:

$$C_i = \sum_{k}^{S} \log(W_k) \cdot U_{k,i} \cdot q_{k,i}$$
 (2)

where  $q_{k,i} = \frac{a_{k,i}}{\sum_{i}^{l} a_{k,i}}$ . In Eq. (2),  $W_k$  is the typical body weight (g) of species "k";  $U_{k,i}$  is a score of the conservation status of species "k" at site "i", based on its IUCN category for the state in which the site is located;  $q_{k,i}$  is another measure of relative abundance of species "k"; and L is the total number of sites. The species richness is implicitly included, as the sum is taken across the "S" species observed in a site, so the higher the number of species, higher the index value will have. Each species "k" has a different contribution to the overall importance of a site, so the species identities are in some way taken into account. The product within the summation represents this contribution.

In terms of the abundance metrics, the difference between  $p_{ki}$ and  $q_{k,i}$  is that the latter is the proportional contribution (from 0 to 1) of site "i" for the total abundance of species "k" among all sites, whereas the former is the contribution of species "k" compared to the total abundance of all other species within site "i". If the total abundance of a given species is largely concentrated on a given site, resulting in a high value of  $q_{k,i}$ , this site should be considered important to the conservation of that species, and its importance will be higher if the species considered is more threatened and larger. The conservation status,  $U_{k,i}$ , was calculated by assigning weights to IUCN categories, from 1 to 5, as following: Not Threatened = 1; Near Threatened = 2; Vulnerable = 3; Endangered = 4 and Critically Endangered = 5. Some species are currently listed under different conservation status in different Brazilian states, presenting different  $U_{k,i}$  values depending on the site under consideration.

We consulted the recent species red lists for the states of São Paulo (www.ambiente.sp.gov.br/listas\_fauna.zip), Espírito Santo (Chiarello et al., 2007) and Rio de Janeiro (Bergallo et al., 2000). This criterion is appropriate because we are primarily concerned with the local persistence of Atlantic Forest mammals, so the regional-scale extinction risk must be important. For example, whitelipped peccaries (T. pecari) are widely considered to be either threatened or critically threatened throughout the Brazilian Atlantic forest (Bergallo et al. 2000; Chiarello et al., 2007) and Mesoamerica (Ceballos and Oliva, 2005) but are not classified as threatened by IUCN red list because this species occurs in large viable populations in much larger areas of Amazonia and the Pantanal wetlands (although this status may change, A. Keuroghlian, pers. comm.). For the State of Alagoas and Paraguay, where regional lists are unavailable, the species were classified according to the red list for Brazil (www.iucnredlist.org). In three areas (Ilha Grande, Morro Grande and Fazenda da Serra) we found high abundance of exotic marmosets (Callithrix jacchus or C. penicillata). These species were excluded from the overall analysis of conservation priorities, as there is little conservation interest in retaining these species outside their original range.

We include body size as an additional component of the site priority index because populations of larger species need larger areas, are generally more prone to local extinction and usually exert important and unique ecosystem functions (Pimm, 1991; Woodward et al., 2005; Cardillo et al., 2005). The measure of body size is complementary to the IUCN criteria, as some larger species may not be considered threatened by IUCN criteria but are at risk of local scale extinction in the highly fragmented Atlantic Forest biome. For this index, body mass is expressed in grams, rather than kilograms, to scale the importance of body weight similarly to that of other terms. For instance, the maximum values of  $U_{k,i}$  and  $log(W_k)$  are, respectively, 5 (for critically endangered species) and 5.378 (for tapir, *Tapirus terrestris*, the largest species).

Finally, we multiplied the index  $C_i$  by a function of site forest area, providing the final index MPi, which we term "Mammalian Priority Conservation Index":

$$MP_i = C_i \cdot A_i^{0.25} \tag{3}$$

where  $A_i$  is the area of site "i". The area was included in the index as a surrogate measure of viability of its populations. In small forest patches, the chance of occurrence of local extinctions is higher due to small population sizes, which enhances the severity of demographic and environmental stochasticity and the detrimental effects of inbreeding (Bull et al., 2007). Also, smaller patches are associated with the negative effects of fragmentation and edges, which often reduce forest habitat quality for large mammals (Laurance et al., 2002; Michalski and Peres, 2007). For this index, the measure of area used for those sites embedded within continuous forest was the legally protected area, rather than the total forest area. We adopt this procedure because there is no guarantee that forests outside conservation units will remain undisturbed in the future, and we required a measure of area to characterize each site. For small isolated forest fragments, we used the fragment area itself.

The potential for a given area to support species can be inferred by the well-known species-area relationship, which is usually described by the power function cAz (Williamson, 1988). The value of the constant "c" is more variable, and depends entirely on the units of measurement. The value of the exponent "z", on the other hand, tends to be relatively invariant within regions (Rosenzweig, 1995). We selected the value 0.25 as it is widely accepted (Grelle et al., 1999; Williamson, 1988). Although exponents found among mainland habitat patches can be somewhat smaller than this value, typically ranging from 0.12 to 0.18 (compared to islands for which z ranges from 0.25 to 0.35), we thereby opted to use 0.25 as the study region covers an area of thousands of square kilometres, including distinct regions of endemism, which tends to inflate the value of z (Rosenzweig, 1995). The index will therefore be higher in larger sites that contain higher species richness, larger populations of large-bodied mammals, more species in higher threat categories, and providing a greater contribution to the overall abundance of its constituent species. Including both a speciesbased index  $C_i$  and site area in the same index  $MP_i$  could be somewhat misleading, as area and species richness tends to be correlated. However, forest patch area was a poor predictor of species richness in our dataset (linear log-log regression:  $R^2 = 0.066$ , p = 0.119). Also, both the site area and the species-based indicator have their own importance. In these terms, we order site importance according to the overall index  $MP_i$  and provide a comparative analysis by plotting  $C_i$  versus site area (raised to 0.25), which allows a more general measure of the conservation requirements of a site. We further note that this index is not aimed to capture every site feature that could determine its conservation value. The index simply includes surrogate measures that are relatively

straightforward to obtain empirically, and it should be interpreted carefully when prioritizing conservation value and habitat management plans.

#### 3. Results

#### 3.1. Determinants of mammal abundances

Thirty-one species of medium and large mammals were detected in the 38 forest sites considered here, ranging from two (Ilhabela) to 15 species per site (Ilha do Cardoso) (Table 1). Mean population abundance across all sites ranged from 0.04 ± 0.08 ind./10 km (Brazilian porcupine, Coendou prehensilis) to  $6.76 \pm 5.13$  ind./10 km (capuchin monkeys, Cebus spp.). Of the species censused, the white-lipped peccary T. pecari was the second most abundant mammal in our Atlantic forest sites  $(4.19 \pm 2.61 \text{ ind.}/10 \text{ km})$ , followed by marmosets *Callithrix* spp. (2.94 ± 3.31 ind./10 km) and howler monkeys Alouatta guariba  $(2.72 \pm 3.15 \text{ ind.}/10 \text{ km})$ . Squirrels (Sciurus spp.) comprised the most widespread taxon, occurring at 33 sites, followed by Cebus spp. (31 sites) and A. guariba (25 sites) (Table 2). Primates comprised by far the most abundant group of species in each forest type and accounted for the highest biomass in montane and submontane forests, while peccaries contributed with the highest biomass in lowland and semi-deciduous forests (Table 2).

Among the response variables, the total mammal abundance. the abundance and biomass of Primates (except Callithrix), Cebus and Sciurus exhibited residuals with significant spatial autocorrelations, so we included spatial predictors from eigenvector filtering analysis. Figs. 2 and 3 show the correlograms for the abundance and biomass estimates, respectively. For Cebus and Sciurus abundance and biomass, the first spatial filter was sufficient to exclude autocorrelation from residuals. For total abundance and primate biomass, it was necessary to include the first three spatial filters, and for primate abundance, the first five spatial filters. Linear models showed that overall mammal abundance estimates were strongly affected by hunting pressure, with sites exposed to higher hunting pressure exhibiting lower abundances (Table 3). Before including the spatial filters, total mammal abundance showed a significant relationship with forest type ( $F_{3,32} = 3.794$ ; p = 0.020), but subsequent analysis with filters showed that such effect were mainly due to the spatial structuring (Table 3). Overall mammal

biomass was significantly related to forest type (biomass being lower in sub-montane sites) and negatively affected by hunting pressure (Table 3, Fig. 4).

Considering the major taxonomic groups of game species separately, we found that most of the variation in abundance and biomass was due to ungulates (Table 4). The abundance and biomass of ungulates was affected by the level of hunting pressure (negatively), and forest type. As with all mammal species combined, ungulates exhibited the lowest abundance and biomass in submontane sites (Fig. 4). Primate abundance and biomass were initially affected by forest type (abundance:  $F_{3,32} = 3.794$ ; p = 0.020; biomass:  $F_{3,32}$  = 3.794; p = 0.020) and hunting pressure (abundance:  $F_{3,32} = 3.794$ ; p = 0.020; biomass:  $F_{3,32} = 3.794$ ; p = 0.020). However, they were not significantly affected by any independent variable after the spatial structure of the data was accounted for. which stresses the importance of geography for this order (Table 4). The abundance of large rodents was significantly affected by forest type (Table 4), being lower at sub-montane and semi-deciduous sites. No consistent pattern was found for either armadillos or carnivores and we failed to consider the data for Cingulata due to small sample sizes.

The two most widespread genera were affected by forest type before spatial autocorrelation was taken into account (*Cebus* abundance:  $F_{3,32} = 3.090$ ; p = 0.041; p = 0.020; *Sciurus* abundance:  $F_{3,32} = 6.561$ ; p = 0.001; *Sciurus* biomass:  $F_{3,32} = 5.037$ ; p = 0.006). After the inclusion of the first spatial filter, *Cebus* abundance and biomass were significantly affected by forest type (abundance:  $F_{3,31} = 3.209$ ; p = 0.036; biomass:  $F_{3,31} = 3.069$ ; p = 0.042), with lower abundances in sub-montane sites and higher abundances in semi-deciduous sites. On the other hand, the abundance and biomass of *Sciurus* were no longer significantly affected by any independent variable after the spatial effects had been taken into account.

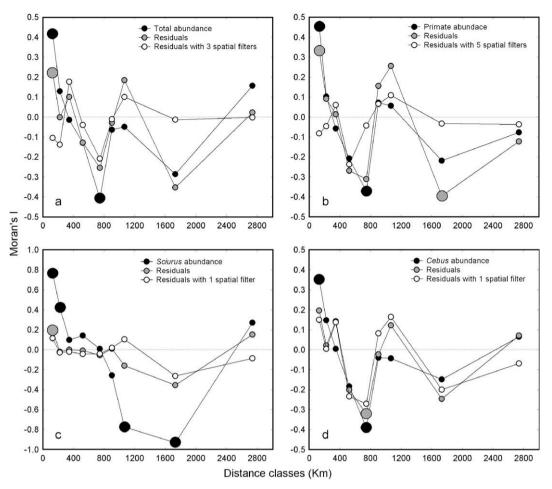
Changes in abundance and biomass, observed mainly in ungulates and primates, were accompanied by significant changes in the assemblage mean body weight driven by differences in hunting pressure. As shown by the abundance and biomass responses in ungulates (Table 4, Fig. 4), hunting pressure had a significantly negative effect over mean mammal body weight  $\overline{W}_i$  ( $F_{1,32} = 5.708$ ; p = 0.023). This association was expected since ungulates were the largest species recorded in all surveys. Therefore, in sites with higher hunting pressure, the mammal assemblages become restricted to individuals of smaller species.

 Table 2

 Summary of the abundances of medium and large-bodied mammal species in each Atlantic forest type. Species sampled at fewer than four sites sampled are not included in this table.

Order	Species	N sites	Lowland	Montane	Semi-deciduous	Sub-Montane
Carnivora	Cerdocyon thous	4	0.16 ± 0.02	P	0.30 ± 0.37	P
	Eira barbara	11	$0.18 \pm 0.05$	0.29	$0.10 \pm 0.06$	$0.05 \pm 0.01$
	Nasua nasua	25	$1.07 \pm 0.63$	1.05	1.52 ± 1.58	$0.70 \pm 0.45$
Cingulata	Dasypus spp.	9	$0.33 \pm 0.01$	1.03 ± 0.34	$0.34 \pm 0.31$	NS
Primates	Alouatta guariba	25	1.33 ± 1.00	$4.80 \pm 2.48$	4.98 ± 3.95	$0.62 \pm 0.49$
	Brachyteles spp.	8	0.30	$0.08 \pm 0.16$	4.47 ± 1.37	1.47 ± 1.60
	Callicebus spp.	11	4.13 ± 2.41	$3.26 \pm 0.31$	$0.38 \pm 0.30$	NP
	Callithrix spp.	16	$4.90 \pm 4.25$	$1.35 \pm 0.14$	2.53 ± 2.76	$0.75 \pm 0.52$
	Cebus nigritus	31	$8.20 \pm 4.86$	$5.78 \pm 2.23$	$8.44 \pm 5.40$	1.48 ± 1.81
	Leontopithecus chrysopygus	4	NP	NP	$0.41 \pm 0.36$	NP
Rodentia	Cuniculus paca	6	$0.72 \pm 0.33$	$2.07 \pm 0.69$	P	0.05 ± 0.01
	Dasyprocta spp.	19	$1.46 \pm 2.05$	P	0.51 ± 0.53	$0.19 \pm 0.18$
	Hydrochaeris hydrochaeris	4	0.05	P	0.17 ± 0.22	P
	Sciurus spp.	33	$3.42 \pm 3.62$	$3.25 \pm 0.50$	1.11 ± 2.30	$0.36 \pm 0.31$
Artiodactyla	Mazama spp	11	$0.32 \pm 0.47$	P	0.22 ± 0.12	$0.09 \pm 0.06$
	Pecari tajacu	17	$2.63 \pm 2.66$	1.08	1.89 ± 1.80	$0.43 \pm 0.36$
	Tayassu pecari	9	$3.36 \pm 2.70$	P	5.71 ± 4.63	3.74
Perissodactyla	Tapirus terrestris	5	P	P	$0.14 \pm 0.03$	0.16

P = present in some areas but not sampled during line transects, NP = species not present in this forest type.



**Fig. 2.** Spatial correlograms for mammal abundances at 38 sites of the Brazilian Atlantic forest: (a) total mammal abundance, (b) primate abundance, (c) *Sciurus* abundance, (d) *Cebus* abundance. Both variables were log-transformed before analysis. Larger circles represent significant values after progressive Bonferroni corrections ( $\alpha_{\text{initial}} = 5\%$ ). Positive and negative Moran's *I* indicate whether the values of a variable are more or less similar, respectively, for pairs of sites at each distance class.

## 3.2. Conservation priorities for mammal conservation

The "hotspot" areas for conservation of medium and large sized mammals were arbitrarily divided into three major classes: higher priority ( $MP_i > 50$ ), medium priority ( $15 < MP_i < 50$ ) and lower priority ( $MP_i < 15$ ). Among the 38 sites considered here, 13 sites were classed as higher, 13 as medium, and 12 as lower priority (Table 1, Fig. 1). Seven lower priority, six medium priority and two higher priority sites are currently legally unprotected (Table 1). Semi-deciduous forest contained the largest number of sites classified as higher priority (five sites), followed by lowland forest (4), montane (3) and sub-montane (1). All montane forests were classed as higher priority because they contained high abundances of several threatened species, but not the highest abundance overall (Table 1).

The  $MP_i$  values were not evenly influenced by its components, the  $C_i$  index, neither by the site area (Fig. 5). Some sites had high  $C_i$ , but a small area, while the opposite was true for other sites even with similar  $MP_i$  values.

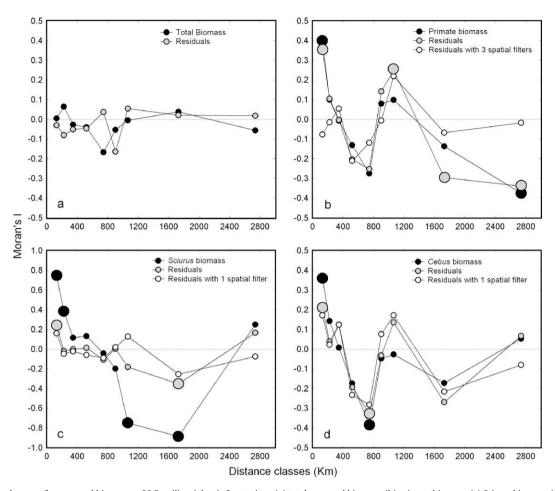
# 4. Discussions and conclusions

# 4.1. Determinants of mammal abundances

This is the first attempt to understand the regional-scale environmental determinants of the abundance of midsized to large-bodied mammal species right across the Atlantic forest biome. Given the distribution of sites in our compilation, we recognize that there are large important Atlantic forest expanses that still deserve urgent intensive censuses, especially in the states of Paraná, Santa Catarina, Minas Gerais, Rio de Janeiro and Bahia. In particular, data on large mammal abundance remain unavailable for large areas, including key protected areas such as Iguaçu National Park (Paraná), Itatiaia and Bocaina National Parks (Rio de Janeiro), Monte Pascoal and Descobrimento National Parks (Bahia) and Rio Doce State Park (Minas Gerais). These areas are known to harbour many endemic mammal species, may retain viable populations of several medium and large mammals and, therefore, should be prioritized for future mammal censuses.

Nevertheless, we found a clear pattern of the major determinants of mammal abundance and biomass throughout the Atlantic forest biome. Forest type (here defined as a composite variable that takes into account floristic composition, rainfall and elevation; *sensu* Oliveira and Fontes, 2000) and level of hunting pressure were important predictors of mammal abundance, whereas forest patch area did not seem to be a major determinant. Lowland and semideciduous forests contained the highest mammalian abundance across the Atlantic forest. These areas also harbour large populations of several threatened species, especially primates. On the other hand, montane and sub-montane forests were associated with relatively low abundances.

The high mammal abundance and biomass in lowland and semi-deciduous forests can be due to the availability of fleshy



**Fig. 3.** Spatial correlograms for mammal biomass at 38 Brazilian Atlantic forest sites: (a) total mammal biomass, (b) primate biomass, (c) *Sciurus* biomass, (d) *Cebus* biomass. Both variables were log-transformed prior to analysis. Larger circles represent significant values after progressive Bonferroni corrections ( $\alpha_{initial} = 5\%$ ). Positive and negative Moran's *I* indicate whether the values of a variable are more or less similar, respectively, for pairs of sites at each distance class.

**Table 3** Multifactorial ANCOVAs for total abundance ( $\log(x + 1)$  Individuals/10 km) and total biomass ( $\log(x + 1)$  kg/10 km). For the overall models:  $R^2 = 0.705$ ; Adj.  $R^2 = 0.420624$ ; F(8,29) = 8.678; P(0,001) for abundance and P(0,001) f

Dependent variable	Effect	SS	df	F	р
Abundance	Intercept	2.963	1	54.99	0.000
	Forest type	0.412	3	2.55	0.075
	Hunting pressure	0.585	1	10.85	0.003
	Log(Area)	0.218	1	4.05	0.053
	First spatial filter	0.070	1	1.29	0.265
	Second spatial filter	0.135	1	2.50	0.125
	Third spatial filter	0.772	1	14.32	0.001
	Error	1.563	29		
Biomass	Intercept	5.608	1	42.74	0.000
	Forest type	2.357	3	5.99	0.002
	hunting Pressure	2.918	1	22.24	<0.001
	Log(Area)	0.010	1	0.08	0.784
	Error	4.199	32		

fruits and overall levels of fruit production (Morellato and Leitão-Filho, 1992; Keuroghlian and Eaton, 2008a). Since 28 of the 31 mammal species censused are partly frugivorous, fruit productivity may largely explain differences in mammal abundances across sites. Fleshy fruit production has been shown to be positively correlated with neotropical primate biomass (Stevenson, 2001). The density of endozoochorous trees is also presumably important. For instance, Almeida-Neto et al. (2008) found a higher percentage of mammal-dispersed species in warmer Atlantic forest sites (low-land and semi-deciduous forests) while the proportion of mam-

mal-dispersed fruits decreases towards higher elevations. This pattern partly explains why montane and sub-montane forests sustain a lower overall mammal abundance and biomass. Keuroghlian and Eaton (2008a) found that white-lipped peccaries (*T. pecari*) in semi-deciduous forests rely on few, but highly productive, tree species bearing fleshy fruits. Differences in floristic composition, habitat structure and soil fertility were also strong predictors of the differences in large mammal assemblage structure between Amazonian *terra firme* and seasonally-flooded (várzea) forests (Haugaasen and Peres, 2005).

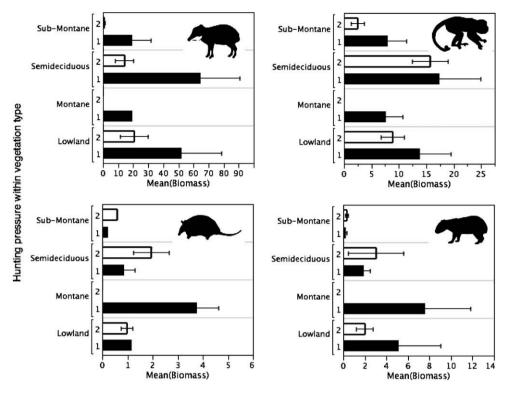


Fig. 4. Mean (±SE) of the biomass of the major game groups (ungulates, primates, armadillos and large rodents) in the Atlantic forest in each forest type and hunting pressure. Black bar hunting pressure moderate-low and white bars high. Note that montane forest sites with level 2 of hunting pressure are unavailable in the data set.

The effect of hunting pressure is expected to be greater in land-bridge islands and isolated forest patches because immigration into these sites from neighbouring source areas cannot balance or restock wildlife populations depleted by game hunters (Peres, 2001). Indeed, when we included an additional categorical variable (island or continent) in the linear model, we found a significant effect of the interaction between this variable and hunting pressure over both total biomass ( $F_{1,30} = 7.509$ , p = 0.010) and ungulate biomass ( $F_{1,30} = 4.784$ , p = 0.037), in which hunting has a stronger negative effect on land-bridge islands. Nevertheless, these analyses showed severe deviations from homogeneity of variances together with an extremely unbalanced design (there were only three true islands in the data set). The degree to which game hunting and habitat isolation operates synergistically is yet to be examined in heavily fragmented parts of the Atlantic forest.

The importance of the Atlantic forest for biodiversity conservation has long been emphasized (Fonseca, 1985). In fact, the Atlantic forest is widely considered as a global biodiversity priority whether this is defined in terms of species richness or the occurrence of endemic and/or threatened species (Myers et al., 2000; Brooks et al., 2002, 2006 Orme et al., 2005; Brooks et al., 2006; Ceballos and Ehrlich, 2006; Gjerde et al., 2007; Hurlbert and Jetz, 2007). However, these studies are too coarse-scale, focus only on presence-absence data, and rarely provide detailed information on specific locations to deploy realistic conservation actions. Very few attempts have been made to refine conservation priorities that can be used by decision makers (Harris et al., 2005; Pardini et al., 2009).

We are aware that the application of our conservation priority index was restricted to medium and large-bodied mammals, but this could be extended to other taxonomic groups, including small non-volant mammals, bats, larger secretive species (felids, tapir and deer), and other vertebrate, invertebrate and plant taxa that could be surveyed at the same sites. For instance, the PETAR (Parque Estadual Turistico do Alto do Ribeira) is one of the few large

protected areas within the State of São Paulo that safeguards a complete mammal fauna including jaguars, the largest primate species, wolly spider monkey, and possibly bush-dogs (Speothos venaticus; see Beisiegel and Ades, 2004). However, we ranked this site as of medium priority because only four mammal species were recorded during the BIOTA sampling program and these were represented by low abundances. Nevertheless, this site is widely considered to be an Important Bird Area because it holds 256 bird species, eight or which are threatened (C.O. Gussoni and M. Galetti, unpublished data). Another illustrative example is Ilhabela. This land-bridge island was ranked as the lowest priority in our study, but uniquely represents the entire distribution of an endemic small mammal [Nelomys (=Phyllomys) thomasi (Olmos, 1997)] and it is one of the most important strongholds of the jacutinga (Aburria jacutinga) (Bernardo et al., unpublished data). Although spatial patterns of conservation priority for different taxa are by no means congruent (Ceballos and Ehrlich, 2006), our index can be refined to accommodate other groups as both site occupancy and abundance data become available (see Kremen et al., 2008). In addition, areas considered lower priority, may have enormous importance for regional conservation (ex. Ribeirão Cachoeira, Gaspar, 2005) and may not be left without resources for their management.

The conservation priority index proposed here takes into account both overall and threatened species richness as well as habitat variables that can indicate priorities for conservation investments. The Semi-deciduous Atlantic forest domain, which is far removed from coastal areas, comprises the most threatened forest type in the entire Atlantic forest biome, and included five of the 13 sites ranked as higher priority. This forest type is located on flat, fertile soils of high agricultural value and retains very few forest fragments larger than 2000 ha (Ribeiro et al., 2009). Even in this densely-populated region where hunting pressure is usually high, most of the remaining fragments still retain threatened mammal species, such as white-eared marmoset *Callithrix aurita*, titi monkey *Callicebus personatus* and the critically endangered black

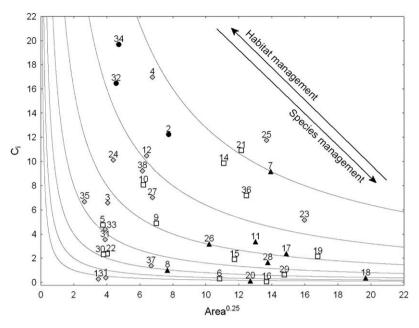
**Table 4** Multifactorial ANCOVAs for total abundance ( $\log(x+1)$  Individuals/10 km) and total biomass ( $\log(x+1)$  kg/10 km) of major game species groups. For ungulate abundance:  $R^2 = 0.325$ , Adj.  $R^2 = 0.220$ , F (5,32) = 3.084, P = 0.022; for ungulate biomass:  $R^2 = 0.339$ , Adj.  $R^2 = 0.236$ , F (5,32) = 3.288, P < 0.016; for Primate (except *Callithrix*) abundance:  $R^2 = 0.688$ , Adj.  $R^2 = 0.601$ , F (8,29) = 7.978, P < 0.001; for Primate (except *Callithrix*) biomass:  $R^2 = 0.693$ , Adj.  $R^2 = 0.608$ , F (8,29) = 8.166, P < 0.001; for Rodentia (except *Sciurus*) abundance:  $R^2 = 0.325$ , Adj.  $R^2 = 0.258$ , F (5,32) = 3.574, P = 0.011; for Rodentia (except *Sciurus*) biomass:  $R^2 = 0.325$ , Adj.  $R^2 = 0.116$ , F (5,32) = 1.970, P = 0.110. Significant effects are in bold.

Dependent variable	Effect	SS	df	F	p
Ungulate abundance	Intercept	0.000	1	0.003	0.955
	Forest type	1.019	3	3.489	0.027
	Hunting pressure	0.841	1	8.645	0.006
	Log(Area)	0.099	1	1.022	0.320
	Error	3.114	32		
Ungulate biomass	Intercept	0.00	1	0.004	0.951
	Forest type	6.88	3	3.862	0.018
	Hunting pressure	4.24	1	7.137	0.012
	Log(Area)	1.63	1	2.741	0.108
	Error	19.00	32		
Primate abundance	Intercept	1.337	1	18.149	0.000
	Forest type	0.369	3	1.668	0.197
	Hunting pressure	0.197	1	2.668	0.114
	Log(Area)	0.050	1	0.681	0.416
	First spatial filter	0.011	1	0.154	0.698
	Second spatial filter	0.272	1	3.691	0.065
	Third spatial filter	1.352	1	18.359	<0.001
	Fourth spatial filter	0.130	1	1.762	0.195
	Fifth spatial filter	0.050	1	0.684	0.415
	Error	1.989	27		
Primate biomass	Intercept	5.094	1	38.22	0.000
	Forest type	0.107	3	0.27	0.849
	Hunting pressure	0.514	1	3.86	0.059
	Log(Area)	0.528	1	3.96	0.056
	First spatial filter	0.183	1	1.38	0.250
	Second spatial filter	0.711	1	5.34	0.028
	Third spatial filter	3.209	1	24.08	<0.001
	Error	3.865	29		
Rodent abundance	Intercept	0.085	1	2.343	0.136
	Forest type	0.494	3	4.550	0.009
	Hunting pressure	0.078	1	2.154	0.152
	Log(Area)	0.000	1	0.007	0.935
	Error	1.158	32		
Rodent biomass	Intercept	0.446	1	2.587	0.118
	Forest type	1.047	3	2.025	0.130
	Hunting pressure	0.256	1	1.486	0.232
	Log(Area)	0.000	1	0.000	1.000
	Error	5.513	32		

lion tamarin Leontopithecus chrysopygus (Bernardo and Galetti, 2004; Cullen et al., 2000). The two large protected forests examined here (Morro do Diabo and Caetetus) not only hold high abundances of medium and large mammals, but also concentrate many highly threatened species (Cullen et al., 2001, 2004). Large unprotected remnants of semi-deciduous forests have already lost more large mammal species, compared to those that are legally protected (Cullen et al., 2004). Semi-deciduous forest fragments continue to be threatened by encroachment from sugar-cane plantations for biofuel production (Scharlemann and Laurance 2008) and several fragments may be suffering from rapid biodiversity collapse due to edge effects, hunting and occasional burnings. Therefore, medium and large fragments of this forest type should be a priority in any regional-scale Atlantic forest conservation plan. Many of these fragments, which are often embedded within large private landholdings including biofuel and citrus or coffee crops, cattle ranches and pulpwood plantations, could be used not only to comply with environmental legislation, but also enhance the prospects for biodiversity conservation, and reduce edge effects and hunting. These companies can use these strategies of good land stewardship to increase their access to expanding domestic and international markets and to national and international credit (Nepstad et al. 2006).

For instance, Fazenda Barreiro Rico is a wealthy cattle ranch with a long tradition of forest protection and has three unprotected fragments (Água Sumida, Monal and Viraeiro), two of which are either of higher or intermediate priority in our analysis. These fragments have already lost several bird and large mammal species in the last 50 years (Magalhães 1999) but still retain an important population of ~600 wolly spider monkeys (Martins, 2005). It is well known that isolated populations of long-lived primates, such as wolly spider monkey, can persist in some small fragments for extended periods (>40 years) before they became extinct (Melo et al., 2005), so augmenting forest cover or connectivity is essential for these isolated populations. However, there are no legal incentives for landowners to promote forest connectivity or reduce hunting in these fragments and this endangered species may face local extinction in a near future.

Lowland forests, by virtue of being easily accessible and highly prized for agriculture and urban development (mainly driven by tourism near coastal areas) is another forest type that has succumbed to high deforestation rates except for southern Bahia, which still retains a considerable forest area. But even in this region the remaining forest cover is rarely undisturbed due to large areas under shade cocoa (*Theobroma cacao*) production, which requires complete understory removal and gradual canopy thinning



**Fig. 5.** Values of the conservation index  $C_i$ , plotted against site area raised to the 0.25 exponent (from general species-area relationships). Black circles: montane vegetation; black triangles: submontane vegetation; gray diamonds: semi-deciduous vegetation; white squares: lowland vegetation. The gray curves are functions along which the product among the two variables have the same value (which gives the index  $MP_i$ ). The curves represent the following values of  $MP_i$  (moving from near the axis to the outermost curve): 2, 4, 8, 16, 32, 64 and 128. The arrows indicate the gradient of priority for recommended conservation measures, depending on the combination of  $C_i$  values and site area. See the text for details. The point labels refers to the study sites: 1 – Água Sumida, SP; 2 – Augusto Ruschi, ES; 3 – Cachoeira, AL; 4 – Caetetus, SP; 5 – Capoeirão, AL; 6 – Caraguatatuba, SP; 7 – Carlos Botelho, SP; 8 – Coimbra, AL; 9 – Córrego do Veado, ES; 10 – Córrego Grande, ES; 11 – Cunha/Santa Virgínia, SP; 12 – Fazenda Rio Claro, SP; 13 – Fazenda Serra, SP; 14 – Ilha do Cardoso, SP; 15 – Ilha Grande, RJ; 16 – Ilhabela, SP; 17 – Intervales, SP; 18 – Jacupiranga, SP; 19 – Juréia, SP; 20 – Jurupará, SP; 21 – Reserva Natural Vale, ES; 22 – M7, ES; 23 – Mbaracayu, Paraguay; 24 – Monal, SP; 25 – Morro Diabo, SP; 26 – Morro Grande, SP; 27 – Mosquito, SP; 28 – Petar, SP; 29 – Picinguaba, SP; 30 – Putiri, ES; 31 – Ribeirão Cachoeira, SP; 32 – Santa Lúcia, ES; 33 – São José, SP; 34 – São Lourenço, ES; 35 – Sarã, SP; 36 – Sooretama, ES; 37 – Tucano, ES; 38 – Viraeiro. SP.

in private landholdings. Protected areas in this region have also been claimed by acculturated Indians (e.g. Pataxó), who once become legal occupants of these reserves have a tremendous impact on forest cover and hunting (Brandt, 1992). The best preserved and largest lowland forest areas occur in northern Espírito Santo: Sooretama Biological Reserve and Reserva Natural Vale, a forest reserve from Vale, an enormous mining corporation previously known as Vale do Rio Doce. These two reserves are contiguous to one another and form a combined forest block of 46,000 ha, most of which is either primary or late secondary forest (Peixoto and Gentry, 1990). With the possible exception of the giant anteater (Myrmecophaga tridactyla), whose last record in the region dates from the late 1960s (Chiarello et al., 2007), these two reserves still safeguard a virtually intact forest mammal fauna, including the two large cats (jaguars P. onca and pumas Puma concolor), and the giant armadillo (Priodontes maximus) (Chiarello, 1999).

# 4.2. Conservation priorities for mammal conservation

We uncovered an interesting pattern by disaggregating the  $MP_i$  into its two components, the conservation index  $C_i$ , which is based on species importance and richness, and the forest patch area (raised to the exponent 0.25). Of the scatter of points distributed in the triangular envelope describing this relationship (Fig. 5), two vertices are of particular concern. In our study areas, we have at one extreme, Santa Lúcia and São Lourenço (both within the State of Espírito Santo) which are characterized by high priority  $C_i$  values but relative small forest areas (although both areas are connected with corridors to other forest patches). The opposite extreme, consisting mainly of the sites Jacupiranga and Juréia (both within the State of São Paulo), have lower priority  $C_i$  values but retain relatively large areas. These diametrically opposite extremes call for very different conservation approaches. The high- $C_i$ /

small-area sites retain higher richness and/or important and threatened species, but the viability of wildlife populations therein is at severe risk of local extinction due to constraints in habitat patch size. Conservation policies at these sites must therefore be focused mainly on the habitat, by enhancing forest cover and quality (Keuroghlian and Eaton, 2008b), or any other habitat management measures that enhances habitat connectivity. On the other hand, the low-C<sub>i</sub>/large-area sites exhibit few species of major conservation concern (which may occur at very low densities), but can presumably provide sufficient amounts of suitable habitat to support larger populations of these species. For these sites, we primarily recommend conservation efforts targeting population management such as species rehabilitation plans and enhanced enforcement of protection such as more effective vigilance against hunting and other extractive activities. This does not imply a clear dichotomy in employing a single approach for each of these extreme situations. Along the continuum between the habitat area and species conservation priority, we can identify a gradient of priorities (Fig. 5). The optimal conservation strategy must therefore be an adequate balance between such priorities, directing different levels of effort to both habitat and species management, depending on which requirements are most limiting within each region or

A possible explanation for the absence or low abundances of threatened species at the largest sites can be related to a sampling artefact. This could happen if populations of some rare species are more patchily distributed than in smaller sites, a well recognized pattern in tropical forests (Diamond, 1975). In this situation, if sampling effort is not proportional to forest patch area, many patchily distributed species could be overlooked in large sites, and the abundance and species richness of these areas would be underestimated when compared to smaller areas. However, this does not seem to be the case. We used multiple regression to

examine the  $C_i$  index as a function of area ( $log_{10}$  ha) and sampling effort (km), and found no significant effect of either sampling effort  $(R^2 = 0.048; F_{1.34} = 0.010, p = 0.923)$  or the interaction between area and effort ( $F_{1.34} < 0.001$ , p = 0.983). Alternatively, we correlated  $C_i$  with an index of relative effort, which was derived by dividing it by the squared root of site area, and again no significant relationship was found. The same was observed when we used species richness as the response variable in both analyses. So, the low abundances and richness of some threatened species, as found in some large sites, likely results from other factors (e.g. high hunting pressure). Although hunting pressure and site area were not significantly correlated across the entire data set, four of the five largest forest sites (Jacupiranga, Juréia, Mbaracayu and Picinguaba) were subjected to high hunting pressure. All of these nominally protected areas are occupied by self-professed indigenous groups or other traditional peoples who live within the reserve boundaries (quilombolas, caicaras), and frequently hunt game vertebrates, harvest edible palms, and practice slash-and-burn agriculture and other extractive activities. At the other extreme, the three sites with the highest  $C_i$  values but with relatively small areas (Caetetus, Santa Lúcia and São Lourenço) are subjected to only low to moderate hunting pressure. Indeed, hunting regime was one of the main determinants of mammal abundances. Nevertheless, it is important to realize that, by virtue of forest area alone, the large sites are extremely important, as only 12% of the original Atlantic Forest cover remains (Ribeiro et al., 2009). The cascading consequences of mammal hunting should be a key priority in future studies (Wright, 2003) and should be designed as part of a systematic ecosystem management plan. This would enhance future attempts to set conservation priorities in the Brazilian Atlantic Forest biome, which should strike a balance between qualitative components (e.g. population sizes) of the remnants forest biodiversity and ecosystem functioning.

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