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EFEITOS DA DEFAUNAÇÃO NA COMUNIDADE DE PEQUENOS MAMÍFEROS NA MATA ATLÂNTICA

CAROLINA LIMA NEVES

Dissertação apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Mestre em Ciências Biológicas – área de concentração Zoologia.

Dezembro - 2010

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Orientador: Prof. Dr. Mauro Galetti

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Comissão Examinadora

Prof. Dr. Mauro Galetti Rodrigues

Prof. Dr. Marco Aurelio Pizo Ferreira

Prof. Dr. Denis Cristiano Briani

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AUTORA: CAROLINA LIMA NEVES
ORIENTADOR: Prof. Dr. MAURO GALETTI RODRIGUES
CO-ORIENTADORA: Profa. Dra. MARIA JOSE DE JESUS SILVA

Aprovada como parte das exigências para obtenção do Título de MESTRE EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA), pela Comissão Examinadora:

Galetti Rodrigues
Prof. Dr. MAURO GALETTI RODRIGUES
Departamento de Ecologia / Instituto de Biociências de Rio Claro

Marco A. Pizo
Prof. Dr. MARCO AURELIO PIZO FERREIRA
Departamento de Zoologia / Instituto de Biociências de Rio Claro

Prof. Dr. DENIS CRISTIANO BRIANI
Fauma Pró Assessoria e Consultoria Ambiental / Rio Claro

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The most important ingredient is a fascination with the wonders of living creatures. …being a biologist does not mean having a job; it means choosing a way of life.” (Ernst Mayr, 1997)

SUMÁRIO

INTRODUÇÃO GERAL

Efeitos da defaunação na comunidade de pequenos mamíferos não-voadores

As interações animal-planta, planta-planta, animal-animal são importantes para a manutenção da integridade das comunidades onde ocorrem (Jordano *et al.* 2006). Janzen (1974) sugeriu que a perda das interações bióticas em áreas tropicais, sujeitas a perturbações de origem antrópica, é um problema de conservação muito mais sutil que a extinção de espécies. Contudo, a rápida (em tempo ecológico) remoção antrópica de alta biomassa ou de diversas espécies da fauna de um ecossistema, fenômeno este definido como defaunação (Dirzo & Miranda 1991), também representa um grande problema para a integridade das florestais tropicais, uma vez que resulta em quebra tanto de interações mutualísticas como agonísticas (Dirzo & Miranda 1991; Wright 2003; Muller-Landau 2007).

A caça é um dos principais causadores do processo de defaunação, estima-se que aproximadamente 60 milhões de animais são mortos ou feridos por caçadores no neotrópico, sendo que os animais cinegéticos mais visados são os representados pelas maiores espécies da floresta (Redford 1992; Peres & Palácios 2007). Fenômeno este que não é diferente em uma área de Mata Atlântica Semidecídua no Estado de SP. Segundo Cullen-Jr *et al.* (2001) as espécies preferidas pelos caçadores dessa região são: a anta (*Tapirus terrestris*), o queixada (*Tayassu pecari*), o cateto (*Pecari tajacu*), o tatu-galhinha (*Dasypus novemcinctus*), a cutia (*Dasyprocta azarae*) e algumas espécies de veados (*Mazama* spp). Já as espécies pequenas (*Callithrix* e *Guerlinguetus*) geralmente não são caçadas e aumentam suas densidades em áreas defaunadas (Galletti *et al.* 2009). Assim como os pequenos roedores são de baixo interesse para os caçadores (Dirzo *et al.* 2007)

A existência de uma defaunação diferenciada, ou seja, espécies animais de médio e grande porte devem ser as primeiras as serem afetadas (Bodmer 1995; Peres 2000, 2001; Dirzo 2001), devido à combinação de características como: baixa densidade populacional, baixas taxas de crescimento populacional e alto valor para caçadores (Redford 1992). Em contraste, as espécies de menor tamanho, que normalmente possuem alta densidade populacional, associada a altas taxas de crescimento populacional e um baixo valor agregado à caça, são menos suscetíveis aos impactos provocados pelos humanos (Peres 2000, 2001; Wright 2003; Cardillo *et al.* 2005). Portanto, a abundância de pequenos mamíferos, principalmente de pequenos roedores, deve permanecer inalterada ou pode ser favorecida pela diminuição ou até mesmo pelo rompimento de interações agonísticas com os mamíferos de médio e grande porte (Wright 2003; Dirzo *et al.* 2007).

Justificativa e relevância do estudo: defaunação na Floresta Atlântica

O Estado de São Paulo ainda concentra os melhores e maiores remanescentes de Floresta Atlântica do Brasil. Como não podia ser diferente no atual cenário de desmatamento do Bioma Mata Atlântica, grande parte desses remanescentes encontra-se inseridos em unidades de conservação. Apesar de serem legalmente protegidas, estas áreas podem sofrer diversos impactos antrópicos, principalmente a prática da caça, que está intimamente relacionada com a composição da matriz no entorno desses parques. Portanto, a pressão de caça é diferenciada nestas UCs conferindo distintos graus de defaunação e, a existência de um gradiente, com áreas altamente perturbadas bem como áreas bem conservadas (Galetti *et al.* 2009). Esses graus de defaunação refletem diretamente na composição de espécies de mamíferos, que geram efeitos indiretos sobre a dispersão e predação de sementes e herbivoria e conseqüentemente, sobre suas implicações na estruturação da comunidade vegetal.

Vários efeitos indiretos da perda de grandes herbívoros nas savanas africanas já foram bem documentados. Por exemplo, foi demonstrado que a remoção de grandes herbívoros causa um aumento na densidade de pequenos mamíferos, particularmente de roedores, provavelmente resultado da diminuição da competição por recursos (Keesing 2000; Caro 2002). Nos ecossistemas temperados da América do Norte, a remoção de predadores de topo (pumas) parece exercer um evidente efeito de cascata trófica (controle top-down) devido ao aumento da abundância de veados e alces (Ripple & Beschta 2004).

Para o Neotrópico, esses efeitos indiretos ainda são pobremente estudados (Wright *et al.* 1994, Wright 2003, Dirzo *et al.* 2007). Além disso, Dirzo & Miranda (1990) se questionaram se outras áreas protegidas de floresta tropical, além da que eles estudaram, estão passando pelo processo de defaunação, sugerindo, portanto, a importância de estudos visando às implicações ecológicas desse processo nestas áreas.

Modelos teóricos sugeriram que a diminuição local de mamíferos de médio e grande porte pode alavancar populações de pequenos mamíferos, em particular de pequenos roedores nas florestas neotropicais (Wright 2003, Dirzo *et al.* 2007). A **figura 1** é uma adaptação de Wright 2003 e sugere como a biomassa e abundância de diferentes grupos de mamíferos deve se comportar diante de um gradiente de defaunação.

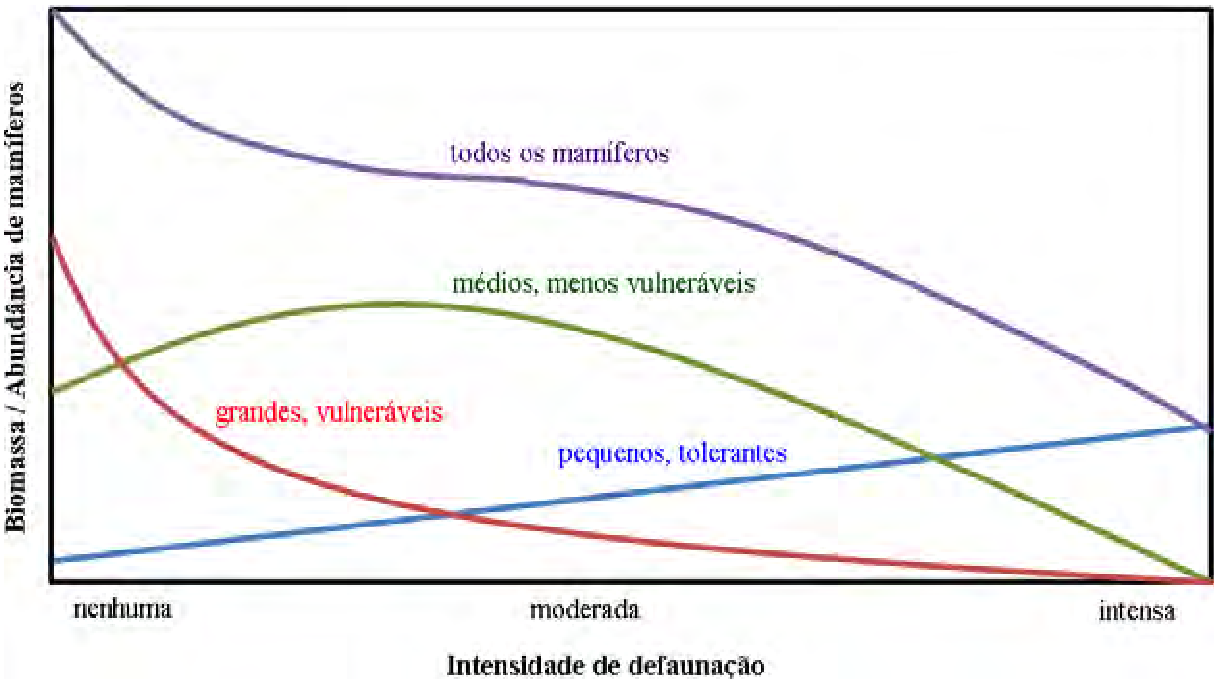

Figura 1. Modelo teórico com predição da estrutura da comunidade de mamíferos em florestas tropicais com pressão de caça resultando em um gradiente de defaunação. Mamíferos de grande porte, espécies preferenciais para a caça, dominam a biomassa da comunidade na ausência dessa pressão, declínam rapidamente à medida que a pressão de caça aumenta. Mamíferos de médio porte, espécies cinegéticas secundárias, inicialmente aumentam em abundância e biomassa devido à diminuição da competição, mas posteriormente declinam devido procura pelos caçadores. Mais especulativamente, os pequenos mamíferos, espécies não caçadas, aumentam por compensação de densidade, sua abundância e biomssa. A biomassa e abundância do total de mamíferos diminui progressivamente à medida que as espécies de grande porte tornaram-se raras e as espécies menores tornam-se mais abundantes. Adaptado de Wright (2003).

Organização temática e objetivos

Os temas abordados nesta dissertação são apresentados sob a forma de dois artigos. Os levantamentos de campo foram realizados em uma área contínua de Mata Atlântica, na qual foram escolhidas duas áreas distando aproximadamente 16 km que apresentavam diferenças entre a abundância e biomassa de mamíferos herbívoros. No **artigo I** comparamos a eficiência de captura entre dois métodos de amostragem de pequenos mamíferos não-voadores: armadilhas de captura-viva e armadilhas de queda. Também analisamos se a qualidade do microhabitat da área de estudo e a influência da sazonalidade (período mais quente e úmido vs. período mais frio e menos úmido) afetam a eficiência de captura de cada tipo de armadilha. Além disso, verificamos se os esforços amostrais diferentes despendidos em cada armadilha poderiam acarretar em viés de amostragem. No **artigo II** testamos a hipótese de que há um aumento na abundância e um declínio na riqueza de espécies de pequenos mamíferos em áreas onde grandes herbívoros estão funcionalmente extintos Além disso, avaliamos os potenciais mecanismos através dos quais os pequenos mamíferos podem responder a essa extinção funcional. Assim como, testamos a influência do microhabitat de cada área de estudo sobre esses parâmetros de comunidade.

Apesar do **Artigo I** ser totalmente metodológico e não tratar do assunto principal dessa dissertação, ele foi necessário, uma vez que esclareceu como os diferentes modelos de armadilhas de captura de pequenos mamíferos não voadores influenciaram na estimativa da diversidade dos mesmos na área de estudo. Portanto, um viés amostral poderia influenciar os resultados do **Artigo II**, prejudicando o entendimento dos efeitos da defaunação na comunidade de pequenos mamíferos, uma vez que durante esse estudo foi essencial o uso de armadilhas de captura.

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CAPÍTULO 1

Artigo I: Hidden biodiversity: effects of trap type, microhabitat and seasonality on small mammals diversity estimation within a tropical rainforest. C.L. Neves, R. Guevara & M. Galetti. *Methods in Ecology and Evolution*. *Em preparação*

Hidden biodiversity: effects of trap type, microhabitat and seasonality on small mammals diversity estimation within a tropical rainforest

Carolina L. Neves[1]*, Roger Guevara[2] & Mauro Galetti[1]

[1]Laboratório de Biologia da Conservação, Departamento de Ecologia, Universidade Estadual Paulista, CP 199, 13506-900 Rio Claro, SP, Brazil.

[2]Red de Biología Evolutiva, Instituto de Ecología AC, AP 63, CP 91000, Xalapa, Ver. Mexico.

*Correspondence author. Email: carollimaneves@gmail.com

Em preparação. Periódico Methods in Ecology and Evolution

Resumo

1. As armadilhas convencionais são amplamente utilizadas em estudos com pequenos mamíferos não-voadores, mas geralmente acarretam um viés de amostragem. Além disso, efeitos da qualidade do microhabitat e da sazonalidade podem influenciar a estimativa da diversidade.

2. Nós comparamos dois métodos de amostragem de pequenos mamíferos: armadilhas de captura viva e de queda, sendo a riqueza de espécies e número de indivíduos variáveis resposta. Os levantamentos de campo foram realizados em uma área contínua de Mata Atlântica. Os efeitos das variáveis de microhabitat e da sazonalidade sobre capturabilidade também foram investigados.

3. As armadilhas de queda capturaram maior número de espécies e indivíduos durante a estação chuvosa, quando comparadas com armadilhas de captura viva. Portanto, as armadilhas de queda foram o melhor método para estimar a riqueza e abundância de pequenos mamíferos, principalmente de espécies semi-fossoriais.

4. Nossos resultados mostraram a importância de considerar o esforço amostral despendido em armadilhas de captura vida e de queda ao se comparar a eficiência de captura entre elas. O uso da abundância relativa resolveu problemas de sub e de superestimativa da capturabilidade em cada tipo de armadilha.

5. Embora o microhabitat seja considerado um importante fator que pode influenciar o número de indivíduos em determinada área de estudo, não encontramos influência do mesmo na capturabilidade de armadilhas de captura viva e de queda na comunidade de pequenos mamíferos. No entanto, verificamos que as estações de captura que apresentaram maior área basal de samambaias e de árvores mortas capturaram mais indivíduos de *Brucepattersonius soricinus*, *Oligoryzomys nigripes* e *Akodon montensis*.

6. Concluímos, portanto que a maioria dos inventários de pequenos mamíferos em regiões tropicais não conseguiu captar a riqueza de espécies verdadeira. Várias espécies consideradas "raras" e listadas como “dados deficientes” no critério da IUCN poderiam ser de fato comuns.

Palavras-chave: Floresta Atlântica, pequenos mamíferos não-voadores, armadilhas de captura-viva, armadilhas de queda, viés de amostragem, Sherman, Tomahawk.

Summary

1. Conventional traps are widely used in studies of non-volant small mammals, but usually lead to sampling bias. Also, microhabitat quality and seasonality effects may influence the estimate of diversity.

2. We compared two small mammal sampling methods: live and pitfall traps. Species richness and number of individuals were our response variables, and field surveys were carried out in a continuous area of the Brazilian Atlantic Forest. Effects of microhabitat variables and seasonality on trappability were also investigated.

3. Pitfall traps captured more number of species and more individuals during the wet season, when compared with live traps. Therefore, pitfall-traps were a better method for estimating the richness and abundance of small mammals, especially semi-fossorial species.

4. Our results showed the importance of considering the sampling effort dispended in live and pitfall traps when comparing the capture efficiency between them. The use of weighted abundance solved trappability problems of underestimation and overestimation in each trap type to capture small mammal*s.*

5. Although the microhabitat is considered an important factor that can influence the number of individuals in the study area, we found no influence of microhabitat on trappability of live and pitfall traps on small mammal community. However, we found that the trap stations with higher basal area of dead trees and ferns captured more individuals of *Brucepattersonius soricinus*, *Oligoryzomys nigripes,* and *Akodon montensis*.

6. We conclude that most small mammal inventories in tropical regions failed to capture the true species richness. Several species considered “rare” and underlisted as data deficient in IUCN criterion could be in fact common.

Key words: Atlantic Rainforest, non-volant small mammals, live-trap, pitfall-trap, sampling bias, Sherman, Tomahawk.

Introduction

The diversity of non-volant small mammals reaches its highest values in neotropical rain forests (Emmons & Feer 1997). Some areas of the Brazilian Atlantic Forest harbor as many as 19-22 marsupial and 33-42 rodent species (InfoNatura 2007). Quantifying the diversity of non-volant small mammals is nonetheless far from being an easy and standardized procedure since sampling bias inherent to trap types, sampling design and microhabitat conditions do exist (Adler & Lambert 1997).

Although different types and sizes of traps and methodological approaches are commonly used to record the alpha diversity of small mammals (c.f., Jones *et al.* 1996; Mangini & Nicola 2006; Monteiro-Filho & Graipel 2006), few studies have applied complementary sampling protocols. Particularly, few studies have used pitfall-traps for non-volant small mammals in addition to be more commonly used live-traps (e.g. Voss & Emmons 1996; Voss *et al.* 2001; Santos-Filho *et al.* 2008).

Pitfall-traps are currently thought crucial to survey the community of non-volant small mammals in the tropics, including those species thought to be rare (Umetsu *et al.* 2006). Many studies have tested the relative trappability of pitfalls and conventional traps (live-traps and snap-traps) for small mammals, but they were conducted mainly in temperate regions (Beacham & Krebs 1980; Williams & Braum 1983; Andrzejewski & Rajska 1972; Chelkowska 1967; Mengak & Guynn-Jr. 1987). However, these types of studies in the tropics are scarce and they show conflicting results: while Umetsu *et al.* (2006) found that pitfall-traps captured more individual and species of small mammals than Sherman traps in a Lower Montane Atlantic Rain Forest, Santos-Filho *et al.* (2006) found the opposite result in a Lower Montane Semideciduous forest.

These contradictory results suggest that not only trap types may bias sampling of small mammals (Astúa *et al.* 2006; O'Farrell *et al.* 1994; Slade *et al.* 1993), but the vegetation type may have deep effects on the effectiveness of different trap types (Jorgensen 2002; Coppeto *et al.* 2006). In consequence at a smaller scale, the microhabitat, where different trap type are lay-down, could not only affect species composition and/or abundance of small mammals (Coppeto *et al.* 2006; Dueser & Shugart-Jr. 1978) but also the effectiveness of different trap types. In the same way seasonality is another factor affecting the species composition, abundance and trappability of small mammals (Adler & Lambert 1997; O'Connel 1989;

Stephenson 1994; Santos-Filho *et al.* 2008). For instance, Bergallo & Magnusson (1999) found that food availability vary seasonally and seems to be the main factor regulating fluctuations of small mammals populations and abundance of several Atlantic forest species. Moreover, many studies have shown a negative relationship between capture rates of small mammals in live-traps and higher food availability in the wet season (Fitch 1954; Adler & Lambert 1997). Therefore, studies that take into account the influence of trap type, allied to microhabitat and seasonality are badly needed.

In this study we compared the effectiveness of pitfall-traps and live traps to sample the community of non-volant small mammals in a continuous area of Brazilian Atlantic forest, and analyzed their correlation with micro-environmental factors and seasonality. Additionally, we verified if differences in sampling effort of different trap types resulted in bias in the estimation of trappability.

Methods

Study region

The study was carried out in the Serra do Mar State Park (SMSP) in eastern São Paulo, southern Brazil (**Fig. 1**). The SMSP is one of the largest areas of continuous Brazilian Atlantic Forest, covering ca. 315,000 hectares (IF 2006) and situated in the Serra do Mar mountain range. About 25% of the remaining forests of Serra do Mar are under protection (Ribeiro *et al*. 2009). The vegetation is classified as Montane Atlantic Rain Forest (Veloso *et al*. 1991). The warm-wet period occurs during summer, while coldest-drier months occur in winter. Mean annual rainfall is about 2,200 mm and monthly mean temperatures range from about 18°C to 22ºC during the coldest and warmest months, respectively (IF 2006).

Sampling sites

The sampling of non-volant small mammals were conducted at two sites, Itamambuca (IT) (45°5’16”W/ 23°19’29”S) and Vargem Grande (VG) (45°14’39”W/23°26’16”S) into the Santa Virginia Nucleus of the SMSP. This Nucleus is located in the northern portion of the park, and has an area of 17,000 ha (IF 2006), with altitudes ranging from 870 to 1,100 m (Tabarelli & Mantovani 1999). Both IT and VG are connected to the Serra do Mar continuum, which cover c.a. 1 million of ha of Atlantic forests (Ribeiro *et al*. 2009).

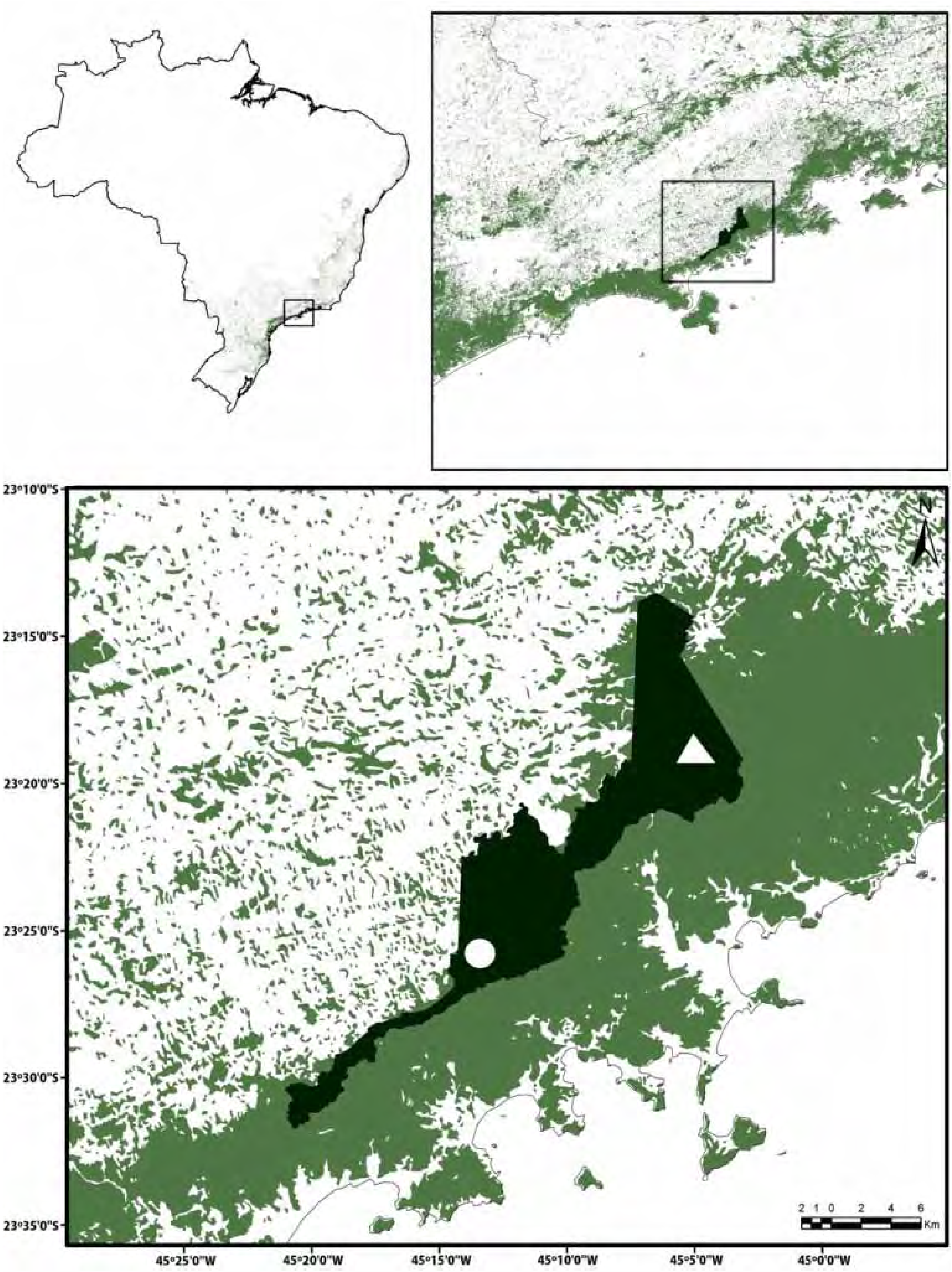

Fig. 1. Location of the study sites Vargem Grande (white circle) and Itamambuca (white triangle) at the Santa Virginia Nucleus (dark green area) of the Serra do Mar State Park (large light-green area), in the context of other remnants of Atlantic rain forest (small light-green areas) in southeast Brazil (Source: SOS Mata Atlântica. Atlas dos Remanescentes Florestais. URL http://mapas.sosma.org.br/).

Mark and recapture of non-volant small mammals

Non-volant small mammals were sampled by means of two standard types of traps: live-traps (Sherman and Tomahawk) and pitfall-traps. We sampled the area bimonthly, from November 2008 through September 2009, over a period of 14 days, with five consecutive nights at each study site. We set up three grids of live-traps and three more grids of pitfall-traps at each site. Live-traps were arranged in 0.6 ha grids (60 x 100 m each) with 24 trap stations 20 m apart. Each trap station received one Sherman trap of different size, randomly chosen (small, 25 x 7.5 x 9.5 cm; medium, 30 x 7.5 x 9.5 cm; large, 37.5 x 10 x 12 cm; H.B. Sherman Trap®, Inc., Tallahassee, Florida, USA). We also randomly set a “Tomahawk”- like trap (45 x 16 x 16 cm; Rosaminas Serviço Engenharia e Comércio ltda. Piraúba, Minas Gerais, Brazil) at six trapping stations. Overall, we had 30 live-traps per grid.

Pitfall-traps were set on grids composed of two parallel lines 30 m apart. Each line received four 60 L plastic buckets (40 cm top diameter, 35 cm bottom diameter, and 56 cm depth) buried with the rim at ground level, spaced every 10 m. The buckets on each line were connected with a 0.5 m tall plastic drift fence that extended an additional 10 m at each end, totaling 50 m of fence. Our sampling efforts consisted of 6840 trap-nights, 5400 for live-traps and 1440 for pitfall-traps.

All grids of live and pitfall traps within a site were spaced at least 100 m from each other to minimize pseudo-replication at the grid level, based on distances moved per night by Atlantic Forest small mammals (Mendel & Vieira 2003; Püttker *et al.* 2006). Both trap types (live and pitfall traps) were baited with a mix of bacon, peanut butter, corn meal and mashed banana in proportions of roughly 1:2.5:6:10. Although pitfall-traps need no bait to work properly, we baited them to minimize starvation of the animals caught, which could spend more than 12 hours in the buckets before being released. We checked and rebaited all traps daily.

At first capture, we marked every individual with a numbered ear-tag (Ear tags, National Band and Tag Co., Newport, Kentucky, USA). All captured animals were released at the station they were trapped. We collected some specimens, of those species that we could not identify based on external morphological characteristics, in order to apply cytogenetic-taxonomic techniques (C.B. Di-Nizo *et al*. unpubl. data). Trapping and handling were carried out under Permit No. 14428-2 of Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

Microhabitat characteristics

At each trap station we recorded 13 microhabitat variables according to four basic guidelines suggested by Dueser & Shugart-Jr (1978). 1. Density of palms seedlings, 2. density of non-palm seedlings, 3. understory density and 4. depth of the litter layer were recorded in four 1 m radius circular plot, each one in four quadrants (north-south and east-west directions) of a 5-m radius circular plot centered at each trap station . Our working "variable" was the arithmetic mean of the four records for each variable. Understory density was estimated with a cross formed by two 1 m PVC sticks graduated every 2-cm. The cross was held horizontally 0.5 m from the ground, and we counted the number of 2-cm marks that came in contact with the understory vegetation and divided this by 100 (total number of marks on the cross). The depth of the litter layer was measured with a ruler graduated in centimeters, which was held vertically in the center of each 1 m circular plot.

We also noted in the center of each trapping station the 5. percentage of canopy cover with a densiometer (Spherical Densiometer Model-C, Robert E. Lemmon, Forest Densiometers sold through Forestry Suppliers, Inc.). Eight variables were recorded in the 5 m circular plot: 6. density of fallen dead logs, 7. density of potential shelters for non-volant small mammals (i.e., ground holes and rock crevices) (Beisiegel 2006), 8. total basal area of *Geonoma* spp., 9. total basal area of *Euterpe edulis*, 10. total basal area of tree ferns, 11. total basal area of other tree species, 12. total basal area of standing dead trees, and 13. bamboo coverage. Basal areas were estimated on the basis of the diameter at breast height (about 1.3 m), and bamboo coverage was estimated on a semi-quantitative scale: 0 = no-bamboo in the circular plot; 1 = bamboo cover < 25%; 2 = 25% - 50%; 3 = 50% - 75%; and 4 = at least 75%. Understory coverage and percentage of canopy cover were transformed into arc-sine values to minimize hard limits, intrinsic to percentage estimates (Zar 1996). Total basal areas of *E. edulis* and *Geonoma* spp were used as microhabitat variables that could indirectly suggest the availability of food resource for small mammals since they were the most abundant palms in the study area and their seeds were predated by most species of rodents in the area (L.A. Galbiati *et al*. unpubl. data). All microhabitat variables were measured once during a six-day period at each trap station in August 2009.

Data analysis

First, we carried out the Fisher *F* test to compare the variances and the Shapiro-Wilk normality test for the total species richness, total rodent richness, total marsupial richness, total raw abundance, and total weighted abundance obtained in each sampling campaign between the two types of trap. Then, we compared the total marsupial richness between trap types by the non-parametric Wilcoxon rank test, since this variable had non-normal errors. The other four variables were compared between trap types by Student´s *t* test.

Raw abundance represents the number of individuals captured regardless of the sampling effort per trap type. Values of weighted abundance were calculated because the grids of live traps contained more traps than those of pitfall traps. To standardize these values, we weighted abundances to represent abundance at 100 trap-nights.

We also compared the total weighted abundance of rodent and of marsupial between trap types, and its correlations with seasonality and microhabitat factor at the trap station level.

To summarize the microhabitat variables we used a principal component analysis (PCA) fitted on the variance/covariance matrix. Because the 13 microhabitat variables were measured in different scales we used the natural logarithmic values to reduce the range of variability of data. Then, we used the scores of the first principal component (PC1) as a surrogate of microhabitat variables.

For these analyses, the weighted abundance values were calculated by multiplying the raw abundance at each live-trap station by 100 and dividing by 5400 (30 traps x 6 grids x 5 nights x 6 sampling periods). The raw abundance at each pitfall-trap station was multiplied by 100 and divided by 1440 (8 traps x 6 grids x 5 nights x 6 sampling periods).

We used linear mixed-effects models in which trap type, seasonality and surrogate of microhabitat variables (see above PC1) were defined as fixed factors. We also modeled the two-way interaction of trap type with seasonality. To control for pseudo-replication (at the trap station level), in the random component of the model we weighed the overall mean of the response variable by the effect of sampling grids nested with study sites. After running more-complex models and finding no significant results with PC1 or with any interaction with PC1, we preferred to use this simplified model described above.

The implications of the use of raw or weighted abundance for evaluating the efficiency of trap type for sampling small mammal species were assessed via a barplot comparison of ratio values. Raw ratio values were calculated by dividing the larger values of raw abundance in one trap type by the smaller values of raw abundance in the other trap type. Weighted ratio values were calculated by dividing the larger values of weighted abundance in one trap type by the smaller values of weighted abundance in the other trap type. The null hypothesis was that pitfall and live-traps did not differ in trappability. Thus, the raw and weighted ratio of abundances in pitfall-traps divided respectively by the raw and weighted ratios of abundances in live-traps would be 1. Since there were deviations of over an order of magnitude from the expected ratio, we log-transformed all ratios in the barplot comparisons.

Since barplot comparisons revealed differences of trappability between raw and weighted abundances for all species in common to the two trap types, we used mixed-effects models with the data of raw and weighted abundances at grid level to statistically compare these differences.

For these analyses, the weighted abundance values were calculated by multiplying the raw abundance in each live-trap grid by 100 and dividing by 900 (30 traps x 5 nights x 6 sampling periods). Those in the pitfall-trap grids were multiplied by 100 and divided by 240 (8 traps x 5 nights x 6 sampling periods).

We also tested the correlations of raw and weighted abundances with the mean scores of PC1 at grid level. Trap type was defined as a fixed factor of the model, whereas in the random component we weighted the overall mean per grid by study sites.

Post-hoc tests were contrasted based on standard errors calculated from the linear predictor, and thus we estimated t values (Warnes 2009). All statistical tests were done in the statistical environment R: (R Development Core Team 2009).

Results

Trap effects on estimated species richness

Overall we recorded 13 rodent and 5 marsupial species. Twelve species were caught in live-traps and 16 in pitfall-traps (**Table 1 and 2**). Ten species were captured by both types of traps (**Table 2**). Eight species were caught by only one trap type: 2 in the live-traps, and 6 in pitfall-traps (**Table 2**).

The results of the *t*-test showed that pitfall-traps captured significantly more rodent species richness (**Table 3**). Both trap types captured almost the same marsupial species (**Table 3**). Only one of five marsupial species was exclusively captured by pitfall-traps (**Table 2**).

Trap effects on estimated abundance: raw vs. weighted abundance

Although the live-traps captured 369 individuals while the pitfall-traps captured 251 individuals (values of raw abundances), a *t*-test revealed no significant difference (t = 1.05, d.f. = 10, P = 0.319). However, once we standardized sampling across trap type, a *t*-test showed that pitfall-traps (17.43 individuals/100 trap-nights) captured 2.6 times more individuals than live-traps (6.83 individuals/100 trap-nights) (t = 2.61, d.f. = 10, P = 0.026).

As is apparent from **Fig. 2,** the raw abundance ratios revealed that four species (*Thaptomys nigrita*, *Akodon montensis*, *Marmosops incanus* and *Didelphis aurita*) were more abundant in live-traps. On the other hand, weighted abundance ratios indicated the opposite for these same species (**Fig. 2**). For the three most abundant species in live-traps (*Trinomys iheringi*, *Philander frenatus,* and *Euryoryzomys russatus*), the graphical comparison showed that the raw data overestimated the importance of live-traps for capturing individuals of these species (**Fig. 2)**. The opposite pattern was shown for the three most abundant species in pitfall-traps (*Oligoryzomys nigripes, Brucepattersonius soricinus,* and *Monodelphis scalops*): the use of raw abundance data underestimated the importance of this trap for capturing individuals of these species (**Fig. 2**).

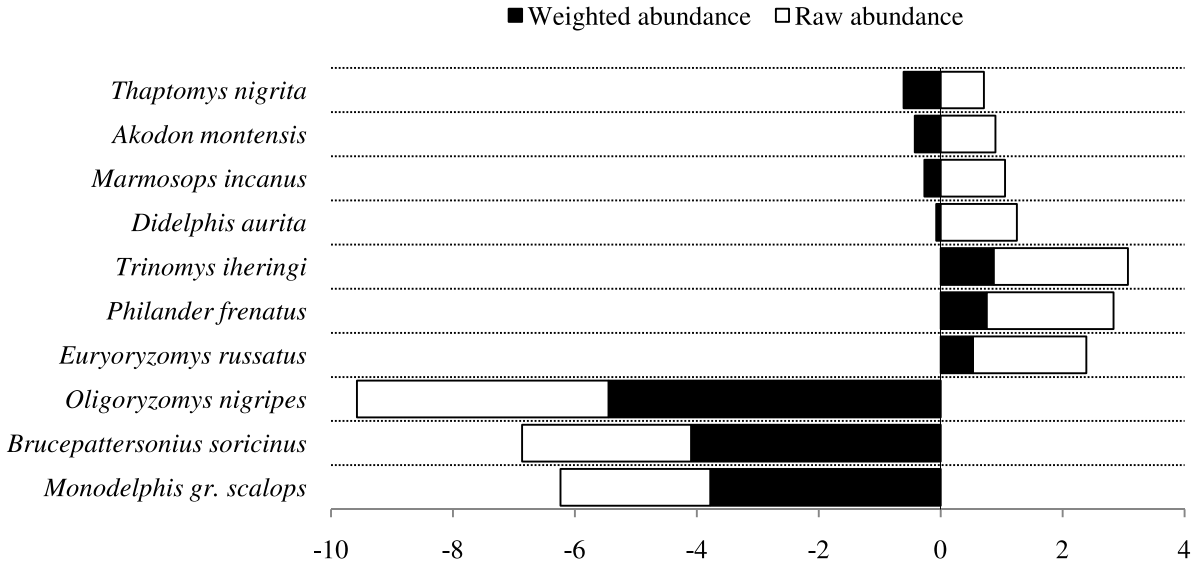

Fig. 2. "Winners" and "losers" at each trap type as represented by the ratio log of raw and weighted abundance. The null hypothesis of equal abundances in each trap type, is represented by the vertical line in the center of frame (expected ratio = 1.0, log expected ratio = 0). Ratios > 0 represent more raw and weighted abundances of each species in live-trap and ratios < 0 represents more raw and weighted abundances of each species in pitfall traps.

In addition, when comparing the results of mixed-effects models for raw and weighted abundance values, we found that the raw abundance data showed that *M. incanus* was on average three times more abundant in live-traps than in pitfall traps (**Table 2**, **Fig. 3a**). However, the weighted abundance data showed no significant differences between trap types (**Table 2**; **Fig. 3b**).

The raw data revealed that *E. russatus* was on average 6.4 times more abundant in live-traps than in pitfall-traps (**Table 2**, **Fig. 3c**). However, this difference was no longer significant when analyzed by the weighted abundance value (**Table 2**, **Fig. 3d**). For *T. nigrita*, we found clearly contrary results. The raw data showed that live-traps captured on average twice as many individuals of *T. nigrita* as did pitfall-traps (**Table 2**, **Fig. 3e**), whereas the weighted abundance data showed that pitfall-traps captured on average twice as many individuals of this species than did live-traps (**Table 2**, **Fig. 3f**).

Thus, for the three species most captured by pitfall-traps (*O. nigripes*, *B. soricinus* and *M.* gr. *scalops*), we found the same results for both the raw and weighted abundance data.

That is these species were captured significantly more often by pitfall-traps (**Table 2**, **Figs. 3 g to m**), but the weighted abundance results revealed that pitfall traps were 3.75 times more efficient in capturing these species compared with the results from the raw data.

Table 1. Number of individuals and weighted abundance (individuals/100 trap-nights) of eight non-volant small mammals that was captured in least one trap type.

Taxa	**Raw abundance**		**Weighted abundance**	
	Live-trap	**Pitfall-trap**	**Live-trap**	**Pitfall-trap**
Didelphimorphia				
Monodelphis sp.	-	5	-	0.35
Rodentia				
Blarinomys breviceps	-	6	-	0.42
Calomys tener	-	1	-	0.07
Juliomys pictipes	-	12	-	0.83
Nectomys squamipes	1	-	0.02	-
Oecomys catharinea	-	2	-	0.14
Rhipdomys cf. *mastacalis*	-	1	-	0.07
Sooretamys angouya	4	-	0.07	-

Table 2. Number of individuals and weighted abundance (individuals/100 trap-nights) in each trap type of the 10 non-volant small mammals that was caught in both type of trap. Also were presented statistical summary of linear mixed effects models at the grid level testing the effects of trap type and of principal component 1 as co-variate. All levels of comparison had one and seven degrees of freedom. Asterisk (*) and doted rectangle indicates $P \leq 0.05$. LI = live-trap; PT = pitfall-trap.

Taxa	**Number of individuals (Weighted abundance)**		**Data modeling**	**Trap type**		**CP1**		**Trap:CP1**	
	LT	**PT**		**F**	***P***	**F**	***P***	**F**	***P***
Didelphimorphia									
Didelphis aurita	7	2	sqrt	3.05	0.12	0.11	0.75	0.01	0.91
	(0.13)	(0.14)	sqrt	0.28	0.61	0.04	0.84	<0.001	0.99
Marmosops incanus	23	8	varPower	5.76	0.05*	0.09	0.77	0.01	0.94
	(0.43)	(0.56)	-	0.17	0.69	0.31	0.59	0.27	0.62
Monodelphis gr. *scalops*	3	35	log+1;varExp	10.67	<0.01*	0.41	0.54	0.54	0.49
	(0.06)	(2.43)	log+1;varExp	15.66	<0.01*	0.46	0.52	0.33	0.59
Philander frenatus	8	1	log+1;varExp	2.47	0.16	3.17	0.12	1.53	0.26
	(0.15)	(0.07)	log+1;varExp	0.68	0.44	1.50	0.26	0.30	0.60
Rodentia									
Akodon montensis	64	26	varExp	1.48	0.26	12.27	0.01*	0.68	0.44
	(1.19)	(1.81)	varExp	1.36	0.28	6.50	0.04*	0.54	0.49
Brucepattersonius soricinus	1	16	log+1;varExp	14.04	<0.01*	0.43	0.53	8.87	0.02*
	(0.02)	(1.11)	log+1;varExp	62.67	<0.001*	0.26	0.62	51.39	<0.01*
Euryoryzomys russatus	147	23	varPower	44.64	<0.001*	0.47	0.51	1.37	0.28
	(2.72)	(1.60)	-	4.01	0.09	0.35	0.57	1.40	0.28
Oligoryzomys nigripes	1	62	log+1;varExp	99.81	<0.001*	0.34	0.58	5.06	0.06
	(0.02)	(4.31)	log+1;varExp	39.71	<0.001*	0.27	0.62	9.91	0.02*
Thaptomys nigrita	101	50	varExp	15.28	<0.01*	4.94	0.06	2.48	0.16
	(1.87)	(3.47)	varExp	9.81	0.02*	0.72	0.42	0.88	0.38
Trinomys iheringi	9	1	log+1	2.90	0.13	3.59	0.10	1.43	0.27
	(0.17)	(0.07)	sqrt; varExp	1.61	0.24	2.60	0.15	0.45	0.52

Table 3. Total number of species and number of species per taxa (N°), Mean per month of capture (Mean), Standard Deviation (SD) and the results of *t*-tests comparing the richness between live and pitfall-traps. Asterisk (*) indicates $P < 0.05$. [1]The nonparametric Wilcox test was conducted for data on species richness of marsupials, since no data normality was detected by Shapiro-Wilk test.

	Live-trap			Pitfall-trap			*t*-test	
	N°	Mean	SD	N°	Mean	SD	*t*	*P*
Total species richness	12	6.80	2.00	16	9.70	2.70	2.035	0.069
Rodent species richness	8	4.50	1.60	11	7.20	2.10	2.423	0.036*
Marsupial species richness[1]	4	2.30	0.80	5	2.50	0.80	W=15.5	0.718

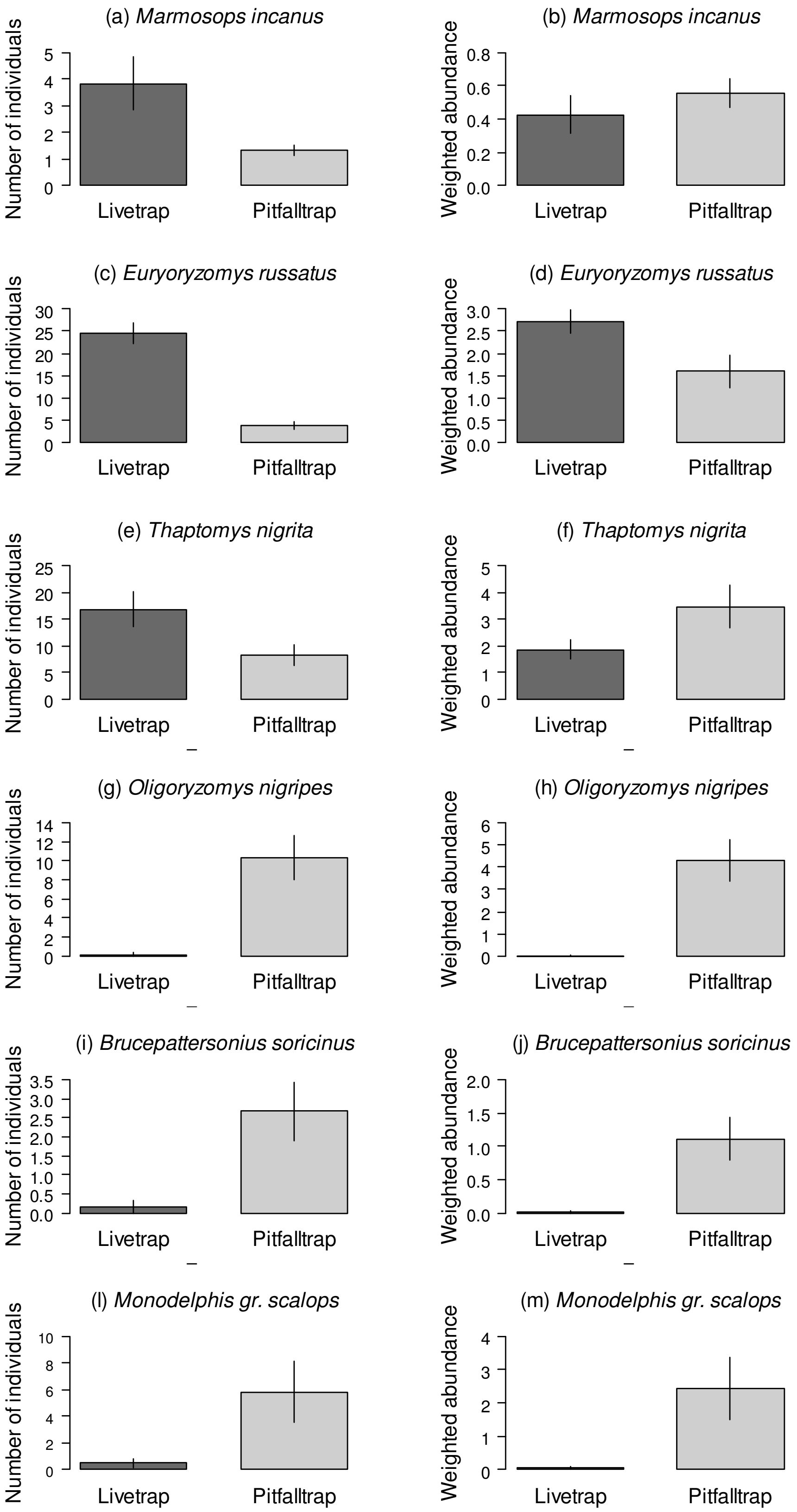

Fig. 3. Mean and SE values of raw (number of individuals) and weighted abundances of six small mammals species (mean ± SE) in each trap type.

Effects of microhabitat and climate seasonality on estimated abundance

PCA accounted for 82% of the variability of the 13 microhabitat variables over the first three components (**Table 4**). Total basal area of tree ferns (0.702) and total basal area of standing dead trees (0.655) had the highest correlation with principal component 1. Total basal area of tree ferns (-0.626) and total basal area of standing dead trees (0.672) had the highest correlation with principal component 2. Total basal area of *E. edulis* showed a high correlation with the principal component 3 (0.917) (**Table 4**). Because the three principal components correlated mostly with the same microhabitat variables, we used only the scores of the first principal component as a surrogate of the microhabitat in further analyses.

Table 4. Results of the principal components analyses carried out to summarized the variation in microhabitat at each trap station. Asterisks (*) indicate the highest (> 0.60) components scores.

	Comp.1	Comp.2	Comp.3
Density of palms seedlings	0.076	0.037	0.030
Density of non-palm seedlings	0.065	0.030	-0.050
Understory density	0.003	-0.004	-0.003
Depth of the litter layer	0.007	-0.016	-0.012
Percentage of canopy cover	-0.002	<0.001	0.002
Density of fallen dead logs	0.077	0.015	-0.033
Density of potential shelters	0.038	0.011	-0.040
Total basal area of *Geonoma* spp.	-0.223	0.050	0.085
Total basal area of *Euterpe edulis*	0.013	0.388	0.913*
Total basal area of tree ferns	0.702*	-0.626*	0.277
Total basal area of other tree species	-0.100	0.015	0.027
Total basal area of standing dead trees	0.655*	0.672*	-0.274
Bamboo coverage	-0.029	-0.002	0.004
Standard deviation	3.243	2.408	2.286
Proportion of variance	40%	22%	20%
Cumulative proportion	40%	62%	82%

Mixed-effects model showed that abundance of rodent was significantly affected by seasonality (F = 39.61; d.f. = 2, 6823; P = <0.0001) but was not affected by microhabitat characteristics (F = 1.89; d.f. = 1, 6813, P = 0.17). A Post-hoc test revealed that did pitfall-traps captured on average six times more individuals of rodent during the wet season than live-traps (t = 3.19, d.f. = 11, P = 0.008; **Fig. 4a**). The rodent abundance in pitfall-traps did not differ between seasons (*t* = 0.78, d.f. = 6823, *P* = 0.436; **Fig. 4a**), but live-traps captured on average three times more individuals of rodent species during the dry season than during the wet season (*t* = 8.23, d.f. = 6823, *P* <0.0001; **Fig. 4a**).There was no difference in rodent abundances between live and pitfall traps during the dry season (*t* = 1.17, d.f. = 11, *P* = 0.265; **Fig. 4a**).

For marsupials, mixed-effects model also showed that there was a significant influence of seasonality on the capture of individuals, in least one kind of trap (*F* = 21.5; d.f. = 2, 6823; *P* = <0.0001.) but was not affected by microhabitat characteristics (*F* = 0.07; d.f. = 1, 6813, *P* = 0.79). A Post-hoc test revealed that pitfall-traps captured on average 10 times more individuals of marsupial during the wet season than did live-traps (*t* = 4.75, d.f. = 11, *P* = 0.0005; **Fig. 4b**), but no trappability differences were found during the dry season (*t* = 0.75, d.f. = 11, *P* = 0.466; **Fig. 4b**). The values of marsupial weighted abundance in live-traps did not differ between the dry and wet seasons (*t* = 1.26, d.f. = 6823, *P* = 0.208; **Fig. 4b**), but pitfall-traps captured on average four times more individuals of marsupial during the wet season than during the dry season (*t* = 5.14, d.f. = 6823, *P* <0.0001; **Fig. 4b**).

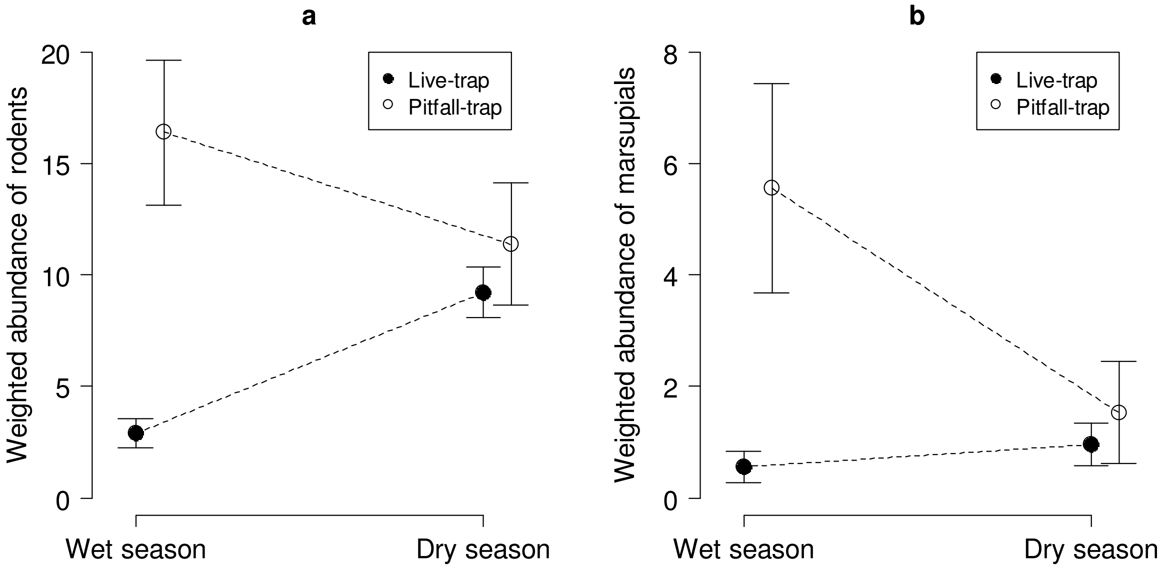

Fig. 4. Mean and 95% CI of (a) rodent weighted abundance and (b) marsupial weighted abundance in live and pitfall traps in each warm-wet and cold-dry seasons.

The surrogate of microhabitat correlated significantly with the raw and weighted abundance of two species: *A. montensis* and *B. soricinus* and significantly only with the weighted abundance of *O. nigripes* (**Table 2**). Since our previous results showed the importance of the use of weighted abundance values in the analysis of trappability, post-hoc tests showed that the weighted abundances of *B. soricinus* and *O. nigripes* in pitfall-traps correlated positively with the scores of principal component 1 ($t > 3.11$, d.f. = 7, $P < 0.03$) whereas their abundance in live-traps was not significantly correlated with microhabitat ($t = 0.51$, d.f.. = 7, $P = 0.62$) (**Figs. 5a and 5b, respectively**). In contrast, *A. montensis* had a significant positive correlation of abundance with the scores on the principal component 1 regardless of trap type ($t = 3.42$, d.f. = 7, $P = 0.01$) (**Fig. 5c**).

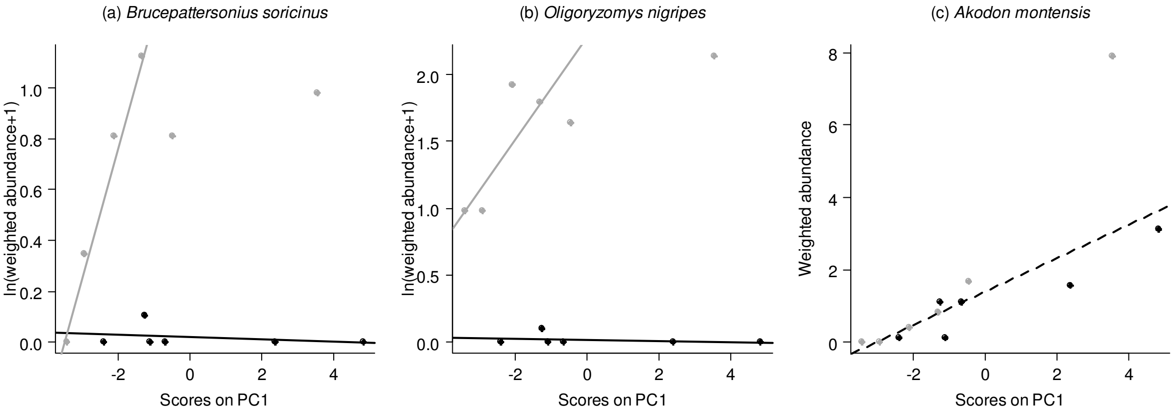

Fig. 5. (a) Positive correlation between the natural logarithmic of *Brucepattersonius soricinus* weighted abundance in each trap type and the mean value at grid level of the first principal component (Scores on PC1); (b) Positive correlation between the *Oligoryzomys nigripes* weighted abundance in each type of trap and the mean value at grid level of the first principal component (Scores on PC1); (c) Positive correlation between the natural logarithmic of *Akodon montensis* weighted abundance and the mean value at grid level of the first principal component (Scores on PC1). Black dots = weighted abundance in live-traps; Grey dots = weighted abundance in pitfall-traps; Black line = trendline of live-traps; Grey line = trendline of pitfall-traps, and Dotted line = trendline of live and pitfall traps.

Discussion

Trap effects on estimated species richness

Pitfall-traps were responsible for capturing three times more individual species than live-traps, especially rare, semi-fossorial and arboreal species (following Fonseca *et al.* 1996; Oliveira & Bonvicino 2006). Therefore, as shown by Umetsu *et al.* (2006), pitfalls provide a better method for estimating small-mammal species richness. However, in our study, this difference was mostly due to capture of rodents, which were sampled 1.4 times more in pitfall-traps than in live-traps.

Most inventories of small tropical mammals have used only live-traps to estimate species richness (Stallings 1989; Passamani *et al.* 2000; Cunha & Rajão 2007; D'Andrea *et al.* 2007; Olifiers *et al.* 2007; Pinto *et al.* 2009; Geise *et al.* 2010). Our results showed that the diversity, especially of rodents, recorded in these studies was probably underestimated due to sampling bias. This bias has likely led to erroneous definitions of the conservation status of small-mammal species, since the effectiveness with which a given population is sampled influences the estimates of parameters of natural populations (Adler & Lambert 1997). Of the approximately 264 species of small mammals in Brazil (Reis *et al.* 2006), 12 (5%) are considered threatened according to the Brazilian list of endangered species A further 30 (11%) are classified as data-deficient, mainly due to the lack of suitable and/or sufficient information to determine their risk of extinction or the conservation status of their populations (Chiarello *et al.* 2008). Almost half (11) of the 30 data-deficient species belong to the genus *Monodelphis*, which comprises rare species that are hardly ever captured by live-traps compared to pitfall-traps (Umetsu *et al.* 2006), once more indicating the sampling gap.

Trap effects on estimated abundance: raw vs. weighted abundance

Considering only the raw numbers of individuals caught, we could not detect differences in trappability between live and pitfall traps. However, when considering the sampling effort, we concluded that pitfall-traps captured 2.6 more individuals than the live-traps, even with a 3.75 times smaller sampling effort in pitfall-traps.

Umetsu *et al.* (2006) found that pitfalls captured twice as many individuals as Sherman traps. However, if we balance this by the sampling effort used in that study (26,208 Sherman-traps for 9,152 pitfall-traps), we can conclude that the pitfall-traps sampled 6 times more individuals than did the Sherman traps.

Our results illustrated the importance of considering the sampling effort expended on live and pitfall traps when comparing their capture efficiencies. The use of weighted abundance solved trappability problems of underestimation and overestimation in each trap type to capture small mammals, and also decreased the risk of misinterpretation, as in the case of four species in this study: *Akodon montensis, Thaptomys nigrita, Didelphis aurita* and *Marmosops incanus.*

Among the four most abundant species captured by pitfalls compared to live-traps, one (*O. nigripes)* is frugivorous-granivorous and scansorial (Fonseca *et al.* 1996). The other three species, *M.* gr. *scalops*, *B. soricinus* and *T. nigrita,* are insectivorous-omnivorous and terrestrial (Fonseca *et al.* 1996), and also exhibit characteristics of semi-fossorial species, such as small eyes, strong claws, and a torpedo-shaped body (Oliveira & Bonvicino 2006). Probably because of their feeding habit, these three species were not attracted by the bait used during this study, and because pitfall-traps do not need bait to work, they were less selective and captured more individuals of these species, as found for 26 other areas of the Atlantic forest (Umetsu *et al.* 2006).

Effects of microhabitat and seasonality on estimated abundance

Although the microhabitat is an important factor that can influence the number of individuals in the study area (Dalmagro & Vieira 2005), we found no influence of microhabitat on the trappability of live and pitfall-traps of the small-mammal community. However, we found that the trap stations with the higher basal area of tree ferns and standing dead trees captured more individuals of *B. soricinus*, *O. nigripes,* and *A. montensis*.

On the other hand, the analytical models showed that the weighted abundances of non-volant small mammals in each type of trap were significantly affected by seasonality. Pitfall-traps captured more individuals than live-traps during the wet season, which is consistent with other studies in the Atlantic Forest (Pardini & Umetsu 2006; Umetsu *et al.* 2006). This marked effect of seasonality could be explained by the greater abundance of food resources in wet season (Bergallo & Magnusson 1999), which could diminish the effectiveness of the bait since live-traps, unlike pitfall-traps, depend on bait attractiveness to work properly (Sealander & James 1958; Williams & Braun 1983). Some studies found reduced trappability in live-traps when food resources are abundant, mainly for frugivorous and granivorous tropical rodent species (Fleming 1971; Rudd 1979; Gliwicz 1984). This pattern is supported by the lack of a difference between captures of rodent individuals during the wet and dry seasons in pitfall-traps, showing that the differences in availability of food between these seasons do not affect the catchability of this kind of trap. Furthermore, there was a difference in capture rates between the two seasons for live-traps, with an increase in the number of captures in the dry season. This again reflects the availability of food, which is lower during the dry season when bait becomes more attractive (Adler & Lambert 1997). Adler & Lambert (1997) found that trappability indices in live-traps were positively related to sampling periods when food resources were scarce.

For marsupials, it seems that food availability does not affect the trappability of live-traps, since we found no differences in capture rates between the wet and dry seasons. Because pitfall-traps do not depend on bait to capture small mammals, we can assume that the greater trappability in the wet season was due to flooding of subterranean shelters, which forced the animals to leave their dens and consequently to be captured by pitfalls. Loretto *et al.* (2005) reported that shelters of the terrestrial marsupial *Metachirus nudicaudatus* are usually beneath the litter layer. Indeed, during this study we caught more individuals captured after nights of intense rain, especially during the wet season. Other hypotheses could explain the lower capture rates of marsupials in the dry season in pitfall-traps. Some studies have found that low temperatures could affect marsupial activity more intensively than rodents and occurrence of torpor has been described for *Monodelphis brevicaudata* (Gardner 2007). Specifically, in this study, *Monodelphis* species showed lower capture rates (75 % less) during the dry season than any other marsupials. Both hypotheses may be plausible, since these species probably construct nests beneath the litter layer, which can be easily flooded during periods of heavy rainfall. Furthermore the presence of torpor may be an attribute of this genus, which should be investigated.

Conclusion

The vast majority of small mammal inventories had failed to capture the real species richness of Neotropical rainforests (**Appendix 1**). Moreover, major studies that applied pitfall methods, introduced another sampling bias by using small traps (e.g., 20 L buckets) (Lyra-Jorge & Pivello 2001; Hice & Schmidly 2002; Pardini 2004; Santos-Filho *et al.* 2006), limiting the capture of species with good jumping or climbing ability (Umetsu *et al.* 2006). Few studies at fragmented forests (Pardini 2004; Pardini & Umetsu 2006; Umetsu *et al.* 2006) and at continuous forest areas (this study) have used both live and large pitfall-traps (60 L) in Brazilian Atlantic Forest. It is no coincidence that the highest species richness of tropical marsupials and rodents has been estimated for these areas (**Appendix 1**). Not only has the species richness of small mammals been generally underestimated, but also their abundance, especially of rodents. Rodents play a key role in forest structure as seed predators and can also transmit diseases to humans (Pardini *et al.* 2010). Several species considered “rare” are underlisted as data deficient, and it is of paramount importance to develop better methods for capture the real picture of the populations of small mammals in rainforests.

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Appendix 1. Information about this study and 21 inventories of non-volant small mammals carried out in areas of Brazilian Atlantic Forest, * data only of ground traps. C = Continuous area and F = Fragmented area. LT = Live-traps and PT = Pitfall-traps

Locality (State)	**Status**	**Sampling sites**	**Sampling effort (trap-nights)**		**Richness**			**Semi-fossorial species**	**References**
			LT	**PT**	**Marsupials**	**Rodents**	**Total**		
Serra dos Órgãos State Park (RJ)	C	6	59,350	-	9	17	26	3	Olifiers *et al*. (2007)
Rio Doce State Park (MG)	C	4	40,490	-	6	12	18	0	Stallings (1989)
Una (BA)	F	8	36,288	10,368	8	12	20	3	Pardini (2004)
Caudaia do Alto (SP)	F	26	26,208	9,152	11	19	30	6	Umetsu *et al.* (2006)
Santa Lúcia Ecological Station (ES)	F	1	21,982	-	8	12	20	0	Passamani *et al*. (2000)
Macacu River watershed (RJ)	F	23	13,800	-	8	9	17	1	Vieira *et al*. (2009)
Poço das Antas (RJ)	F	8	13,498		7	5	12	1	Pires *et al*. (2002)
Intervales State Park/ Saibadela (SP)*	C	1	9,782	-	4	7	11	0	Vieira & Monteiro-Filho (2003)
Mata do Paraiso (MG)	F	1	8,676	-	4	13	17	1	Lessa *et al.*(1999)
Morro Grande Forest Reserve (SP)	F	6	6,048	2,112	9	14	23	5	Pardini & Umetsu (2006)
Rio Doce State Park (MG)	C	1	5,880	-	5	6	11	0	Grelle (2003)
Fonte Grande State Park (ES)	F	1	5,724	-	4	2	6	0	Caldara-Jr. & Leite (2007)
Sumidouro (RJ)	F	6	5,700	-	2	10	12	0	D'Andrea *et al*. (2007)
PESM/Santa Virgínia Nucleous (SP)	**C**	**2**	**5,400**	**1,440**	**5**	**13**	**18**	**4**	**This study**
Anchieta (ES)	F	4	3,331	-	7	1	8	1	Passamani *et al*. (2005)
Intervales State Park/Barra Grande (SP)*	C	1	2,359	-	4	8	12	3	Vieira & Monteiro-Filho (2003)
Viana (ES)	F	6	2,160	-	9	8	17	1	Pinto *et al*. (2009)
Santa Teresa (ES)	F	1	1,950	-	5	5	10	0	Passamani & Ribeiro (2009)
Serra do Mar of Parana	C	1	1,920	-	1	5	6	1	Caceres (2004)
Parque Estadual do Desengano (RJ)	C	1	756	180	5	14	19	2	Modesto *et al.* (2008a)
Serra da Concórdia (RJ)	F	1	756	180	2	4	6	1	Modesto *et al*. (2008b)
Angra dos Reis (RJ)	C	1	512	-	5	4	10	0	Cunha & Rajão (2007)

CAPÍTULO 2

Artigo II: Indirect effects of large herbivores on the diversity of small mammals in the Atlantic Rainforest. C.L. Neves, R. Guevara & M. Galetti. *Ecology. Em preparação*

Indirect effects of large herbivores on the diversity of small mammals in the Atlantic Rainforest

Carolina L. Neves[1], Roger Guevara[2] & Mauro Galetti[1]

[1]Laboratório de Biologia da Conservação, Departamento de Ecologia, Universidade Estadual Paulista, CP 199, 13506-900 Rio Claro, SP, Brazil.

[2]Red de Biología Evolutiva, Instituto de Ecología AC, AP 63, CP 91000, Xalapa, Ver. Mexico.

*Correspondence author. Email: carollimaneves@gmail.com

Em preparação. Periódico Ecology.

RESUMO

A caça, a perda de habitat e a fragmentação nas florestas tropicais são as principais ameaças para a maioria das espécies de grandes herbívoros. Modelos teóricos sugerem que a extinção local desses mamíferos pode desencadear um aumento nas populações de espécies não cinegéticas, como os pequenos mamíferos. Este aumento que tem sido atribuído ao relaxamento na competição entre estes grupos. No entanto, praticamente todos os estudos que testaram esta hipótese foram realizados nas savanas Africanas, um bioma pobre em espécies em termos de pequenos mamíferos. Florestas tropicais possuem a maior diversidade de pequenos mamíferos, mas nenhum estudo efetivamente testou se a redução da abundância de grandes herbívoros afeta as populações de pequenos mamíferos. Nós comparamos a riqueza de espécies e abundância de pequenos mamíferos não-voadores ao longo de 12 meses em duas áreas com diferentes abundâncias de grandes herbívoros na Mata Atlântica. Encontramos que essas áreas compartilham 72% das espécies de pequenos mamíferos, mas diferem significativamente em relação à abundância de roedores, mas não de marsupiais. A área com menor abundância de grandes herbívoros, particularmente queixadas (*Tayassu pecari*), apresentou a maior abundância de roedores, sendo que essa diferença só pôde ser verificada pelas armadilhas de queda. Os roedores mais afetados pela extinção funcional de herbívoros de grande porte foram as espécies fossoriais, ao invés dos granívoros, o que sugere que a interferência, mais do que a competição, pode ser o mecanismo que explica este padrão. Esta é a primeira demonstração empírica dos efeitos indiretos de grandes herbívoros na diversidade de roedores em florestas tropicais.

Palavras-chave: Brasil, compensação de densidade; caça; microhabitat; efeitos top-down, *Tayassu pecari*.

ABSTRACT

Most species of large herbivores in tropical forests is threatened by hunting, habitat loss and fragmentation. Theoretical models suggest that local extinction of these mammals can trigger the populations of non game species, such as small mammals, an increase that has been attributed to the relaxation of competition between these groups. However, virtually all studies that tested this hypothesis have done in African savannas, a species-poor biome in terms of small mammal diversity. Rainforests hold the highest diversity of small mammals and none studied have effectively test if the reduced abundance of large herbivores affects the populations of small mammals. We compared the species richness and abundance of small mammals over 12-mont period in two areas with different abundances of large herbivores in the Brazilian Atlantic rainforest. We found that these areas share 72% of its species, but differs significantly on the abundance of rodents, but not of marsupials. The area with the lowest abundance of large herbivores, particularly white lipped peccaries (*Tayassu pecari*), showed the greatest abundance of rodents, but this difference was captured only by pitfall traps. The rodent species that were affected most by the local extinction of large herbivores were the fossorial species, rather than the granivorous ones, which suggest that interference, rather than competition may be the mechanism that explains this pattern. This is the first empirical demonstration of the indirect effects of large herbivores on the diversity of rodents in rainforests.

Key words: Brazil, density compensation; hunting; microhabitat; top-down effect, *Tayassu pecari*.

INTRODUCTION

Large herbivores are known to have an important impact on the composition and dynamics of ecological communities (Janzen 1981; Dirzo and Miranda 1991 Wright 2003). Direct effects of these species include their role as herbivores, seed predators, seed dispersers and trampling seedlings (Wright 2003; Galetti *et al*. 2006; Stoner *et al*. 2007). Indirect effects of large herbivores have been studied particularly in temperate and savanna ecosystems (Keesing 1998; Keesing 2000; Caro 2002; Ripple and Beschta 2004).

Large herbivores have lower biomass in rainforests compared to savannas or open temperate ecosystems (Butler 2006) and their impact on the ecosystem have been focused only on the direct impact (Bodmer 1991; Barreto *et al.* 1997; Galetti *et al.* 2001). In the neotropical rainforests, the populations of large herbivores are declining are a result of subsistence hunting, fragmentation and habitat loss (Redford 1992; Peres 1996; Galetti *et al.* 2009). The functional extinction of large herbivores, as well as the associate top predator fauna, in rainforests has led the term “empty forest” (Redford 1992).

The selective pressure of hunting target mostly large bodied vertebrates (Redford 1992; Peres and Palacios 2007), which may trigger the populations of small-bodied species that may once be controlled by large species through predation, competition or interference, a phenomenon called “density compensation” (MacArthur *et al.* 1972). Theoretical models have suggested that the local extinction of large herbivores will release the population of small mammals, particular rodents, in neotropical forests (Wright 2003; Dirzo et al. 2007). The only empirical test of this hypothesis can be found in the studies of newly isolated land-bridge islands (Adler 1996). Very high densities of a species of small rodents (*Proechimys semispinosus*) were found on islands with a high degree of defaunation in Panama (Asquith *et al.* 1997). However, most of rainforests are not totally empty forests (Redford and Feinsinger 2001), and top down forces controlling small rodents have never tested in continental forests.

We hypothesized in areas where large herbivores are functionally extinct we predict an increase of small mammal abundance and a decline in species richness. In addition, we evaluate the potential mechanisms by which small mammals might be responding to the functional extinction of large herbivores, (1) comparing the density of the dominant fruiting trees that might explain major differences in small mammal abundance, (2) measuring the microhabitat characteristics used for each small mammal species. We hypothesized that microhabitats more protected from the trampling effects of large herbivores will have higher abundance irrespective of the area.

METHODS

Study areas

Sampling of non-volant small mammals was conducted at two sites in the Brazilian Atlantic forest, Itamambuca (IT) (45°5'16"W/ 23°19'29"S) and Vargem Grande (VG) (45°14'39"W/23°26'16"S) into Santa Virginia Nucleus (see **Figure 1 – Artigo 1**) that has an area of 17,000 hectares. This site is located in the northern portion of the Serra do Mar State Park (SMSP) (IF 2006), with altitudes ranging from 870 m to 1,100 m (Tabarelli and Mantovani 1999). The Serra do Mar massif cover a continuous area of 1 million of ha of Atlantic forests (Ribeiro *et al.* 2009). Vegetation can be classified as Montane Atlantic Rain Forest (Veloso *et al.* 1991).

The warm-wet period occurs during summer, while coldest-drier months occur in winter. Mean annual rainfall is about 2,200 mm and monthly mean temperatures range from about 18°C to 22ºC during the coldest and warmest months, respectively (IF 2006).

The abundance of large herbivores in both study areas has been censured in some detail with camera traps and linear transects (Rocha Mendes 2010). The main results are summarized in **Figure 2**. Itamambuca and Vargem Grande have similar species composition of large mammals, but Vargem Grande has marked differences in biomass and abundance of large herbivorous compared to Itamambuca, especially of the white-lipped peccary *Tayassu pecari,* (**Table 1**, **Figure 2**). Biomass of large-bodied mammals were 47 fold in Itamanbuca than in Vargem Grande (**Table 1**).

Table 1. Abundance (individuals/10km) and relative biomass (kg / 10 km) in two class size of mammals in each study sites according to data census of linear transects. Methodological details in Rocha-Mendes (2010).

Class size	Itamambuca		Vargem Grande	
	Abundance	**Biomass**	**Abundance**	**Biomass**
Medium-bodied (1 - 15 kg)	1.87	7.73	1.32	5.55
Large-bodied (> 15 kg)	8.22	284.03	0.12	6.03

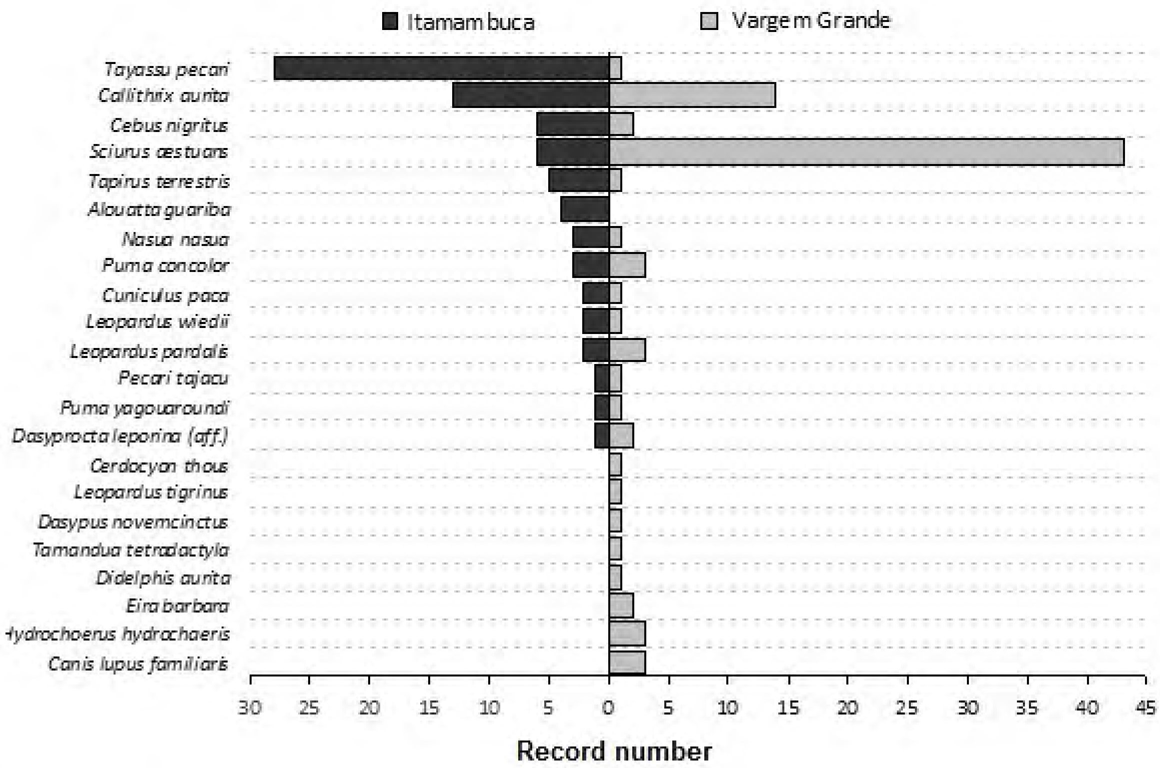


Figure 2. Record number of non volant mammals (data of census by linear transect summed with data of camera traps) in Itamambuca and Vargem Grande sites. Methodological details in Rocha-Mendes (2010).

Mark and recapture of non-volant small mammals

Sampling of non-volant small mammals was done using two standard types of traps: live-traps (Sherman and Tomahawk) and pitfall-traps. We sampled bimonthly over a period of 14 days, which five consecutive nights at each site during one year (November 2008 to September 2009). We set up three grids of live-traps and six transects of pitfall-traps at each site. Live-traps were arranged in a 0.6 ha grids (60 x 100 m each) with 24 trap stations spaced every 20 m. Each trap station received one Sherman trap of different size, randomly chosen (small, 25 x 7.5 x 9.5 cm; medium, 30 x 7.5 x 9.5 cm; large, 37.5 x 10 x 12 cm; H.B. Sherman Trap®, Inc., Tallahassee, Florida, USA). We also randomly set a “Tomahawk”-like trap (45 x 16 x 16 cm; Rosaminas Serviço Engenharia e Comércio ltda. Piraúba, Minas Gerais, Brazil) at six trapping stations. Overall, we had 30 live-traps per grid.

Pitfall-traps were set on grids composed of two parallel lines 30 m apart. Each line received four 60 L plastic buckets (40 cm top diameter, 35 cm bottom diameter, and 56 cm depth) buried with the rim at ground level, spaced every 10 m. The buckets on each line were connected with a 0.5 m tall plastic drift fence that extended an additional 10 m at each end, totaling 50 m of fence. The same sampling effort was applied in each study area, consisted of 3420 trap/nights, 2700 for live-traps and 720 for pitfall-traps per site.

All grids of live and pitfall traps within a site were spaced at least 100 m from each other to minimize pseudo-replication at the grid level, based on distances moved per night by Atlantic Forest small mammals (Mendel and Vieira 2003; Püttker *et al.* 2006). Both trap types (live and pitfall traps) were baited with a mix of bacon, peanut butter, corn meal and mashed banana. Although pitfall-traps need no bait to work properly, we baited them to minimize starvation of the animals caught, which could spend more than 12 hours in the buckets before being released. We checked and rebaited all traps daily.

At first capture, we marked every individual with a numbered ear-tag (Ear tags, National Band and Tag Co., Newport, Kentucky, USA). All captured animals were released at the station they were trapped.

Microhabitat variables

Microhabitat used by small mammals was characterized by measuring 13 microhabitat variables (**Appendix 1**) at each trap station according to four basic guidelines suggested by Dueser and Shugart-Jr (1978). All variables were measured once during a six-day period in August 2009. The first four variables were recorded in four 1-m radius circular plot, each one in four quadrants (north-south and east-west directions) of a 5-m radius circular plot centered at each trap station. On these cases our working “variable” was the arithmetic mean of the four records of each variable. Variables 6 to13 were recorded in the 5-m circular plot. Basal areas were estimated on the basis of the diameter at breast height (about 1.3 m). Basal areas were estimated on the basis of diameter at breast height (about 1.3 m). Percentages of understory coverage and of canopy cover were transformed into arc-sine values to minimize hard limits, intrinsic to percentage estimates (Zar 1996). Total basal areas of *E. edulis* and *Geonoma* spp were used as microhabitat variables that could indirectly suggest the availability of food resource for small mammals since they were the most abundant palms in the study area and their seeds were eaten by most species of rodents in the area (L.A. Galbiati *et al*., unpubl.data).

DATA ANALYSIS

Species richness was calculated as the total number of non-volant small mammals species captured in each sampling month at each study site. The mean species richness do not met the assumptions of equal variance (Fisher *F* test) and normality (Shapiro-Wilk normality test), so the variation of species richness between locations was analyzed by the non-parametric Wilcoxon rank test.

Microhabitat variable were summarize by a principal component analysis (PCA) fitted on the variance/covariance matrix. We used the natural logarithmic values of the 13 variables as a way to reduce the range of variability across variables, since each microhabitat variables were measured in different scales. Then we used the scores of principal component 1 (PC1) as a surrogate of microhabitat variables.

We compared total abundance, total abundance of rodents and total abundance of marsupials between study sites and its correlation with microhabitat factor at the trap station level. We used linear mixed-effects models in which study sites and PC1 were defined as fixed factors and we modeled also the two-way interaction of study sites with trap type (live and pitfall-traps). Previously, we found that pitfall-traps captured 2.6 more individuals than the live-traps, even with a 3.75 times smaller sampling effort in pitfall-traps in both study areas (C.L. Neves, R. Guevara and M. Galetti, unpubl. data). In the random component of the model we weighed the overall mean of the response variable by the effect of grids nested with seasons, to control for pseudo-replication (at the grid level) and for effects of seasonality. Seasonality effects on abundances in each type of trap were found at both study areas (C.L. Neves, R. Guevara and M. Galetti, unpubl. data). For more robust analyses, the models for each abundance values were simplified by excluding non-significant variables (considering $P < 0.05$).

For these analyses, we weighted the values of total abundance, rodent total abundance and marsupial total abundance to represent abundance at 100 trap-nights. We multiply the numbers of individuals at each study area by 100 and dividing by 3420 (30 traps x 3 grids of live-traps x 5 nights x 6 sampling periods plus 8 traps x 3 grids x 5 nights x 6 sampling periods).

The effect of defaunation on the abundance of each species, captured in common between the areas of study, were analyzed by generalized linear models (GLM) with "*Chi-square"* test to compare the variances. For these analyses we used as dependent variable the values of weighted abundance of small mammals (number of individuals/100 trap-nights) at the grid level. The weighted abundance values were calculated by multiplying the number of individuals in each grid of live-traps by 100 and dividing by 900 (30 traps x 5 nights x 6 sampling periods). Those in the grids of pitfall-traps were multiplied by 100 and divided by 240 (8 traps x 5 nights x 6 sampling periods). The independent variables were the study sites, the type of trap and the surrogate of microhabitat variables (CP1). We tested correlation of abundances with CP1. Furthermore, we tested the two-way interaction of study site with trap type, study site with CP1 and trap type with CP1. For species that showed no significant double effects (considering $p < 0.05$), we tested only single effects by glm with F test to compare the variances of two samples.

Post-hoc tests were contrasted based on standard errors calculated from the linear predictor, and thus we estimated t values (Warnes 2009). All statistical tests were done in the statistical environment R: (R Development Core Team 2009).

RESULTS

Defaunation effects on species richness

Overall we recorded 18 species of small mammals, being 13 rodent and five marsupial species. Seventeen species were captured at Itamambuca and 14 at Vargem Grande. Four species were captured exclusively in Itamambuca, while one was only captured in Vargem Grande. The Wilcoxon test showed that species richness were captured on average 1.3 fold at Itamambuca compared with Vargem Grande ($W = 31$; $P = 0.04$) (**Figure 3**).

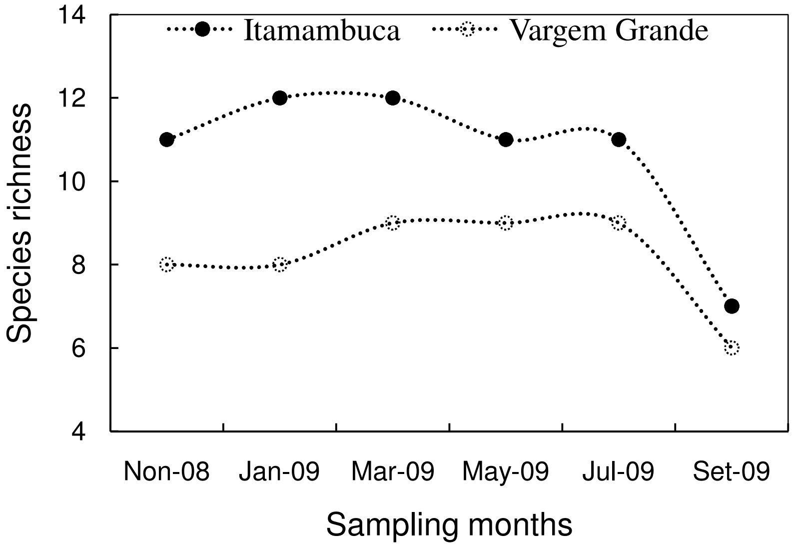


Figure 3. Species richness of non-volant small mammals per sampling months in Itamambuca (*solid circles*) and in Vargem Grande (*open circles*), sites with higher and lower abundance of white-lipped peccary, respectively.

Defaunation effects on abundance

Although 367 individuals were captured in Itamambuca while 253 were captured in Vargem Grande, mixed-effects model revealed no significant difference ($F = 0.12$; d.f. = 1, 21; $P = 0.72$). However, mixed-effects model showed that type trap significantly affected the values of rodent abundance, in least one site ($F = 14.19$; d.f. = 2, 21; $P < 0.0001$). Post-hoc test showed that pitfall-traps captured on average twice the number of individuals in Vargem Grande than in Itamambuca (t = 2.15, d.f. = 21, P = 0.04; **Figure 4a**). There was no significant difference of mean values of abundance between Vargem Grande and Itamambuca for live-traps (t = 0.42, d.f. = 21, P = 0.68; **Figure 4a**).

For marsupials, mixed-effects models also showed that there was a significant influence of trap type on the capture of individuals (*F* = 3.83; d.f. = 2, 21; *P* = 0.04). However, post-hoc test revealed that values of marsupial abundance in live-traps did not differ between Itamambuca and Vargem Grande (*t* = 0.01, d.f. = 21, *P* = 0.99; **Figure 4b**), also there were no differences of marsupial abundances in pitfall-traps between study areas (*t* = 1.30, d.f. = 21, *P* = 0.20, **Figure 4b**). Only that pitfall-traps captured on average 2.6 fold individuals than did live-traps in both study sites (*t* = 3.00, d.f. = 21, *P* = 0.007, **Figure 4b**).

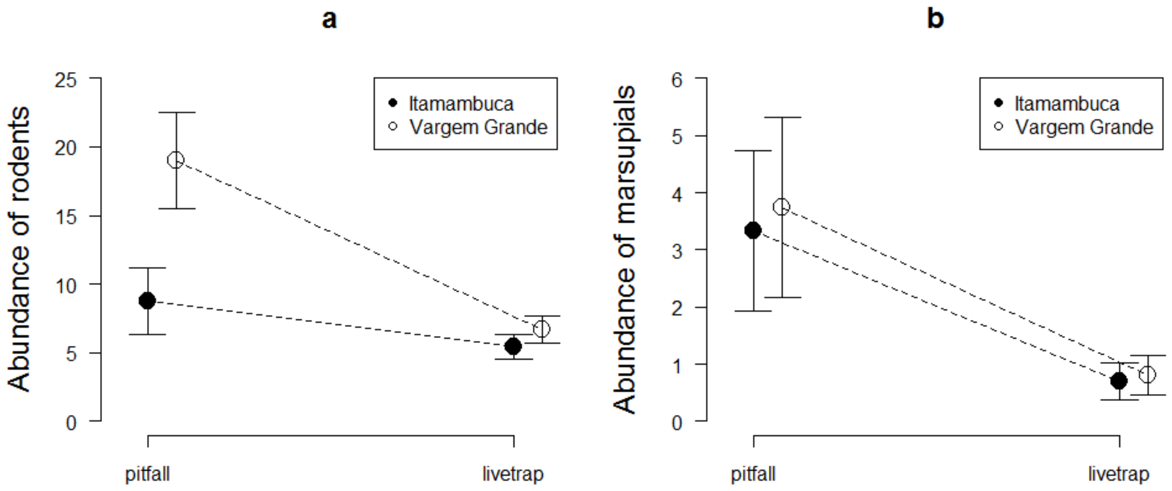


Figure 4. Mean and 95 % CI of weighted abundance values (individuals/100 trap.nights) of rodent (a), and marsupial (b) per trap type (live and pitfall traps) in Itamambuca (*solid circles*) and in Vargem Grande (*open circles*), sites with higher and lower abundance of white-lipped peccary, respectively.

The GLM with *F* for single effects revealed that *Thaptomys nigrita* was on average 2.6 times more abundant in Vargem Grande than in Itamambuca (**Table 2**, **Figure 5a**). Also, GLM showed a significant influence of trap type on the capture of individuals (**Table 2**). Pitfall-traps in Vargem Grande were responsible for capturing on average 3 fold individuals of *T. nigrita* than did pitfall-traps in Itamambuca (**Figure 5a**). Live-traps in Vargem Grande were responsible for capturing on average 2 fold individuals of *T. nigrita* than did live-traps in Itamambuca (**Figure 5a**).

Furthermore, the influence of trap type on the capture of individuals was found for *Monodelphis* spp. and *Euryoryzomys russatus*, in least one study site (**Table 2**). Pitfall-traps in Vargem Grande were responsible for capturing on average almost the same number of *Monodelphis* spp. than did pitfall-traps in Itamambuca (1.2 fold) (**Figure 5b**). Live-traps in

Vargem Grande were responsible for capturing on average 2 fold individuals of *Monodelphis* spp. than did live-traps in Itamambuca (**Figure 5b**). For *E. russatus*, pitfall-traps in Vargem Grande were captured on average 2.3 fold individuals than did live-traps in Itamambuca (**Figure 5c**). Live-traps in Itamambuca were responsible for capturing on average almost the same number of *E. russatus* than did live-traps in Vargem Grande (1.2 fold) (**Figure 5c**).

Table 2. Weighted abundance (individuals/100 trap.nights) in each study site of non-volant small mammals and statistical summary of GLM with *F* test at the grid level testing the effects of site (IT – Itamambuca and VG - Vargem Grande). All levels of comparison had one and three degrees of freedom. Asterisk (*) indicates $P \leq 0.05$. [a]GLM for the genus *Monodelphis* was performed with the sum of weighted abundances of the tow species *Monodelphis gr. scalops* and *Monodelphis* sp.

Taxa	**Weighted abundance**		**Data modeling**	**Study sites**		**Trap type**		**CP1**	
	IT	**VG**		***F***	***P***	***F***	***P***	***F***	***P***
Didelphimorphia									
Didelphis aurita	0.11	0.16	-	0.28	0.61	0.00	0.97	0.02	0.88
Marmosops incanus	0.50	0.49	-	0.64	0.45	0.13	0.73	2.23	0.17
Monodelphis spp. [a]	1.27	1.56	inverse	2.07	0.19	19.05	<0.01*	3.35	0.10
Philander frenatus	0.15	0.07	sqrt	0.03	0.87	0.26	0.62	27.03	<0.001*
Rodentia									
Euryoryzomys russatus	1.95	2.37	-	0.78	0.40	5.35	0.04*	0.08	0.79
Juliomys pictipes	0.69	0.14	-	1.26	0.29	3.38	0.10	0.02	0.88
Thaptomys nigrita	1.50	3.85	-	11.40	0.01*	15.56	<0.01*	2.77	0.13
Trinomys iheringi	0.22	0.02	-	1.14	0.32	0.90	0.37	0.28	0.61

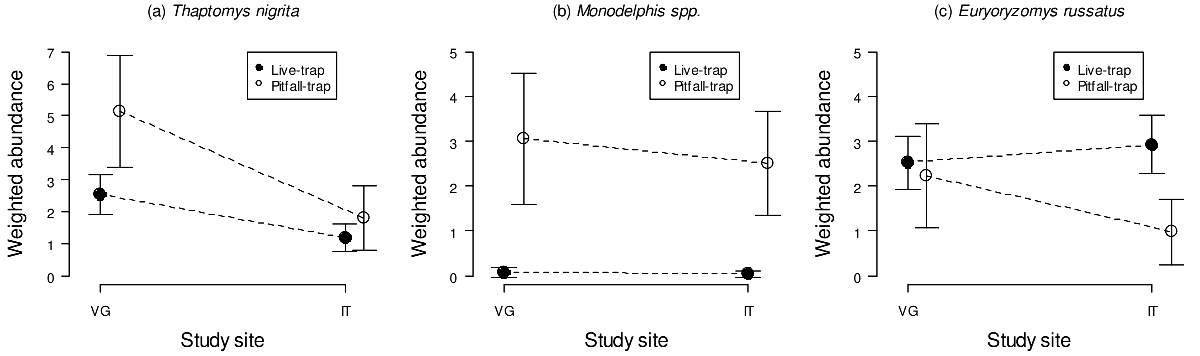


Figure 5. Mean and 95 % CI of weighted abundance values of the species (a) *Thaptomys nigrita*, (b) *Monodelphis* spp., and (c) *Euryoryzomys russatus* per location (IT- Itamambuca and VG – Vargem Grande) in live-traps (*solid circles*) and in pitfall-traps (*open circles*).

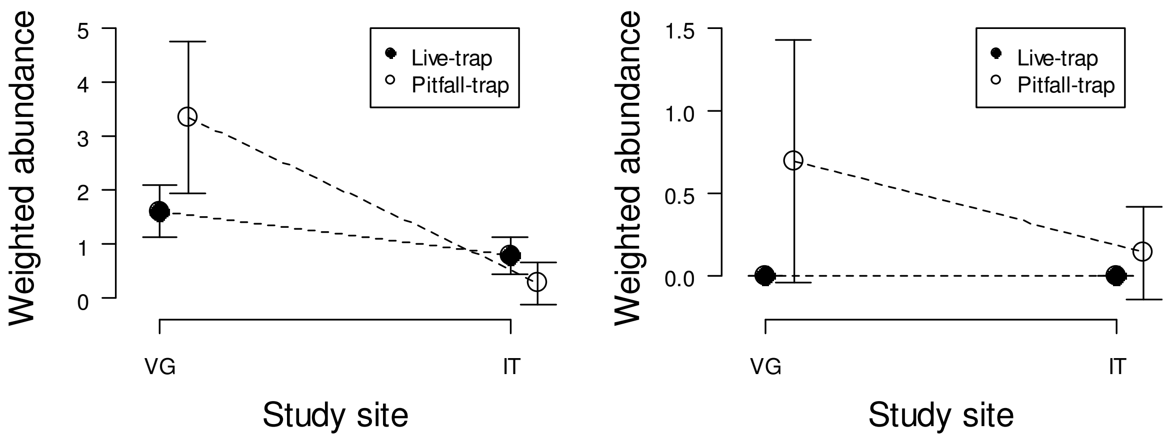
The GLM with "*Chi-square"* anova revealed that *Akodon montensis* was on average 5 times more abundant in Vargem Grande than in Itamambuca (**Table 3**, **Figure 6a**). Also, GLM showed a significant influence of trap type on the capture of individuals (**Table 3**). Pitfall-traps in Vargem Grande were responsible for capturing on average 12 fold individuals of *A. montensis* than did pitfall-traps in Itamambuca (**Figure 6a**). Live-traps in Vargem Grande were responsible for capturing on average 2 fold individuals of *A.montensis* than did live-traps in Itamambuca (**Figure 6a**).

Abundance of *Blarinomys breviceps* was on average 5 fold in Vargem Grande than in Itamambuca (**Table 3**, **Figure 6b**). Also, GLM showed a significant influence of trap type on the capture of individuals (**Table 3**). Since any individual of *B. breviceps* was captured by live-traps, we found that only pitfall-traps in Vargem Grande were responsible for capturing on average 5 fold individuals of *B. breviceps* than did pitfall-traps in Itamambuca (**Figure 6b**).

For *Brucepattersonius soricinus* and *Oligoryzomys nigripes*, GLM revealed the same pattern. These species were on average 2 times more abundant in Vargem Grande than in Itamambuca (**Table 3, Figure 6 c,d**). Also, there was a significant influence of trap type on the capture of individuals of both species (**Table 3**). Pitfall-traps in Vargem Grande were responsible for capturing on average 2 fold individuals of *B. soricinus* and *O. nigripes* than did pitfall-traps in Itamambuca (**Figure 6 c,d**). Live-traps in Itamambuca captured only one individual of both species, while none individual was captured by live-traps at Vargem Grande (**Figure 6 c,d**).

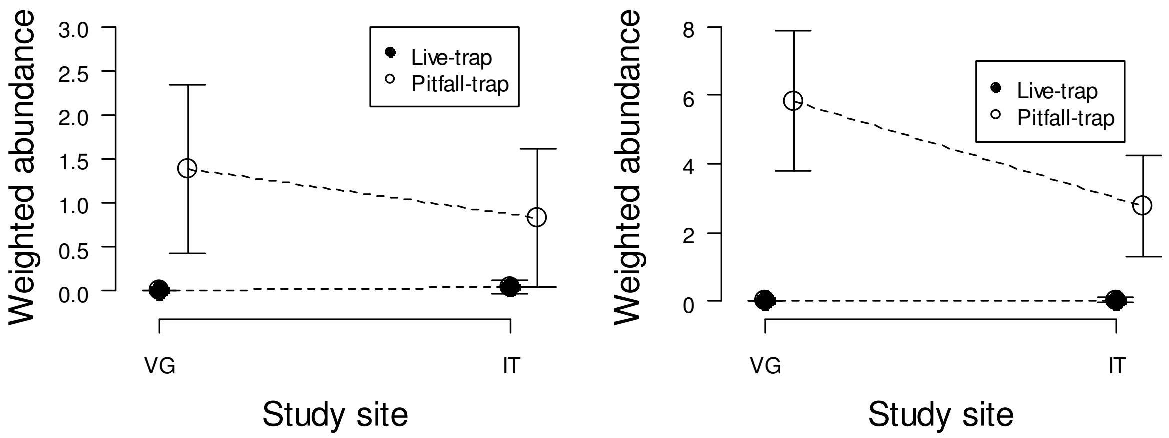
Table 3. Weighted abundance (100 trap.nights) in each study site of rodent species and statistical summary of GLM with *Chi-sq* test at the grid level testing the effects of site (IT - Itamambuca and VG - Vargem Grande). All levels of comparison had one and three degrees of freedom. Asterisk (*) indicates P ≤ 0.05.

Taxa	**Weighted abundance**		**Data modeling**	**Study sites**		**Trap type**		**CP1**		**Trap:CP1**		**Site:CP1**	
	IT	**VG**		***Chi-sq***	***P***	***Chi-sq***	***P***	***Chi-sq***	***P***	***Chi-sq***	***P***	***Chi-sq***	***P***
Rodentia													
Akodon montensis	0.53	2.46	-	90.81	<0.001*	88.36	0.12	30.89	<0.001*	7.00	<0.001*	-	-
Blarinomys breviceps	0.07	0.35	inverse	46.10	<0.001*	21.51	<0.001*	19.72	0.18	-	-	7.05	<0.001*
Brucepattersonius soricinus	0.44	0.69	log	106.76	0.04*	40.96	<0.001*	37.23	0.049*	-	-	7.00	<0.001*
Oligoryzomys nigripes	1.41	2.92	log	298.08	<0.001*	33.49	<0.001*	30.26	0.07	-	-	7.00	<0.001*



(a) *Akodon montensis*

(b) *Blarinomys brevicpes*



(c) *Brucepattersonius soricinus*

(d) *Oligoryzomys nigripes*

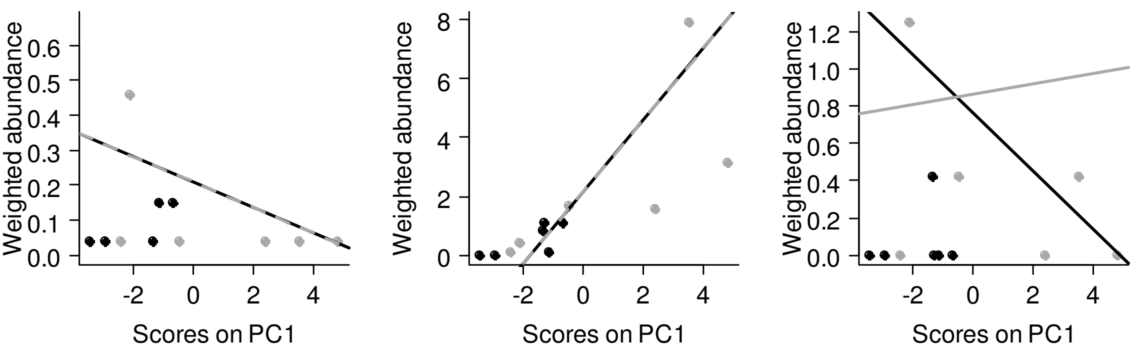
Figure 6. Mean and 95 % CI of weighted abundance values (individuals/100 trap.nights) of the species (a) *Akodon montensis*, (d) *Blarinomys breviceps*, (c) *Brucepattersonius soricinus,* and (d) *Oligoryzomys nigripes* per location (IT- Itamambuca and VG – Vargem Grande) in live-traps (*solid circles*) and in pitfall-traps (*open circles*).

Microhabitat effects on abundance

The principal component analysis accounted for 82% of the variability of the 13 microhabitat variables over the first three components. Total basal area of tree ferns (0.702) and total basal area of standing dead trees (0.655) had the highest correlation coefficients with the first principal component, whereas total basal area of tree ferns (-0.626) and total basal area of standing dead trees (0.672) had the greatest correlation coefficients with principal component two, and solely total basal area of *E. edulis* showed a high correlation index with the third principal component (0.917). Because the three principal components correlated mostly with the same microhabitat variables we used only the scores on the first principal components as surrogate of the microhabitat in further analysis.

Mixed-effects models showed that abundances of small mammals in each type of trap was not affected by microhabitat characteristics (F = 1.20; d.f. = 1, 6813, P = 0.27), neither for rodents (F = 2.16; d.f. = 1, 6813, P = 0.14) or marsupial abundance (F = 0.12; d.f. = 1, 6813, P = 0.73).

The surrogate of microhabitat correlated significantly with the weighted abundance of one species of marsupial, *Philander frenatus* (**Table 2**), and one rodent, *A. montensis* (**Table 3**). The abundance of *P. frenatus* had a significant positive correlation of abundance with the CP1 regardless of trap type (**Figure 7a**). In contrast, *A. montensis* had a significant positive correlation of abundance with the scores on the principal component 1 regardless of trap type (**Figure 7b**). Therefore, CP1 correlated significantly with the weighted abundance of three rodent species, *Blarinomys breviceps*, *Brucepattersonius soricinus* and *Oligoryzomys nigripes*, in least one site. Post-hoc tests showed that the weighted abundances of *B. breviceps* in Itamambuca correlated negatively with the scores of principal component 1 (t = 2.97; d.f. = 7; P = 0.02) whereas abundance in Vargem Grande was not significantly correlated with microhabitat (t = 1.98, d.f. = 7, P = 0.09) (**Figure 7c**). Thus, the weighted abundances of *B. soricinus* and *O. nigripes* in Itamambuca correlated positively with CP1 ($t > 5.13$, d.f. = 7, $P <$ 0.01) whereas their abundance in live-traps was not significantly correlated with microhabitat ($t > 0.76$, d.f. = 7, $P > 0.46$) (**Figures 7 d and 7e**, respectively).


(a) *Philander frenatus* (b) *Akodon montensis* (c) *Blarinomys breviceps*

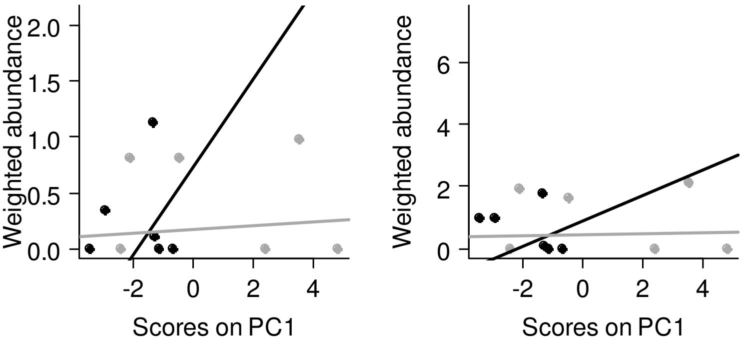

(d) *Brucepattersonius soricinus* (e) *Oligoryzomys nigripes*

Figure 7. (a) Negative correlation between the weighted abundance of *Philander frenatus* and the mean at grid level of the principal component 1 (Scores on PC1); (b) Positive correlation between the weighted abundance of *Akodon montensis* and the scores on PC1; (c) Negative correlation between the weighted abundance of *Blarinomys breviceps* in Itamambuca and mean at grid level of the scores on PC1, (d) Positive correlation between weighted abundance of *Brucepattersonius soricinus* in Itamambuca and mean at grid level of the scores on PC1, and (e) Positive correlation between weighted abundance of *Oligoryzomys nigripes* in Itamambuca and mean at grid level of the scores on PC1. Correlation between weighted abundances of *B. breviceps, B. soricinus and O. nigripes* in Vargem Grande and the mean at grid level of the scores on PC1were not significantly. Black dots = number of individuals in Itamambuca; Grey dots = number of individuals in Vargem Grande; Black line = trendline of Itamambuca; and Grey line = trendline of Vargem Grande. Dotted line = trendline of Itamambuca and Vargem Grande.

DISCUSSION

Defaunation effects on species diversity

The area with higher abundance of large herbivores had higher species richness. This same patterned was showed for herpetofauna richness in the African savannas (Nasseri *et al.* 2010). These authors found that areas with heavy habitat modification by elephants activities had higher species richness. This positive evidence of ecosystem engineers processes was also revealed for the peccaries on the anurofauna in the Peruvian Amazonas (Beck *et al.* 2010). None studied, so far, have attributed the positive ecological engineers effects of peccaries on non-volant small mammals richness.

On the other hand, we found a contrary patterned for abundance values of small mammals. The area with low abundance of large herbivores consistently had higher abundance of rodents, but not of marsupials. Other variables that usually control the abundance of rodents, such as fruit availability (Bergallo and Magnusson 1999), predation (Fonseca and Robinson 1990; Wang 2002) and microhabitat differences (Dueser and Shugart-Jr 1978; Coppeto *et al.* 2006) were not important for explaining the overall abundance of rodents in the area with low abundance of large herbivores. Mesopredators, such as medium (*Leopardus pardalis*) or small felids (*L. wiedii*,) and the South American coati *Nasua nasua* do not differ between areas (Rocha-Mendes 2010), and the marsupial *Didelphis aurita* had small values of relative abundance, only 0.11 individuals/100 trap-nights in Itamambuca and 0.16 individuals/100 trap-nights in Vargem Grande, which do not differ significantly between this areas (see **Table 2**).

Microhabitat differences between sites might not be responsible for influence the overall diversity of small rodents. But specifically, we found influence of microhabitat on *P. frenatus* and *Akodon montensis* regardless of sites, not explaining the differences on abundance between sites. We found a positive correlation between abundances of *B. soricinus* and *O. nigripes* and microhabitat quality at Itamambuca, once more, not explaining the differences on abundance between sites, since these species were not more abundant in this site compared with Vargem Grande, despite the positive correlation. However, we found a negative relationship between abundance of *B. breviceps* and microhabitat quality at Itamambuca, suggesting that higher abundances of the lipped peccaries could modify the microhabitat and have a negative effect on abundance of this species.

Neither fruit availability might be responsible for influence the overall higher diversity of small rodents on Vargem Grande. Rocha-Mendes (2010) found that the density of the dominant palm *Euterpe edulis* was 1.6 times higher in the area with lower abundance of peccaries (Vargem Grande), which might explain the differences in the abundances of rodents by providing greater amount of seed. However, the rodent species that increase their abundance in the area with low herbivores were mainly insectivorous-omnivorous.

Since the major difference between areas is the abundance of white lipped peccaries (*Tayassu pecari*), it is likely that this ungulate might influence the diversity of small rodents. White lipped peccaries have an important direct effect on plant communities in the study site, especially through seed predation, herbivory and trampling (Rocha-Mendes 2010). But what are the mechanisms that peccaries control rodent abundance? We envision at least two mechanisms: direct competition for same food resources or indirect effects such as habitat modification.

White lipped peccaries have a generalist diet, eating mainly seeds (Tiepolo and Tomas 2006), and might compete with small rodents for seed sources. However, the rodent species that increased their abundances in the area with low herbivores where not the most granivorous ones (L. Galbiati *et al*. unpubl. data). We would expect that *Trinomys iheringi* or *Euryoryzomys russatus*, recognizably the most granivores species, would favor in the absence of peccaries but we fail to find this pattern. The rodent species that increase their abundance in the area with low herbivores were mostly with fossorial or semi-fossorial habits, *T. nigrita*, *B. breviceps* and *B. soricinus*, indicating that habitat modification is the major mechanism that might explain how white lipped peccaries control the rodent diversity in these forests.

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Appendix 1. Designation and sampling methods for 13 variables measuring the forest microhabitat structure.

Microhabitat variable	Sampling methods
1. Density of palms seedlings	We counted the palm seedlings.
2. Density of non-palm seedlings	We counted other seedlings, except of palms.
3. Understory density	We estimated this variable with a cross formed by two 1-m PVC sticks graduated every 2 cm. The cross was held horizontally 0.5 m from the ground, and we counted the number of 2-cm marks that came in contact with the understory vegetation and divided this by 100 (total number of marks on the cross)..
4. Depth of the litter layer	This variable was measured with a ruler graduated in centimeters, which was held vertically in the center of each 1-m circular plots.
5. Percentage of canopy cover (CA)	This variable was measured with a densiometer (Spherical Densiometer Model-C, Robert E. Lemmon, Forest Densiometers sold through Forestry Suppliers, Inc.).
6. Density of fallen dead logs	We counted all fallen dead logs with diameter > 10 cm.
7. Density of potential shelters for non-volant small mammals	We counted ground holes or rock crevices (Beisiegel 2006).
8. Total basal area of *Geonoma* spp.	Sum of basal area of each *Geonoma* spp.
9. Total basal area of *Euterpe edulis*	Sum of basal area of each *Euterpe edulis* with DBH > 10 cm.
10. Total basal area of tree ferns	Sum of basal area of each Fern tree with DBH > 10 cm.
11. Total basal area of other tree species	Sum of basal area of each tree with DBH > 10 cm (except the *Geonoma* spp., Fern and *Euterpe edulis* basal areas).
12. Total basal area of standing dead trees	Sum of basal area of each stand dead log with DBH > 10 cm.
13. Bamboo coverage	This variable was measured in a semi-quantitative scale of density, 0 = 0%; 1 = 1 to 25%; 2 – 26 to 50%; 3 – 51 to 75%; 4 = 76 to 100%. In the 5m radius circle

CONSIDERAÇÕES FINAIS

Esta dissertação contribui para uma maior compreensão dos efeitos indiretos da extinção funcional dos grandes herbívoros sobre a comunidade de pequenos mamíferos na Floresta Atlântica. Segundo o modelo teórico, o incremento na abundância de espécies de mamíferos de pequeno porte seria devido à ruptura da competição com os animais de grande porte. Entretanto, demonstramos empiricamente que a perda dos grandes herbívoros resultou em um aumento na abundância de roedores fossoriais, que provavelmente, não competem por recursos com os grandes herbívoros. Provavelmente, a interferência provocada pela extinção ecológica dos grandes herbívoros se dá de maneira indireta sobre os pequenos roedores, através da modificação do microhabitat para estes mamíferos. Contudo, as variáveis de microhabitat medidas durante este estudo não conseguiram representar a modificação no ambiente provocada pelos queixadas. Por outro lado, a sazonalidade climática foi um importante fator responsável pelas diferenças encontradas em relação à eficiência das armadilhas utilizadas durante o estudo. Nossos resultados mostraram uma inédita e estreita relação entre os pequenos e os grandes mamíferos. Portanto, este conjunto de dados deve ser utilizado como base para novas pesquisas nessa área de conhecimento, sendo as armadilhas de queda imprescindíveis para a detecção dos efeitos da defaunação.