

Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants

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ARTICLE INFO

Article history:

Received 18 September 2008

Received in revised form 29 January 2009

Accepted 4 February 2009

Available online 20 March 2009

Keywords:

Small fragments
Island biogeography
Matrix use
Rodents
Marsupials
Economic activity

ABSTRACT

The remaining Atlantic Forest fragments are structurally isolated by a matrix of pastures, plantations, or urban areas, and most remnants are small (<100 ha). Island biogeography theory has been used to predict the effects of such fragmentation in the remaining fragments, but human activities and land use around fragments may be equally important. A related question is which aspects of land use have a strong effect on biodiversity. We compare the relative importance of fragment size and isolation vs. land use around fragments as determinants of composition and richness of small mammals in Atlantic Forest fragments. We also compare two aspects of land use around fragments, economic activity (peri-urban, agriculture, cattle), and property ownership (peri-urban, low income rural producers, affluent rural producers). Small mammals were surveyed in 21 fragments varying from 12 to 250 ha, and in two sites of continuous forest in the Macacu River watershed, State of Rio de Janeiro, Brazil, from 1999 to 2007. The effects of land use, fragment size and isolation were formulated as eleven candidate models, compared by Akaike Information Criteria. In the models selected, species composition was associated more strongly with fragment size, followed by isolation, with a smaller effect of property ownership. Species richness was determined mostly by fragment isolation, but also by a negative effect of agriculture when it was the dominant economic activity. Regardless of the critics to island biogeography theory, fragment isolation and size were by far the most important determinants of species composition. Economic activity and property ownership allowed the detection of subtle but important effects of land use on species composition and richness.

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1. Introduction

Many landscapes are currently composed of small remnants (e.g. less than 1000 ha), where conservation of a single large reserve is not an option (Tscharntke et al., 2002). This is the case of many regions of the coastal Atlantic Forest of Brazil, where fragments of original forest are structurally isolated from each other by a matrix of human settlements, pastures, plantations, and roads (Tabarelli et al., 2005). A few large remnants of Atlantic Forest still exist, but most of them are less than 50 ha (Ribeiro et al., 2009), and persisted in the landscape mainly because of its steep terrain, for preservation of headsprings, or because of mandatory legal reserves (Fiszson et al., 2003).

Empirical experimental and observational evidence established the importance of preserving small fragments for conserving biodi-

versity in fragmented landscapes (Lindenmayer et al., 2002; Tscharntke et al., 2002; Vieira et al., 2003; Pardini, 2004; Pardini et al., 2005, 2009; Bodin et al., 2006; Metzger et al., 2009). In some cases the fauna and flora associated with small fragments may not even occur in large fragments (Bodin et al., 2006; Fonseca et al., 2009; Vieira et al., 2003; Pardini et al., 2009). The implications for conservation strategies are manifold (Tscharntke et al., 2002), but in the Atlantic Forest conserving small fragments is not simply an option but a requirement to maintain the remaining and highly endangered biodiversity of this biome.

Because of the extensive application of island biogeography theory (MacArthur and Wilson, 1967), fragment size and isolation were usually considered as the main determinants of species composition, abundance, and richness (Lovejoy et al., 1986; Soulé et al., 1988; Newmark, 1996). Nowadays it is broadly accepted that a considerable part of the variation in species richness and composition among fragments is not explained by fragment size or isolation, particularly in landscapes where most fragments are small

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(Laurance and Bierregaard, 1997; Lomolino and Perault, 2001; Haila, 2002; Tschantke et al., 2002; Michalski and Peres, 2005; Bodin et al., 2006; Kupfer et al., 2006). The type of matrix and its effects have received considerable more attention (Driscoll, 2004; Manning et al., 2004; Kupfer et al., 2006; Umetsu et al., 2008).

Several studies have described how populations in forest fragments are influenced by the surrounding matrix (e.g. Hinsley et al., 1995; Stouffer and Bierregaard, 1995; Gascon et al., 1999; Mazerolle and Villard, 1999; Metzger, 2000; Lindenmayer et al., 2001; Renjifo, 2001; Tischendorf et al., 2003; Dormann et al., 2007; Umetsu et al., 2008). Kupfer et al. (2006) defended a shift in focus, away from a patch-based perspective based on fragment size and isolation to a landscape mosaic perspective, focusing on gradients of habitat conditions: the intervening matrix can serve either as suitable habitat, conduit, barrier or filter for native species in fragments, and for invasive species. They also point out how matrix quality and structure is usually linked with human-related processes.

The emphasis on the role of anthropogenic disturbances, matrix quality and structure on ecological processes and biodiversity poses new questions to conservation biology. Anthropogenic disturbances on remaining forest fragments may differ according to the economic activity in the matrix surrounding fragments. Plantations may provide additional food sources and some shelter for animals, allowing occupation of the matrix or dispersal (Norton et al., 2000; Cook et al., 2002; Silva et al., 2005; Anderson et al., 2007), whereas cattle ranching in extensive pastures may not offer much shelter or food, and the structure of forest may be further disturbed if cattle is allowed to enter the fragment (Horvath et al., 2001; Maron and Lill, 2005). Fragments in urban areas suffer other kind of disturbances, related to higher number of humans in the surroundings, or visiting the fragment (Hansen et al., 2005; Guirado et al., 2007; Markovchick-Nicholls et al., 2008). Disturbance caused by hunting, cutting, noise, wildfire, and predation by domestic cats and dogs is directly related to distance from human settlements (Theobald et al., 1997; Olifiers et al., 2005). Some species respond to human presence similarly to the presence of a potential predator, avoiding or underutilizing areas close to human populations (Frid and Dill, 2002).

Alternatively, anthropogenic disturbances may also differ according to property ownership, which is associated with historical land use and impacts on remnants of original habitats (Cabral and Fiszon, 2004; Lunt and Spooner, 2005). Rural properties owned by low income families in the tropics almost invariably use forest fragments for several utilitarian and subsistence purposes (Peres and Michalski, 2006). In a region of the Atlantic Forest of Brazil studied by Cabral and Fiszon (2004), properties of low income are small, and cutting, hunting, pet predation, and wildfire are more common in fragments surrounded by several small rural properties. Economic activity, however, differs between these low income owners, some producing vegetables other raising cattle (Cabral and Fiszon, 2004). Large rural properties are owned by companies or affluent producers, which also may be involved in cattle ranching and agriculture. However, cattle ranching and pasture differ between small and large property owners. In small rural properties cattle is raised more loosely in the property, frequently entering the forest fragment and causing further disturbance, which is less frequent in the more confined cattle of large properties (Cabral and Fiszon, 2004). Pasture is also grown more loosely in small properties, grasses sometimes reaching 1 m high, whereas in large properties pasture is sown regularly and kept short. Also, when fragments are surrounded by one or two large properties human density around the fragment is lower, and the access to the fragments is usually restricted. These factors may limit impacts on forest fragments compared to fragments surrounded by small properties (Cabral and Fiszon, 2004). Properties owned by peri-ur-

ban settlers have yet a third land use because (1) owners do not depend as much on the land for survival, and (2) do not need to maintain 20% of their property as legal reserve, which rural properties are required by Brazilian law. Therefore, the impacts on forest fragments are likely to differ between peri-urban and rural properties.

Small mammals (rodents and marsupials) are especially useful to study the impacts of environmental variables because of their importance in natural systems, either as seed dispersers (Grelle and Garcia, 1999; Cáceres, 2002), pollinators (Janson et al., 1981; Gribel, 1988; Goldingay et al., 1991; Vieira et al., 1991), arthropod predators (Freitas et al., 1997; Santori et al., 1997; Cáceres and Monteiro, 2001; Carvalho et al., 2005), and as a resource for carnivores, owls, and snakes (Wright et al., 1994). Species of small mammals respond differently to habitat fragmentation, particularly in the Atlantic Forest of Brazil (Olifiers, 2002; Pardini, 2004; Viveiros de Castro and Fernandez, 2004; Pardini et al., 2005, 2009; Puttker et al., 2008). Most small mammals endemic to the Atlantic Forest do not occupy anthropogenic habitats, requiring remnants of native vegetation to persist (Umetsu and Pardini, 2007; Umetsu et al., 2008; Pardini et al., 2009), but the effects of different land uses on the composition of small mammals in forest fragments has not been evaluated yet.

Our first objective was to determine the relative importance of island biogeography vs. matrix features as determinants of biodiversity of small mammals in a fragmented Atlantic Forest landscape. Deforestation patterns associated with property ownership were studied in the same region by Cabral and Fiszon (2004). Additionally, we compared two aspects of land use and matrix features: economic activity and property ownership.

2. Methods

2.1. Study area

Study sites were located in the Macacu river watershed, in the municipalities of Guapimirim (22°2'S and 42°59'W), Cachoeiras de Macacu (22°28'S and 42°39'W), and Itaboraí (22°44'S and 42°51'W), Rio de Janeiro State, Brazil (Fig. 1). The climate is mild-humid-mesotermic (Nimer, 1989), and vegetation is classified as dense evergreen forest ("Ombrófila Densa"; IBGE, 1991).

The processes of loss and fragmentation of the original Atlantic Forest started early in the colonization of the State of Rio de Janeiro by Europeans, mostly the Portuguese colonizers (Dean, 1996). The region of the Macacu river was first occupied by human settlements by the end of the XVI century, but the fragmentation process was significantly intensified in the 1960s, following the construction of a major highway, facilitating access by the human population. Since then, population growth rates in Guapimirim, Cachoeiras de Macacu and neighboring municipalities have accelerated, with higher growth rates than Rio de Janeiro city and the Brazilian average rate (Fiszon et al., 2003; Cabral and Fiszon, 2004). Increased human densities and land property claims on the border of conservation units increased the pressure over Atlantic Forest remnants of the region (Cabral and Fiszon, 2004). Nevertheless, the Macacu river watershed is considered to maintain a large portion of forested areas compared to other watersheds that feed the Guanabara Bay (Secretária de Estado de Meio Ambiente e Desenvolvimento Urbano, Rio de Janeiro, 2005).

2.2. Field methods

Small mammals were surveyed in 23 sites of the Macacu River watershed, from 1999 to 2007 (Appendix, Fig. 1). Twenty-one of these sites were forest fragments varying from 12 to 250 ha, and two sites (sites 22 and 23) were at the base of the Serra dos Órgãos

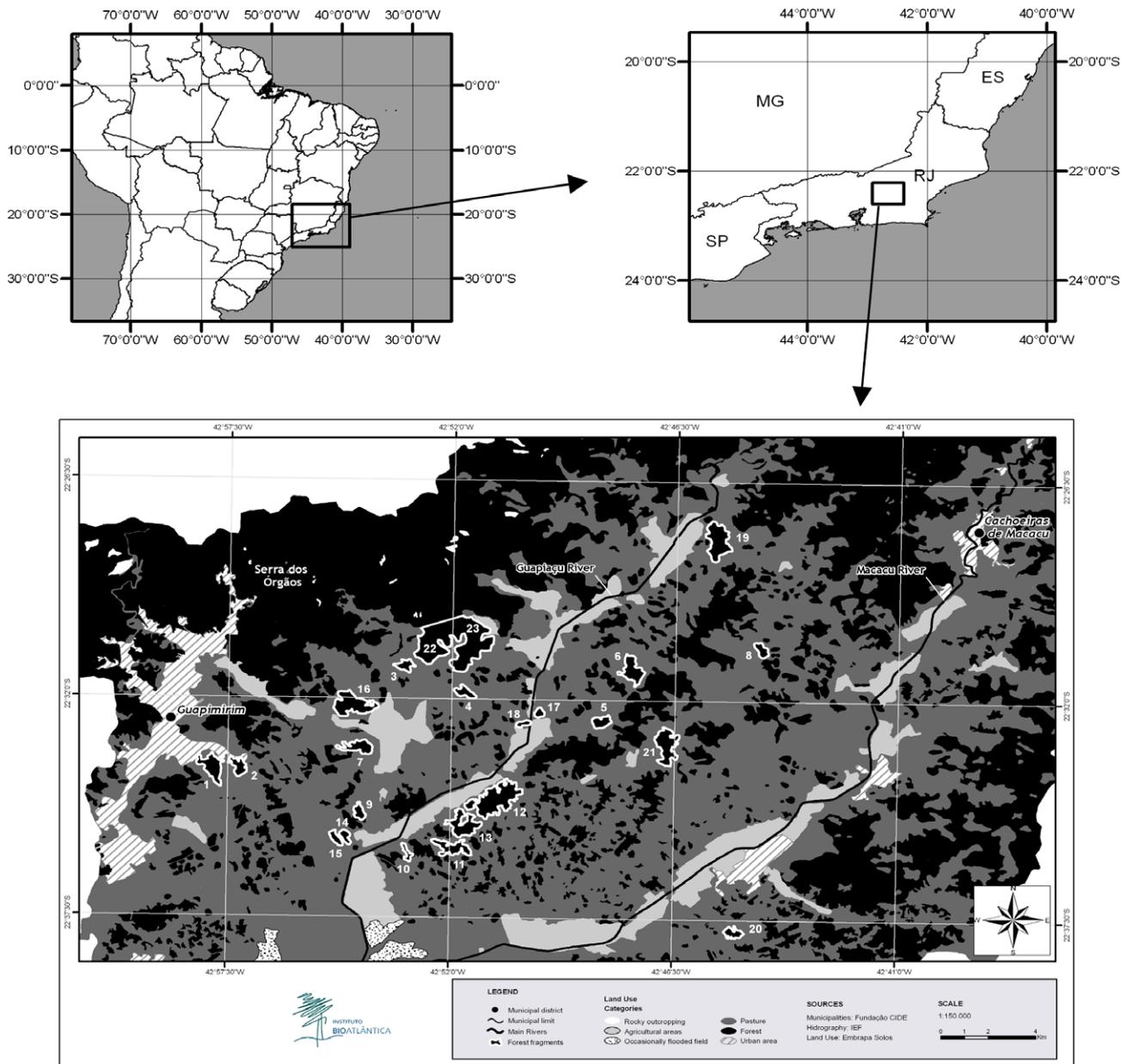


Fig. 1. Study area in Brazil and Rio de Janeiro State, and image of vegetative cover in the Macacu River watershed.

range, part of the Serra do Mar, one of the largest continuous stretches of Atlantic Forest (Atlântica/INPE/ISA, 1998; Ribeiro et al., 2009; Fig. 1). These two sites were in the same altitude range of forest fragments (100–250 m). Potential sites were chosen based on aerial photographs (1:20,000 scale) taken in 1996 by Fundação CIDE, an information agency of the Rio de Janeiro State Government. Fragments of different sizes, degree of isolation, and with different features of the surroundings were selected, but also favouring fragments with well defined borders and more circular shape. Ease of access and permission by owners were final practical criteria to select sites. The first 13 sites were sampled twice, one time in the rainy season and another in the drier season, from 1999 to 2001. Because no difference in species composition between seasons was detected, the remaining 10 sites were sampled only once, from 2005 to 2007. Only the first sampling session was used for the sites sampled twice. The potential effects of seasonal and interannual variation in relative abundances were not considered in the models, increasing the residual, unexplained variation term of the models. If these (and other) unaccounted factors are indeed

important, the residual term will be large relative to variance explained by the independent variables, and the all models will fit the data poorly, being equally plausible.

A constant sampling effort of 600 trap-nights per fragment was used. The cumulative number of species tended to reduce its rate of increase since the first night of trapping. On the 3rd day generally ca. 80% of all species were already captured, hence our sampling effort and design was likely to have sampled most species of the local assemblages. It was intended only to be a rapid, but comparable survey, not a complete one. In each site, four 280-m long transects were established, from the center to the edge of the fragments, each transect oriented to a different cardinal direction, generally north, south, east and west. Transects had 15 trap stations 20 m apart, sampled for five consecutive nights, and trap stations had two livetraps, one Tomahawk and one Sherman. In six trap stations of each transect, one of the traps was set from 1 to 3 m above the ground, alternating the type of trap set above the ground between trap stations. Traps were checked early in the morning and rebaited if necessary. A mixture of peanut based

butter (Amendocrem[®]), banana, oats and bacon were used as bait. Animals trapped were removed from the area at least during the trapping session. From 1999 to 2001 animals were euthanized, and deposited in the Museu Nacional – Universidade Federal do Rio de Janeiro. From 2005 to 2007, only unidentified animals were euthanized. Animals identified with certainty were housed in individual plastic cages, fed *ad libitum*, and released at their original sites of capture at the end of the trapping session.

2.3. Landscape metrics

Size and isolation of fragments were measured on a digital map of the Macacu River watershed generated from georeferenced Landsat 5 TM satellite image obtained from 1999 to 2007, using ArcView 3.1. Fragment isolation was measured as the shortest distance to nearest fragment or area of continuous forest, but only fragments larger than 10 ha were considered. This was the size of the smallest fragment considered for analysis (Olifiers, 2002; Appendix). To include the two sites of continuous forest in the analyses, they were attributed an extremely large “fragment” size (10,000 ha), and an extremely low value of isolation (1 m). However, to determine if their inclusion introduced any bias in the results, the analyses were run with and without the two sites in the continuous forest.

Economic activities and property ownership in the matrix surrounding fragments were determined based on a series of satellite images of the period, aerial photographs (1969, 1976, and 1996), interviews with local residents and owners surrounding the 11 fragments studied from 1999 to 2001 (Cabral and Fiszon, 2004), and visiting properties, generally during the sampling of small mammals of a fragment. Not all properties around a fragment actually reached the border of the fragment, but still could affect small mammals, either by its type of ownership or economic activity. Thus, all properties within 100 m from the fragment border were considered to determine the category of property ownership and economic activity surrounding a fragment.

Economic activity in the matrix surrounding fragments was restricted to cattle ranching, agriculture, mixed use, and peri-urban areas. The major economic activities in the matrix where fragments are inserted are cattle ranching (semi-confined or unconfined), and plantations of vegetables, mostly manioc (*Manihot esculenta*), “inhamé” (*Colocasia esculenta*), “jiló” (*Solanum gilo*), and sweet potato (*Ipomoea batatas*). With the increase in the urban population of Guapimirim, Cachoeiras de Macacu, and Itaboraí some forest fragments are surrounded by peri-urban settlements.

Property ownership was based on the classification of Cabral and Fiszon (2004). Fragments were classified as surrounded by 1–2 large rural properties, more than three small rural properties, and properties in peri-urban areas. Three patterns of property ownership were identified. Fragments surrounded by 1–2 large properties had the same characteristics of land occupation, soil use, and accessibility to fragments (semi-confined cattle ranching, pastures regularly mown and sown, reduced use of the fragment for timber extraction or by the cattle), hence were grouped in a single category (similar to Type 1 of Cabral and Fiszon, 2004, which included only fragments within a single large property). Fragments surrounded by more than three small rural properties had a more intense use of the fragment, cattle was raised unconfined and frequently entering the fragment, and pasture height and composition varied greatly (Type 2 of Cabral and Fiszon, 2004). Fragments were defined as peri-urban when surrounding properties were mostly peri-urban settlements, where lawns and yards are more frequent, cattle is rare, and a variety of small animals (chicken, piglets, ducks) and subsistence plantations occur sparsely (within Type 3 of Cabral and Fiszon, 2004).

There is some overlap in the classification by economic activity or property ownership because peri-urban fragments and sites in continuous areas were the same in the two classifications.

Richness was considered simply as the number of species in each fragment. Abundance data per species (no. of individuals captured per fragment) were used as dependent variables instead of presence–absence because abundance provides an additional information that is lost from presence/absence data. Moreover, the number of individuals captured can be considered directly proportional to abundance when catch per trap-night is low, less than 0.2 (Caughley, 1977), when competition for traps is unlikely. Therefore, the frequency of captures should be proportional to abundance. The fixed sampling effort allowed direct comparison of abundance estimates, based on the number of individuals captured. For species composition, species abundances were the dependent variables, hence each model was multivariate in nature, and formulated as a Canonical Correspondence Analysis, CCA. This is an ordination method frequently used for presence–absence or species abundance data, and can be viewed as an extension of correlation analysis to multivariate data (Legendre and Legendre, 1998). For species richness there was only one dependent variable, hence each model was formulated as a linear regression.

2.4. Models and their comparison

A total of eleven models were formulated, four combining property ownership with fragment size and isolation, four combining type of economic activity with fragment size and isolation, and three with the possible combinations of fragment size and isolation only. The relative likelihood of the eleven models given the data on species composition or species richness was compared with the Akaike Information Criteria corrected for small sample sizes, AICc, and derived Akaike differences, Δ_i (difference between the AICc of model i and the model of lowest AICc), and Akaike weights, w_i , which indicate the probability that the model is the best model (Burnham and Anderson, 2002). Values of AICc for multivariate and univariate models can be obtained by an estimate of their residual sum of squares, RSS, which is the maximum likelihood estimate for multivariate normally distributed data (Burnham and Anderson, 2002). Models were selected by first eliminating models with $\Delta_i > 10$, which are considered to have “almost no support from the data” (Burnham and Anderson, 2002: 170). Because one of the main objectives of the study is to compare typical island biogeography variables with variables that consider the matrix features, the selected model had to include a combination of the two types of variables, yet have a low AICc and corresponding high w_i .

3. Results

A total of 742 individuals of 17 species of small mammals were captured, eight marsupials and nine rodents (Table 1). Species richness in the forest fragments varied from 3 to 10, whereas the two sites in the continuous forest had 10–11 species of small mammals (Table 1). One species was captured exclusively in the continuous area, the rodent *Trinomys dimidiatus*, whereas three marsupials were captured exclusively in fragments, *Caluromys philander*, *Gracilinanus microtarsus*, and *Philander frenatus* (Table 1). Fragment size varied from 12 to 250 ha, and fragment isolation from 10 to 1500 m. However, fragment size and isolation were uncorrelated ($r = -0.259$, $R^2 = 0.067$).

Models including both fragment size and isolation, fragment isolation, or fragment size alone were the most likely models to explain species composition given the data (Table 2). Models that included features of the surroundings (property ownership or dominant economic activity) also had some support ($\Delta_i < 10$), but

Table 1

Number of individuals captured and number of sites where small mammal species occurred in the Macacu River watershed, from 1999 to 2007.

	No. of fragments a species was captured	No. of individuals captured in fragments	No. of individuals captured in continuous forest	Catch per 1000 trap-nights in fragments	Catch per 1000 trap-nights in the continuous forest
Marsupialia					
<i>Caluromys philander</i>	2	2	0	0.2	0.0
<i>Didelphis aurita</i>	20	168	54	13.3	45.0
<i>Gracilinanus microtarsus</i>	1	1	0	0.1	0.0
<i>Marmosops incanus</i>	6	26	6	2.1	5.0
<i>Metachirus nudicaudatus</i>	12	34	2	2.7	1.7
<i>Micoureus paraguayanus</i>	18	51	1	4.0	0.8
<i>Monodelphis</i> sp.	1	1	1	0.1	0.8
<i>Philander frenatus</i>	14	155	0	12.3	0.0
Rodentia					
<i>Akodon cursor</i>	16	156	19	12.4	15.8
<i>Nectomys squamipes</i>	4	6	8	0.5	6.7
<i>Oecomys catherinae</i>	4	4	3	0.3	2.5
<i>Oligoryzomys nigripes</i>	2	4	1	0.3	0.8
<i>Euryoryzomys</i> sp.	2	7	19	0.6	15.8
<i>Oxymycterus dasytrichus</i>	2	4	1	0.3	0.8
<i>Phyllomys</i> sp.	2	3	2	0.2	1.7
<i>Rhipidomys</i> sp. n.	1	1	1	0.1	0.8
<i>Trinomys dimidiatus</i>	0	0	1	0.0	0.8
Species richness range	3–10		10–11		

comparatively less than models with fragment size and isolation (high AICc and low w_i in Table 2). The lower support of models with features of the matrix is mostly because the extra parameters added did not result in a proportional increase in the likelihood and variance explained (one parameter for each level of the categorical variable considered, hence four parameters for property ownership, and five for economic activity) (Table 2). For the same reason, models including property ownership were more likely than models considering the type of economic activity, the extra parameter involved in models with type of economic activity did not result in a proportional increase in likelihood (Table 2).

One of our objectives is to determine the relative importance of fragment size, isolation, and features of the surroundings. However, models with the lowest AICc (1–3) did not include any feature of the surroundings, hence were not appropriate for this objective. Model 6 was chosen to be considered in further analyses because it included the three variables present in all models with lower AICc (fragment size, isolation, and property ownership), yet fit the data as well as Models 4 and 5. Excluding the two sites in the continuous forest did not affect the order of the selected models for species composition.

The first axis of the selected model (Model 6) represented mostly fragment isolation, but also a contrast with part of the variation in fragment size (Fig. 2a). Fragment isolation had a large negative standard coordinate in the first axis (−0.787), whereas fragment size had a positive coordinate (0.498). Isolated fragments

were unique in the abundance of the marsupial *G. microtarsus*, but also *P. frenatus* (Fig. 2a). The second axis was basically variation in fragment size regardless of its isolation (Fig. 2a.), with a large positive coordinate for fragment size (0.827). Abundances of four rodents were positively correlated with fragment size, *T. dimidiatus*, *Nectomys squamipes*, *Euryoryzomys* sp., and *Rhipidomys* sp. n. (Fig. 2a). Only the rodent *T. dimidiatus* was captured exclusively in the continuous forest, whereas the other rodents were more abundant in the continuous forest but captured in fragments as well. Taken together the first two axes explained 84.05% of the variation in species composition, hence this is the variation explained by fragment size and isolation.

Property ownership appeared on the third axis, distinguishing between fragments surrounded by peri-urban areas and by small rural properties (Fig. 2b). The third axis explained 8.23% of species composition, a small but important part of variation. The rodents *Oecomys catherinae*, *N. squamipes*, and the marsupial *Marmosops incanus* were more abundant in fragments near peri-urban areas, whereas the rodents *Oxymycterus dasytrichus*, *Phyllomys* sp., and the marsupials *G. microtarsus*, *C. philander*, and *Micoureus paraguayanus* were more abundant in fragments surrounded by small rural properties (Fig. 2b).

The model of lowest AICc when considering species richness as the dependent variable was also the one including both fragment size and isolation, but only when the two sites in the continuous forest were considered (Table 3, Models 1a–6a). When these sites

Table 2

Fit and selection statistics of models affecting composition of small mammal species in the 23 forest sites studied. Total inertia (proportional to total variation) was 1.366 for all models, constrained inertia is proportional to variation explained by the CCA axes, RSS = residual sum of squares, K = number of parameters in the model, $n = 23$, AICc = Akaike Information Criteria corrected for small ratio sample size/number of parameters, w_i = Akaike weight (probability that the model is the best K-L model among the models in the set).

Model		Constrained inertia	RSS	K	AICc	Δ_i	w_i
1	Fragment size and isolation	0.378	0.988	2	−67.787	0.000	0.425
2	Fragment isolation	0.220	1.146	1	−66.800	0.987	0.260
3	Fragment size	0.202	1.164	1	−66.437	1.350	0.217
4	Property ownership and fragment isolation	0.487	0.879	5	−61.565	6.222	0.019
5	Property ownership	0.342	1.024	4	−61.352	6.435	0.017
6	Property ownership, fragment size and isolation	0.610	0.756	6	−61.305	6.482	0.017
7	Property ownership and fragment size	0.428	0.938	5	−60.070	7.717	0.009
8	Economic activity	0.411	0.955	5	−59.641	8.146	0.007
9	Economic activity and fragment isolation	0.529	0.837	6	−58.951	8.836	0.005
10	Economic activity and fragment size	0.493	0.872	6	−58.008	9.779	0.003
11	Economic activity, fragment size and isolation	0.638	0.728	7	−57.954	9.833	0.003

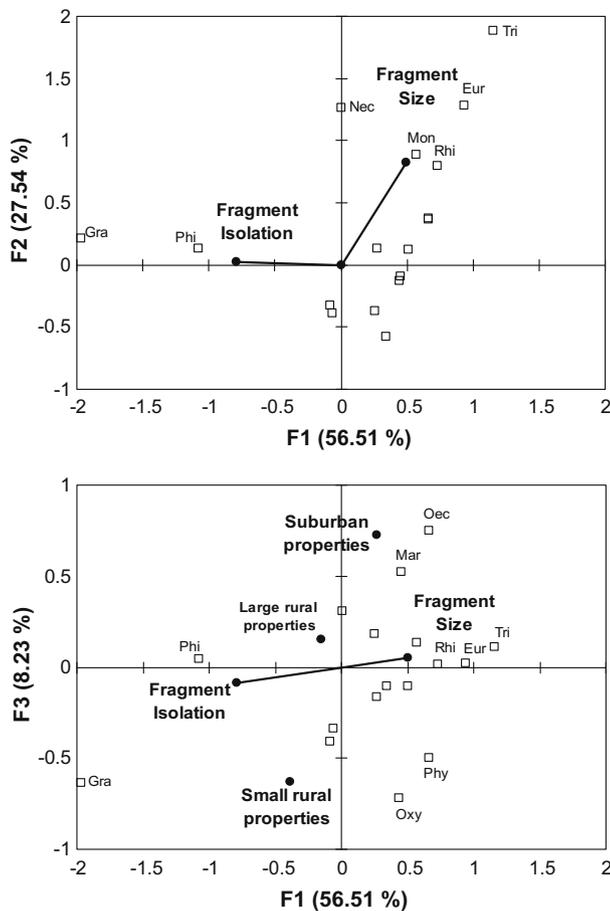


Fig. 2. Ordination of small mammal species composition on the first three factors (F1–F3) of a Canonical Correspondence Analysis based on fragment size, isolation, and property ownership around forest fragments (peri-urban, small rural properties, large rural properties, continuous area). To avoid an excessive amount of information, only species with scores higher than the mean score of factor were labeled. Species acronyms: Tri = *Trinomys dimidiatus*, Eur = *Euryzomys* sp., Rhi = *Rhipidomys* sp. n., Nec = *Nectomys squamipes*, Mon = *Monodelphis* sp., Gra = *Gracilinanus microtarsus*, Phi = *Philander frenatus*, Oec = *Oecomys catherinae*, Mar = *Marmosops incanus*, Oxy = *Oxymycterus dasytrichus*, Phy = *Phyllomys* sp.

were excluded, most models with $\Delta_i < 10$ included fragment isolation (Table 3, Models 1b–7b). Models including fragment size as an independent variable had the poorest fit to the data, with the lowest Akaike weights, w_i (Models 6b and 7b in Table 3). Models con-

sidering fragment isolation or economic activity had the highest fit, with the lowest AICc and largest w_i . Thus, the model including only economic activity (Model 2b) had a better fit to the data of species richness than models including property ownership (Models 4b and 5b), a result opposite to the obtained for species composition.

Model 3b was chosen for analysis because it included the two variables present in the models with lower AICc, fragment isolation and economic activity, and yet had the third lowest AICc and highest w_i . The fit of Model 3b and 4b is very similar, but only Model 3b included the two variables present in isolation in Model 1b and 2b, and Model 3b explained about 10% more variation than Model 4b (R^2 about 0.10 larger). The two variables in Model 3b were likely to be associated with species richness, and we want to compare their relative importance. Another reason for choosing Model 3b was its more linear and precise estimates of species richness up to values of 4–5 species (Fig. 3). Overall, estimation of species richness was more precise for values of up to 4–5 species, but for estimates between 5 and 6 species were highly uncertain, regardless of the model (Fig. 3).

When only fragments are considered, species richness tended to be higher in fragments surrounded by peri-urban, cattle, and mixed matrices compared to fragments surrounded by agriculture (Fig. 4). Fragment isolation was negatively related to species richness (Fig. 4).

4. Discussion

The use of island biogeography theory to understand and predict effects of habitat fragmentation has been increasingly criticized based on empirical evidence (Brotons et al., 2003; Watson et al., 2005; Pavlacky and Anderson, 2007), and conceptual arguments (Cook et al., 2002; Haila, 2002). A landscape approach has been proposed as an alternative paradigm, based on concepts centered on individual organisms, such as Umwelt, and a continuum of environmental effects (Manning et al., 2004; Fischer and Lindenmayer, 2006). Results such as those obtained in our study suggest that these may not be mutually exclusive conceptual backgrounds or alternative paradigms. Indeed, island biogeography variables (fragment size and isolation) were the most important variables to explain variation in species composition, considering the whole range of variation in fragment size (from 12 to thousands of hectares), or considering only fragments from 12 to 250 ha. Nevertheless, property ownership added a small, but important component of variation.

Island biogeography was conceived to explain species richness, and does not consider ecological attributes of species (MacArthur

Table 3
Fit and selection statistics for the models with species richness as the dependent variable supported by the data ($\Delta_i < 10$). (A) Including two sites in a continuous forest, and (B) considering only forest fragments. AICc = Akaike Information Criteria corrected for small ratio sample size/number of parameters.

Model	Independent variables	MSE	R^2	K	AICc	Δ_i	w_i
A. Including two sites in the continuous forest (n = 23)							
1a	Fragment size and isolation	2.545	0.575	3	25.537	0.000	0.695
2a	Economic activity	2.254	0.661	6	28.307	2.770	0.174
3a	Economic activity and fragment isolation	2.134	0.697	7	29.950	4.413	0.076
4a	Property ownership	2.850	0.547	5	31.226	5.689	0.040
5a	Property ownership, fragment size and isolation	2.602	0.630	7	34.505	8.969	0.008
6a	Economic activity, fragment size and isolation	2.265	0.697	8	34.743	9.206	0.007
B. Only fragments (n = 21)							
1b	Fragment isolation	2.640	0.238	2	22.950	0.000	0.626
2b	Economic activity	2.357	0.391	5	25.572	2.622	0.169
3b	Economic activity and fragment isolation	2.236	0.456	6	27.191	4.240	0.075
4b	Property ownership and fragment isolation	2.573	0.335	5	27.410	4.460	0.067
5b	Property ownership	2.981	0.185	4	28.199	5.249	0.045
6b	Property ownership, fragment size and isolation	2.733	0.336	6	31.401	8.451	0.009
7b	Economic activity, fragment size and isolation	2.383	0.457	7	31.784	8.834	0.008

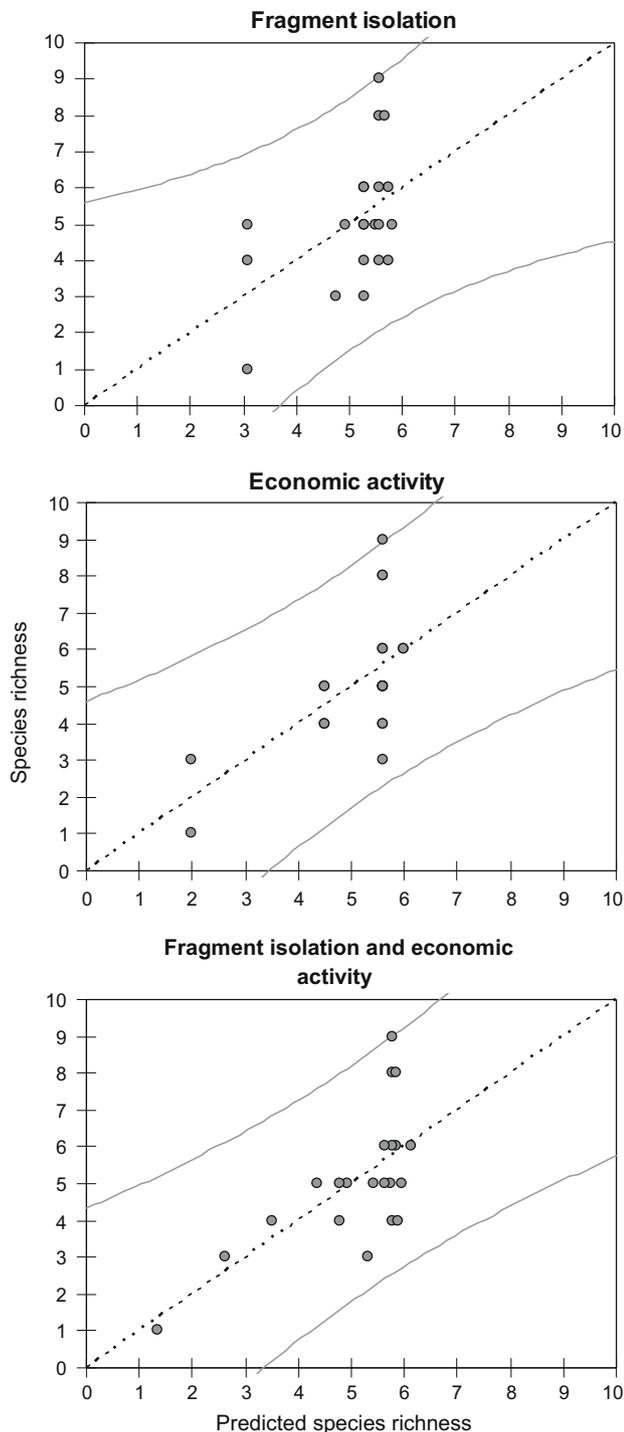


Fig. 3. Predicted and observed species richness in forest fragments based on fragment isolation, economic activities in the matrix (Peri-urban, Agriculture, Cattle, Mixed), and the two variables combined in a single linear regression model. Only fragments were considered, excluding two sites sampled in a continuous area of Atlantic Forest.

and Wilson, 1967). Thus, the dominant effects of fragment size and isolation on species composition are somewhat surprising. Species composition could change with fragment isolation because species do differ in their abilities to cross the matrix between fragments (e.g. Pires et al., 2002; Lira et al. 2007; Forero-Medina and Vieira, 2009). Large fragments could differ in species composition if they were more diverse in habitats or resources, or if the structure of local assemblages were affected by fragment size. Regardless of the causes, the strong effect of fragment size and isolation on species

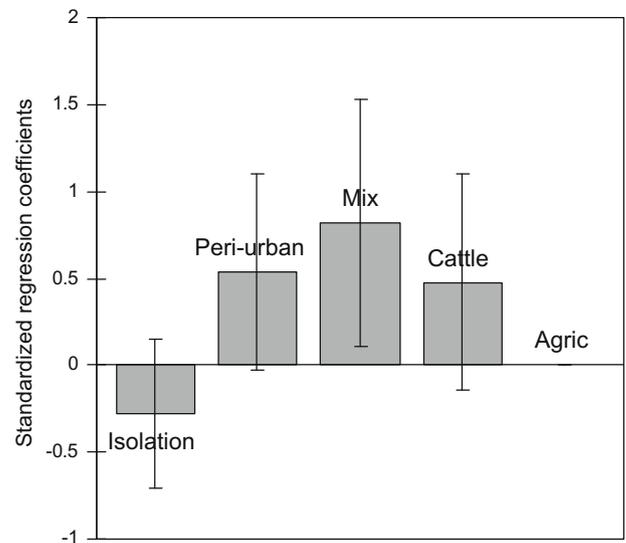


Fig. 4. Effects of isolation of forest fragments and economic activities in the surroundings on species richness of small mammals. Only fragments were considered, excluding two sites sampled in the continuous area of Atlantic Forest. Standardized regression coefficients were obtained from a linear regression with isolation of fragments and economic activity in the matrix as independent variables. Economic activity was categorical and represented by dummy variables in the regression, where Agriculture was coded as the reference treatment. Vertical bars are confidence limits of the coefficients.

composition indicates that they should not be disregarded in spite of contentions about the suitability of island biogeography theory to predict habitat fragmentation effects.

For species richness, however, fragment size was important only when the continuous forest was included in the analysis. When only fragments were considered, richness was determined mostly by fragment isolation, not fragment size, with a small effect of the type of economic activity in the matrix. Thus, when the size of forest fragments ranged less than an order of magnitude, from 12 to 250 ha, the more isolated the fragment, the poorer it was on species. This result agrees with the conclusions of Watling and Donnelly (2006), which reviewed of faunal responses to habitat patchiness across several studies. Area and isolation were the two most important variables explaining variance in species richness and assemblage structure among patches, area having a larger explanatory power than isolation. However, the effect of area was mainly a consequence of a greater range in patch areas relative to isolation.

Isolated fragments surrounded by a matrix used for agriculture had the poorest assemblages of small mammals. Apparently, the vegetables grown in the matrix – mostly manioc (*M. esculenta*), “inhamé” (*C. esculenta*), “jiló” (*S. gilo*), and sweet potato (*I. batatas*) – did not serve as supplementary food resource for most species of small mammals. These plantations form relatively open habitats at the soil level compared to abandoned or occasionally used pastures, especially after the harvest, when the field is mown, remaining bare soil until the young plants of the new harvest start to grow. The success of individual movements between fragments is certainly reduced, increasing fragment isolation. Similar results were also observed in woodlands of England surrounded by plantations of wheat and oilseed rape, where dispersal by mice and voles is limited after the harvest (Fitzgibbon, 1997), and for meadow voles in North America, where transition probabilities (=movement) between habitat patches also are associated with vegetation height in the matrix (Russell et al., 2007). Agrotoxics are frequently used in plantations of “jiló”, another potential factor reducing success of movements between fragments. These are ten-

tative hypotheses that could be tested with data on individual movements in fragments surrounded by different matrix types.

The two types of human activities (economic activity in the matrix vs. property ownership) had different effects on species composition and richness. Fragments surrounded by peri-urban and small rural properties did not differ in species richness (Fig. 4), but their composition was distinct (Fig. 2b). Indeed, presence of agriculture or pastures, and distance from residences influenced significantly the species composition of small mammals in other areas of Atlantic Forest in the Rio de Janeiro State (Oliveira et al., 2005). Thus, peri-urban and small rural properties must differ in their effects on forest fragments, and consequently on small mammal species. This result further indicates that species richness should not be used as the sole measure of the effects of human activities (Su et al., 2004).

Fragment isolation and economic activity in the matrix explained much of the variation in species richness, but only values on the extremes of species richness range. Most unexplained variance was concentrated around estimates of 5–6 species, with observed richness of 4–9 species (Fig. 3). This suggests that future studies trying to understand and predict species richness in fragments less than 1000 ha should consider focusing on fragments of intermediate to high species richness rather than fragment size.

The natural history of most small mammals captured is unknown, which hampers the development and test of specific hypotheses about the associations involved. However, tentative hypotheses are possible based on the information available. For example, the marsupial *M. incanus* was studied in nearby continuous forest (Cunha and Vieira, 2002; Macedo et al., 2007). It uses mostly the ground and understory, never reaching the canopy (Cunha and Vieira, 2002), and feeds more on arthropods than marsupials of the canopy, such as *C. philander* (Leite et al., 1996). Peri-urban households do not use the nearby forest fragment as much as small rural properties, which frequently extract timber, or allow cattle to penetrate in the forest fragment (Fizon et al., 2003; Cabral and Fizon, 2004). Thus, it is possible that fragments near peri-urban areas have more rich or diverse understory, which would favor *M. incanus*. Such *post hoc* hypotheses are testable, and possible to be formulated for other species, such as *T. dimidiatus* and continuous forests, or *Oxymycterus* and fragments surrounded by small rural properties.

4.1. Conservation implications

The landscape of the Macacu River watershed consists of many small fragments (<100 ha) in a heterogeneous matrix, varying in the type of properties and in the economic activity from place to place, a typical pattern in the Atlantic Forest (Pardini et al., 2009; Ribeiro et al., 2009), and in most fragmented biomes (Bodin et al., 2006). Therefore, results of this study have implications for a variety of fragmented biomes.

Regardless of the critics to the use of island biogeography theory to understand habitat fragmentation, fragment isolation and size were by far the most important determinants of species composition in the Macacu River watershed. Therefore, in spite of the recent emphasis on alternative approaches such as ability to use matrix (Pires et al., 2002; Lira et al., 2007; Forero-Medina and Vieira, 2009), and landscape heterogeneity (Pardini et al., 2009), island biogeography must still be considered in the design and implementation of conservation strategies. Nevertheless, the inclusion of aspects of land use around fragments is likely to improve the effectiveness of these strategies. The inclusion of property ownership and economic activity around fragments allowed the detection of subtle but important effects, particularly property ownership in the case of species composition. For species richness, isolation and economic activity around fragments were more important than fragment size and property ownership.

Acknowledgments

Renata Pardini, Emerson M. Vieira, and Jean Paul Metzger made invaluable comments on early versions of this manuscript. Angela Marcondes, Nélio P. Barros, and the Instituto BioAtlântica (IBIO) provided invaluable logistical support. Sabrina Costa and Edson Santiami offered essential assistance in the compilation of the maps used in Fig. 1. Financial support was provided by grants from Projetos Demonstrativos Ambientais (PDA/MMA), Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira (PROBIO-MMA/GEF), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ). The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) also provided a MSc fellowship to Natalie Oliveira, and currently a doctoral fellowship to Ana C. Delciellos.

Appendix A. Characteristics of sites sampled and their surroundings

Sites	Date	Season	Area (ha)	Isolation (m)	Property ownership surrounding fragments	Economic activity surrounding fragments
1	September 1999	Dry	50	360	Properties in peri-urban areas	Peri-urban area
2	September 1999	Dry	27	40	Properties in peri-urban areas	Peri-urban area
3	October 1999	Rainy	33	210	<2 Large rural properties	Mixed agriculture-cattle
4	October 2000	Rainy	28	610	>3 Small rural properties	Mixed agriculture-cattle
5	November 1999	Rainy	16	170	<2 Large rural properties	Mixed agriculture-cattle
6	October 2000	Rainy	37	160	>3 Small rural properties	Mixed agriculture-cattle
7	October 1999	Rainy	41	120	<2 Large rural properties	Mixed agriculture-cattle
8	December 2000	Rainy	70	250	<2 Large rural properties	Mixed agriculture-cattle
9	December 2000	Rainy	18	90	<2 Large rural properties	Mixed agriculture-cattle
10	March 2001	Rainy	10	140	>3 Small rural properties	Mixed agriculture-cattle
11	March 2001	Rainy	22	70	>3 Small rural properties	Mixed agriculture-cattle
12	August 2005	Dry	243	520	>3 Small rural properties	Mixed agriculture-cattle
13	April 2006	Rainy	96	290	>3 Small rural properties	Mixed agriculture-cattle
14	June 2006	Dry	20	160	<2 Large rural properties	Cattle ranching
15	June 2006	Dry	19	310	<2 Large rural properties	Cattle ranching

(continued on next page)

Appendix A (continued)

Sites	Date	Season	Area (ha)	Isolation (m)	Property ownership surrounding fragments	Economic activity surrounding fragments
16	September 2006	Dry	116	10	<2 Large rural properties	Mixed agriculture-cattle
17	November 2006	Rainy	16	1400	<2 Large rural properties	Cattle ranching
18	November 2006	Rainy	15	1400	>3 Small rural properties	Agriculture
19	March 2007	Rainy	166	320	>3 Small rural properties	Agriculture
20	May 2007	Dry	36	1490	>3 Small rural properties	Mixed agriculture-cattle
21	July 2007	Dry	96	290	>3 Small rural properties	Cattle ranching
22	September 2000	Dry	10000	1	Continuous forest	Continuous forest
23	September 2000	Dry	10000	1	Continuous forest	Continuous forest

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