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ECOLOGIA TRÓFICA DE PEQUENOS MAMÍFEROS NÃO VOADORES EM UMA ÁREA CONTÍNUA DE MATA ATLÂNTICA

RAISA REIS DE PAULA RODARTE

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 Zoologia.

Junho - 2013

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TÍTULO: Ecologia trófica de pequenos mamíferos da Floresta Atlântica: uma abordagem isotópica

AUTORA: RAISA REIS DE PAULA RODARTE

ORIENTADOR: Prof. Dr. MAURO GALETTI RODRIGUES

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Ao Samuel G. Tomasin, com amor.

“... Hoje me sinto mais forte,
Mais feliz, quem sabe. Só levo a certeza
De que muito pouco sei,
Ou nada sei

Conhecer as manhas e as manhãs
O sabor das massas e das maçãs

É preciso amor pra poder pulsar
É preciso paz pra poder sorrir
É preciso a chuva para florir

Penso que cumprir a vida
Seja simplesmente
Compreender a marcha
E ir tocando em frente

Como um velho boiadeiro
Levando a boiada
Eu vou tocando os dias
Pela longa estrada, eu vou
Estrada eu sou ...

Todo mundo ama um dia,
Todo mundo chora
Um dia a gente chega
E no outro vai embora

Cada um de nós compõe a sua história
Cada ser em si
Carrega o dom de ser capaz
E ser feliz.”

Tocando em frente – Almir Sater

"Have the courage to follow your heart and intuition.

They somehow already know what you truly want to become"

Steve Jobs

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Resumo

Ao longo de décadas ecólogos tentam entender quais são os mecanismos que promovem coexistência de espécies. Florestas tropicais abrigam a maior diversidade de pequenos mamíferos do planeta, portanto espécies dentro deste grupo podem compartilhar recursos similares. Nesse trabalho buscamos entender as relações tróficas entre roedores e marsupiais através da análise de isótopos estáveis de carbono e nitrogênio em três áreas contínuas de Mata Atlântica brasileira. Nosso principal objetivo foi compreender como diferentes espécies são capazes de coexistir em uma rica comunidade de pequenos mamíferos em relação a recursos alimentares. Nós verificamos se o tamanho corporal está relacionado às razões isotópicas de carbono e nitrogênio para cada espécie e testamos a hipótese de que espécies de tamanho corpóreo similar apresentam nichos tróficos distintos. Para isso, coletamos amostras de pelos de 57 indivíduos de marsupiais e 204 indivíduos de roedores. Encontramos que roedores apresentam nicho trófico mais amplo com espécies distribuídas em três níveis tróficos (granívoras, onívoras e insetívoras) enquanto os marsupiais estão inseridos em um único nível trófico, alimentando-se exclusivamente de invertebrados. Observamos também alta sobreposição de dieta entre marsupiais e alguns roedores onívoros, provavelmente devido ao consumo de invertebrados e fungos. Em geral, não houve correlação entre o tamanho corporal e os valores isotópicos dos marsupiais, mas para três espécies de roedores (*Euryoryzomys russatus*, *Thaptomys nigrita* e *Trinomys iheringi*) houve correlação significativa entre o tamanho do corpo e um dos isótopos. Para os marsupiais, a dieta por si só não explica a coexistência entre espécies, que parece estar mais relacionada à separação de uso do espaço vertical. Por outro lado, para os roedores a dieta e o tamanho corporal foram suficientes para explicar a coexistência de um número elevado de espécies, mostrando que a comunidade está organizada em diferentes guildas. Identificar mecanismos cruciais na determinação da estrutura e composição de comunidades é o primeiro passo para entender relações interespecíficas e, dessa forma os fatores que promovem ou facilitam a coexistência entre as espécies. Esperamos que nossos resultados, os quais foram obtidos em áreas contínuas, sejam usados como base em estudos futuros sobre coexistência de espécies em comunidades de pequenos mamíferos em áreas fragmentadas e defaunadas.

Palavras-chave: Nicho trófico. Coexistência. Isótopos estáveis. Roedores. Mata atlântica. Marsupiais.

Abstract

For many decades ecologists try to understand what the mechanisms that promote species coexistence are. Tropical rainforests support the greatest diversity of small mammals in the world, therefore species within that group may share similar resources. In this paper we seek to understand the trophic relationship between rodents and marsupials through the analysis of stable carbon and nitrogen isotopes within three continuous areas of the Atlantic forest of Brazil. We were particularly interested in understanding how different species are able to coexist in a rich small-mammal community with respect to sharing food resources. We verified if body size is related to carbon and nitrogen stable isotope ratios for each of the species and tested the hypothesis that species with similar body size have distinct trophic niches. We collected hair samples for isotopic analysis from 57 individuals of marsupials and 204 individuals of rodents. We found that rodents have a broad trophic niche with species distributed in three trophic levels (granivores, omnivores and insectivores) while marsupials are mainly within one trophic level, feeding exclusively on invertebrates. We found a strong diet overlap among marsupials and some omnivorous rodents, probably due to consumption of invertebrates and fungi. In general, there was no correlation between body size and isotopic values for marsupials, but for three species of rodents (*Euryoryzomys russatus*, *Thaptomys nigrita* and *Trinomys iheringi*) there was significant correlation between body size and one of the isotopes. For marsupials, diet by itself does not seem to explain species coexistence. Marsupials seem to be more related to different vertical use of space. On the other hand, for rodents diet together with body size was sufficient to elucidate the high number of coexisting species because we could show that the community was organized into different guilds. Identifying the mechanisms that are crucial to determine the structure and composition of a community is the first step to understanding inter-specific relations, thus the factors that promote or facilitate species coexistence. We hope that our results, which were obtained in continuous areas, will be valuable as a baseline in future studies on species coexistence within small mammal communities in fragmented or defaunated forests.

Keywords: Trophic niche. Coexistence. Stable isotopes. Rodents. Atlantic forests. Marsupials.

SUMMARY

Article: TROPHIC NICHE DIFFERENTIATION AMONG RODENTS AND MARSUPIALS IN THE ATLANTIC RAINFORESTS

Raisa R. Rodarte, Mauro Galetti, Marcelo Moreira, Carolina L. Neves. Em preparação.

Anexo A - BROCARDO, C.R., RODARTE, R., BUENO, R.S., CULOT, L. & GALETTI, M. Non-volant mammals of Carlos Botelho State Park, Paranapiacaba Forest Continuum. Biota Neotrop. 12(4): http://www.biotaneotropica.org.br/v12n4/pt/abstract?inventory+bn02512042012

Trophic niche of small mammals

Trophic niche differentiation among rodents and marsupials in the Atlantic rainforests

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INTRODUCTION

How different species can coexist in a community is a central issue in ecology (Hutchinson 1959, MacArthur 1964), and numerous theories have been proposed to explain such phenomenon (Elton 1927, Hutchinson 1957, Chesson 2000). In general, species that occur together are required to exhibit ecological differences in at least one niche dimension (Hutchinson 1957, Pianka 1994, Chesson 2000) such as: (1) period of foraging (Gutman and Dayan 2005, Castro-Allerano and Lacher 2009), (2) space (MacArthur 1964) or (3) food (Leite et al 1996, Ben-Moshe et al 2001). Another relevant factor in resource partitioning is the difference in body size in species that share the same resource (Hutchinson 1957). Brown (1973) and Bloch et al. (2011) found that species of similar body size occur together less frequently than expected by chance.

Rainforests are particularly suitable to test how species can coexist because several species co-occur in a complex environment. The Atlantic rainforest holds one of the greatest diversity of small mammals in the Neotropics (Pardini and Umetsu 2006, Amori et al 2013) harboring approximately 120 species of rodents and marsupials along its distribution range (Paglia et al 2012) with up to 23 species living sympatrically (Pardini and Umetsu 2006). Species coexistence can be determined in large part by interspecific competition for food resources (Brown et al 1979). Hence, for a stable co-occurrence, most of the species need to present differences in trophic niches. Trophic niches are essential in understanding life history strategies and ecological interactions (Kawanishi et al 2012), however they remain poorly described for small mammals in the neotropics. Data on the diet of rodents and marsupials are often obtained through direct observations of feeding activity in the field (Paschoal and Galetti 1995), analysis of fecal samples (Leite et al 1996, Carvalho et al 2005) or gut content (Casella and Cáceres 2006, Pinotti et al 2011). However there are some criticisms regarding the use of these traditional methods. The gut content and fecal analyses may not accurately determine diets because these methods only reveal undigested food remains and temporal food consumption (Herrera et al 2002). Moreover in forested habitats the direct observations of small mammals diets are difficult due to their small size and mostly nocturnal activity. In contrast, the use of stable isotope technique might provide a better approach to characterize trophic relationships in a community (Zhao et al 2004, Young et al 2010, Kawanishi et al 2012).

Stable carbon and nitrogen isotopes are commonly used in ecological studies to infer food sources (DeNiro and Epstein 1978, 1981, Ambrose and DeNiro 1986, Nakagawa et al 2007) and discriminate among trophic niches (Kawanishi et al 2012, Dammhahn et al 2013). When the isotopic compositions of important food items differ, isotopic ratios of animal tissues can serve as natural tracers of resource use and habitat exploitation (Ambrose and DeNiro 1986) because animal tissues are synthesized and maintained by nutrients that are assimilated through the diet. Stable isotopes provide information about the assimilated food on different time scales ranging from hours to decades depending on the tissue analyzed (Tieszen et al 1983). Hard tissues (e.g. hair) accumulate information on diet over a long period, probably several weeks and months (Tieszen et al 1983, Boutton et al 1984), which corresponds to the average lifetime of most small mammals (Krebs et al 2007). Here, we examined whether diet is an important mechanism to promote small mammal species coexistence in a continuous rainforest by testing the hypothesis that species with similar body size have distinct trophic niches.

MATERIAL AND METHODS

Study site

This study was carried out in three continuous Brazilian Atlantic forests. The three sites, Itamambuca - ITA (45°5'W/23°19'S), Vargem Grande - VG (45°14'W/23°26'S) and São Miguel Arcanjo - CB (48°06'W/24°13'S) basis are located in Serra do Mar massif, the largest remnant of continuous Atlantic forest with an area of 1 200,000 ha (Ribeiro et al 2009) (Figure 1). All of these areas have similar altitudes, climate and vegetation. The altitudinal gradient ranges from 700 to 1,100 meters (Tabarelli and Mantovani 1999) and vegetation is classified as Montane Atlantic Rainforest (Oliveira-Filho and Fontes 2000). The annual average temperatures range from 15 to 22 °C, with the hot-wet period occurring during summer while the cold-dry months occur in winter (IF 2008).

The small mammal fauna at these three continuous areas are comprised of 25 species, nine marsupials and 16 small rodents (Table 1S) (Brocardo et al 2012, Neves 2010).

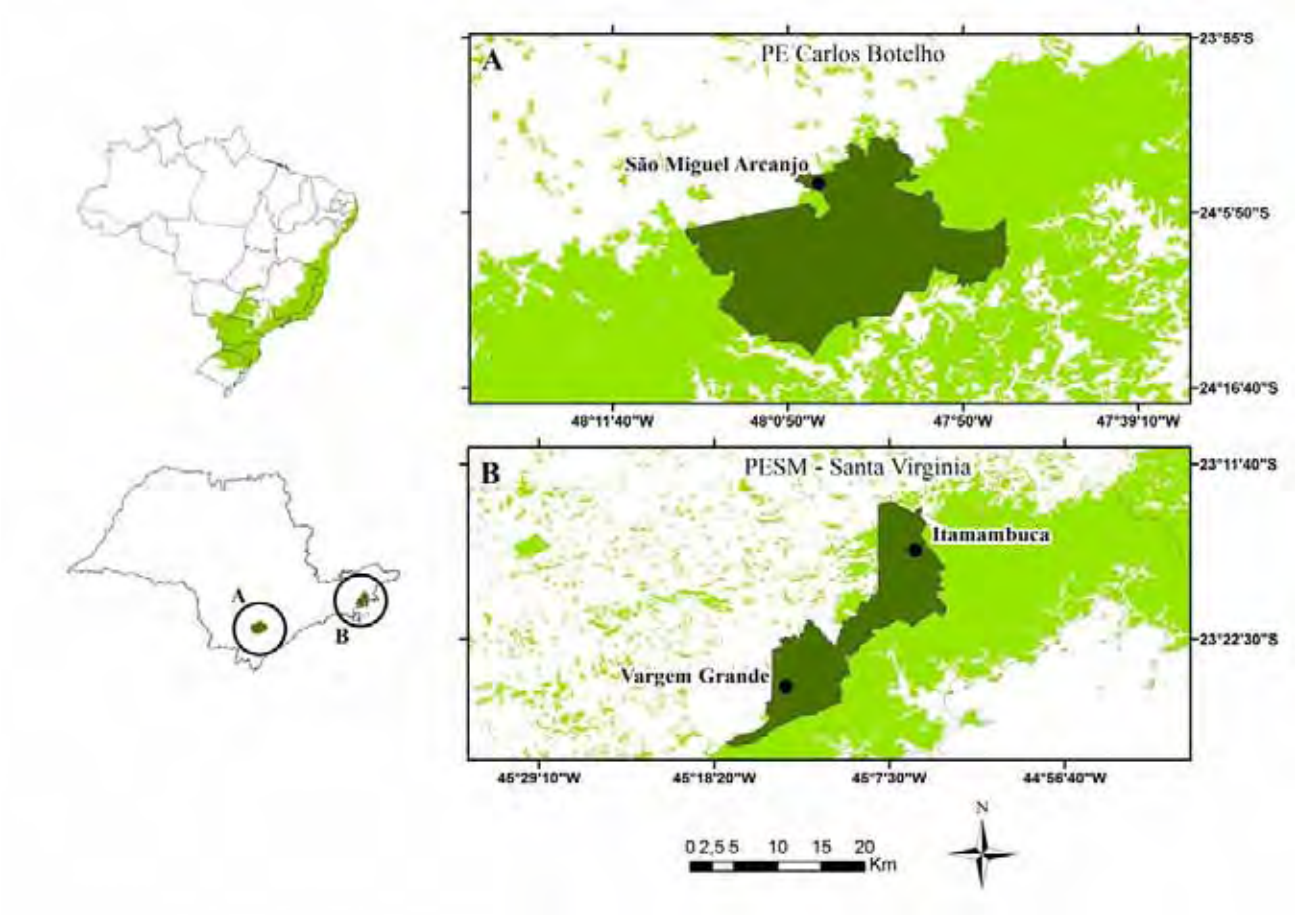

Figure 1. Localization of the three Atlantic forest areas in São Paulo state. (A) Carlos Botelho State Park (in dark green) and the upper part of the park, São Miguel Arcanjo basis evidenced by a black dot. (B) The Santa Virginia nucleus (in dark green) and their both bases (Itamambuca e Vargem Grande) indicated by black dots. In light green we have the current distribution of the Brazilian Atlantic Forest. (Map by: Bruno Borges)

Sampling of small mammals and food resources

The small mammal sampling took place bimonthly throughout one year, totaling six field trips equally distributed in the dry and wet seasons. During each field trip, we trapped five consecutive nights. To optimize our sampling we used both live traps and pitfall traps. Overall, our sampling effort consisted of 3420 trap-nights, being 2700 for live-traps and 720 for pitfall-traps per site. All individuals captured were marked with a numbered ear tag (Ear Tags, National Band and Tag Co., Newport, Kentucky, USA), identified, weighed and measured. We collected hair samples for the stable isotope analysis and then released the animal at the same spot where trapped. See Supplemental material for details of small mammals trapping.

In addition, food resource samples were collected concomitantly to small mammals inside the grids or along the pitfall transects for a stable isotope habitat baseline. In an attempt to identify the maximum resource availability at the trapping sites, we sampled food items that were recorded in previous studies on diet of rodents and marsupials in Atlantic forest (Leite et al 1996, Cáceres 2004, Pinotti et al 2011). We took several plant tissues, animal prey and fungi of which we organized into four categories (invertebrates, fungi, fruits and leaves).

Stable isotope analysis

Prior to the analysis, all food samples were oven-dried at 40ºC to remove traces of water and subsequently cut into fine pieces for analysis. We only used the small mammal species and food items that were sampled sufficiently ($n > 5$).

We estimated trophic niche and diet overlap by analyzing the $\delta^{13}C$ and $\delta^{15}N$ values of small mammals' hair and food resources. The $^{13}C/^{12}C$ ratio informs about the consumers' reliance on primary producers with different photosynthetic pathways (C3 or C4) while the $^{15}N/^{14}N$ ratio is used to define trophic relationships between consumers and its diet (Newsome et al 2007). Nitrogen and carbon isotope concentrations were determined by Continuous Flow Isotope Ratio Mass Spectrometry, using a Thermo Delta Plus mass spectrometer (Bremen, Germany) coupled to a Carlo Erba CHN 1110 elemental analyzer (Milan, Italy). The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios were evaluated and compared to calibrated gas ratios using Pee Dee Belemnite carbonate and atmospheric N_2, respectively according to the formula:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where X refers to ^{13}C or ^{15}N and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of sample and standard, respectively. The results were defined in delta notation (δ) and reported in parts per mil (‰) in relation to international patterns. Precision was estimated by the SD of 44 replicates of an internal standard along the sample analyses as 0.09 and 0.12 ‰ for C and N, respectively. All data were analyzed by technicians from Isotope Ecology Laboratory at Center for Nuclear Energy in Agriculture (CNEA).

Data analysis

Prior to any analysis, we checked if isotopic signatures of food sources were different among the areas (Figure 1S). As we found a similar isotopic baseline for all categories we performed statistical analysis without discriminating the areas. We also checked our data for normality and homoscedasticity through Shapiro Wilk's and Bartlett tests, respectively. As our dataset were not normally distributed nor presented homogeneity of variances, we performed a non-parametric Kruskal-Wallis test to examine significance of differences between species relative to isotopes**.** We also did a post-hoc test (Mann-Whitney pairwise comparison) to identify which species were statistically different for each isotope.

In order to verify trophic relationships among species we analyzed the isotopic data in $\delta^{13}C$ - $\delta^{15}N$ bi-plots as proposed by Layman et al. (2007). We delimited the isotopic space covered by rodents, marsupials and food items to evaluate diet overlap. We also used mean values and standard deviations of each species, as well as the range of $\delta^{13}C$ and $\delta^{15}N$ values to characterize the small mammal community. The range was measured by the distance between the minimum and maximum values of each isotope. The total range of $\delta^{13}C$ may indicate the variety of carbon sources used by the animals while of $\delta^{15}N$ may inform the trophic position within a food web. The small mammal species were categorized by their carbon source use as C3 or C4 plant consumers. They were also classified by nitrogen levels as frugivore-granivores or insectivores based on the relative dominance of fruits and invertebrates in the diet, or as omnivores if diets included significant quantities of both fruits and insects, and/or other diet sources. To check if body mass and isotopes are related and could facilitate the coexistence of species, we did a linear regression with ^{13}C and ^{15}N isotopic signatures of species and its body

mass.

All the analysis were done using the statistical environment R, version 2.15.2 (R Development Core Team 2009) and the program PAST, version 2.17 (Hammer et al 2001).

RESULTS

Of the 25 species registered, we performed stable isotope analyses using hair samples from 20 species (12 rodents and eight marsupials). Altogether we analyzed 408 samples comprised of 147 of food sources and 261 hairs of small mammals' (57 from marsupials and 204 from rodents) (Tables 1, 1S). But of these 20 species, eight had less than six individuals sampled. Therefore we analyzed only data from 12 species, being seven rodents and five marsupials.

Small mammal species showed a broad range of isotopic signatures (Table 1). The total $\delta^{13}C$ range of species in the small mammal community was 19.6, varying from - 8.7 to - 28.3 ‰ which indicates that in the community there are species relying on C3 and C4 plants. For $\delta^{15}N$, the total extent was 8.1 (minimum of 3.4 to 11.6 ‰), which indicates that species may be distributed in three trophic levels. Rodents had a broad isotopic niche while marsupials had a narrow one**.**

We analyzed four categories of food items (fruits, fungi, invertebrates and leaves) and observed differences among them for both isotopes ($H(\chi^2)=64.005$, $p=0.001$ to $\delta^{15}N$; $H(\chi^2)=54.167$, $p=0.001$ to $\delta^{13}C$). Invertebrates and fungi were more enriched and had similar $\delta^{15}N$ median values, whereas fruits and leaves were depleted in this isotope (Figure 2S). All food items were depleted in $\delta^{13}C$, with leaves showing the widest variation (Table 2S, Figure 2S).

Marsupials – The combined results from the marsupial species presented a slight variation in $\delta^{13}C$ (-25.48 to -22.77 ‰) and also in $\delta^{15}N$ (6.47 to 10.79 ‰) values (Table 1). The species were depleted in ^{13}C-isotope suggesting the carbon comes mostly from C3 plants. They all presented high and similar $\delta^{15}N$ values ($H(\chi^2)=1.269$, $p=0.866$) which is evidence for a diet rich in insects. Our results also show that marsupials fed mostly on invertebrates and/or fungi (Figure 2). Results from post-hoc Mann Whitney pairwise comparisons showed significant differences in $\delta^{13}C$ among some species, with *Metachirus nudicaudatus* and *Philander frenatus*

having higher median values (Figure 3S-B). For $\delta^{15}N$, there was no significant difference between species (Figure 3S-A). We also found a strong overlap between marsupials and some rodents, as *Thaptomys nigrita* and *Akodon montensis* (Figure 2).

Body mass had no correlation with none of the isotopes (R^2=0.03, p=0.18 for $\delta^{13}C$ and R^2=0.01, p=0.40 for $\delta^{15}N$), except for a marginally positive correlation in *M. nudicaudatus* (R^2=0.55, p=0.05) in which heavier individuals had higher $\delta^{13}C$ values (Table 3S, Figure 3). In general marsupials present a wide variation in body mass, with *Didelphis aurita* (1078 g) and *Monodelphis scalops* (36 g) being the heaviest and lightest species respectively (Table 1S).

Rodents – The combined results did not show a similar pattern for any isotope ($H(\chi^2)$ = 114.08, p<0.001 for $\delta^{15}N$; $H(\chi^2)$ =100.01, p<0.001 for $\delta^{13}C$) since each species behave differently (Figure 4S). *Brucepattersonius soricinus* had the highest value of $\delta^{15}N$, and was classified as insectivore, whereas *Euryoryzomys russatus* and *Trinomys iheringi* were mostly frugivorous-granivorous rodents. The species *A. montensis* and *T. nigrita* showed intermediate values of ^{15}N-isotope and were classified as omnivorous together with *Necromys lasiurus* and *Oligoryzomys nigripes* (Figure 4S-A). However these latter two rodents used a distinct primary carbon source, markedly from C4 plants. According to median $\delta^{13}C$ values, we can categorize the rodent community into three groups: C3 plant consumers, C4 plant consumers and mixed feeders (Figure 4S-B). Post hoc analysis showed significant differences both in $\delta^{13}C$ and $\delta^{15}N$ among most species, although not between every species pair. In relation to $\delta^{13}C$, *O. nigripes* and *N. lasiurus* were statistically different from the other five species. And for $\delta^{15}N$, *B. soricinus* was the only species statistically distinct from all others.

The small rodents consumed all food items although with some specificities. The frugivorous-granivorous species (*E. russatus* and *T. iheringi*) fed mostly on fruits while insectivores (*B. soricinus*) and omnivores consumed mostly invertebrates and/or fungi. For *N. lasiurus* and *O. nigripes* we were unable to sample food items with similar isotopic signature (Figure 2).

We found a correlation between body mass and both isotopes for rodents (R^2=0.13, p< 0.001 for $\delta^{13}C$ and R^2=0.36, p<0.001 for $\delta^{15}N$) particularly for some species. Body mass was

positively correlated to $\delta^{13}C$ for *T. iheringi* (R^2=0.12, p=0.021) and negatively correlated to $\delta^{15}N$ for *E. russatus* (R^2=0.28, p<0.001) and *T. nigrita* (R^2=0.27, p< 0.001) (Table 3S). For *E. russatus* and *T. iheringi*, both granivorous and C3 plant consumers, differences in body mass could facilitate species coexistence. In contrast, for *O. nigripes* and *N. lasiurus* the hypothesis was rejected due to the body size similarity.

Table 1. Mean and standard deviations (inside parenthesis) of $\delta^{13}C$ (‰ PDB) and $\delta^{15}N$ (‰ Air) values from hair samples collected of 20 small mammal species in the Atlantic rainforests. The isotopic data were defined in delta notation (δ) and reported in parts per mil (‰) of international standards.

	Mean and SD values of $\delta^{13}C$ and $\delta^{15}N$ (‰)									
	ITA			**VG**			**Carlos Botelho**			
	Mean$\delta^{13}C$	Mean$\delta^{15}N$	n	Mean$\delta^{13}C$	Mean$\delta^{15}N$	n	Mean$\delta^{13}C$	Mean$\delta^{15}N$	n	n total
Order/Family/Species										
Didelphimorphia										
Didelphidae										
Didelphis aurita	-24.99	9.66	1	-24.63 (±0.81)	6.79 (±0.45)	3	-23.51 (±0.45)	8.38 (±1.28)	2	6
Gracilinanus microtarsus	-	-	-	-	-	-	-25.16 (±0.39)	5.58 (±0.46)	2	2
Marmosops incanus	-24.82 (±0.37)	9.59 (±1.13)	3	-24.35 (±0.91)	8.11 (±0.97)	8	-24.83 (±0.30)	7.87 (±0.84)	4	15
Metachirus nudicaudatus	-	-	-	-	-	-	-23.95 (±0.48)	8.35 (±0.62)	7	7
Monodelphis americana	-	-	-	-	-	-	-24.67	7.97	1	1
Monodelphis iheringi	-24.34 (±0.51)	9.48 (±0.36)	2	-	-	-	-	-	-	2
Monodelphis scalops	-	-	-	-	-	-	-24.68 (±0.29)	8.01 (±0.91)	6	6
Philander frenatus	-25.15 (±0.47)	8.02 (±0.44)	2	-	-	-	-23.73 (±0.37)	8.25 (±0.68)	21	23
Rodentia										
Cricetidae										

Akodon cursor	-	-	-	-	-	-	-24.1 (±1.02)	8.4 (±1.78)	5	5
Akodon montensis	-24.89 (±0.66)	8.43 (±0.89)	6	-24.77 (±2.09)	6.54 (±0.33)	5	-17.42 (±6.42)	7.91 (±1.77)	7	18
Blarinomys breviceps	-	-	-	-23.690	10.07	1	-	-	-	1
Brucepattersonius soricinus	-23.48 (±0.15)	9.87 (±0.29)	3	-23.25 (±0.30)	10.62 (±0.69)	3	-17.85 (±7.13)	9.50 (±1.94)	2	8
Delomys sublineatus	-	-	-	-	-	-	-25.53 (±1.17)	5.17 (±1.33)	4	4
Euryoryzomys russatus	-24.87 (±0.69)	6.24 (±0.64)	3	-25.16 (±1.0)	5.38 (±0.91)	21	-25.34 (±0.87)	5.89 (±1.04)	56	80
Juliomys pictipes	-	-	-	-	-	-	-25.42 (±1.1)	7.74 (±1.94)	4	4
Necromys lasiurus	-	-	-	-	-	-	-11.76 (±1.65)	6.76 (±1.60)	6	6
Oligoryzomys nigripes	-14.87 (±3.57)	6.75 (±0.47)	3	-14.14 (±2.71)	6.18 (±1.08)	3	-10.35 (±1.01)	6.76 (±3.19)	5	11
Sooretamys angouya	-25.32 (±0.1)	3.07 (±0.77)	3	-	-	-	-	-	-	3
Thaptomys nigrita	-24.06 (±0.84)	7.80 (±0.91)	11	-24.71 (±0.48)	8.59 (±0.96)	10	-23.55 (±0.88)	7.40 (±0.52)	16	37
Echimyidae										
Trinomys iheringi	-24.44 (±0.71)	4.84 (±1.13)	7	-26.60	5.15	1	-25.72 (±0.91)	4.97 (±0.83)	36	44

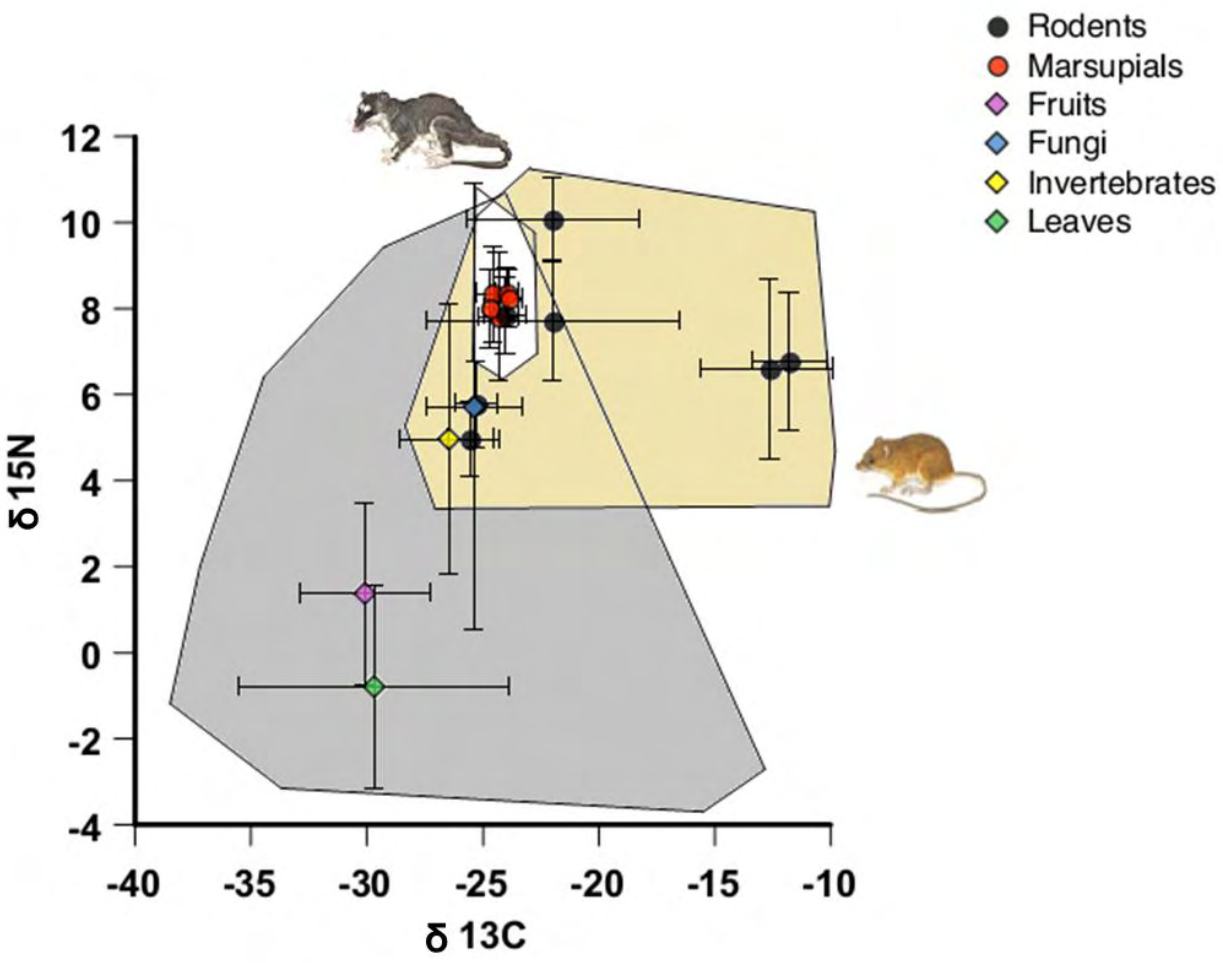

Figure 2. Mean and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ values from hair samples of rodents (black dots), marsupials (red dots) and each type of food resource. The delimited areas represent the isotopic space of all food sources (in gray) and small mammals (marsupials – white; rodents – cream colors.

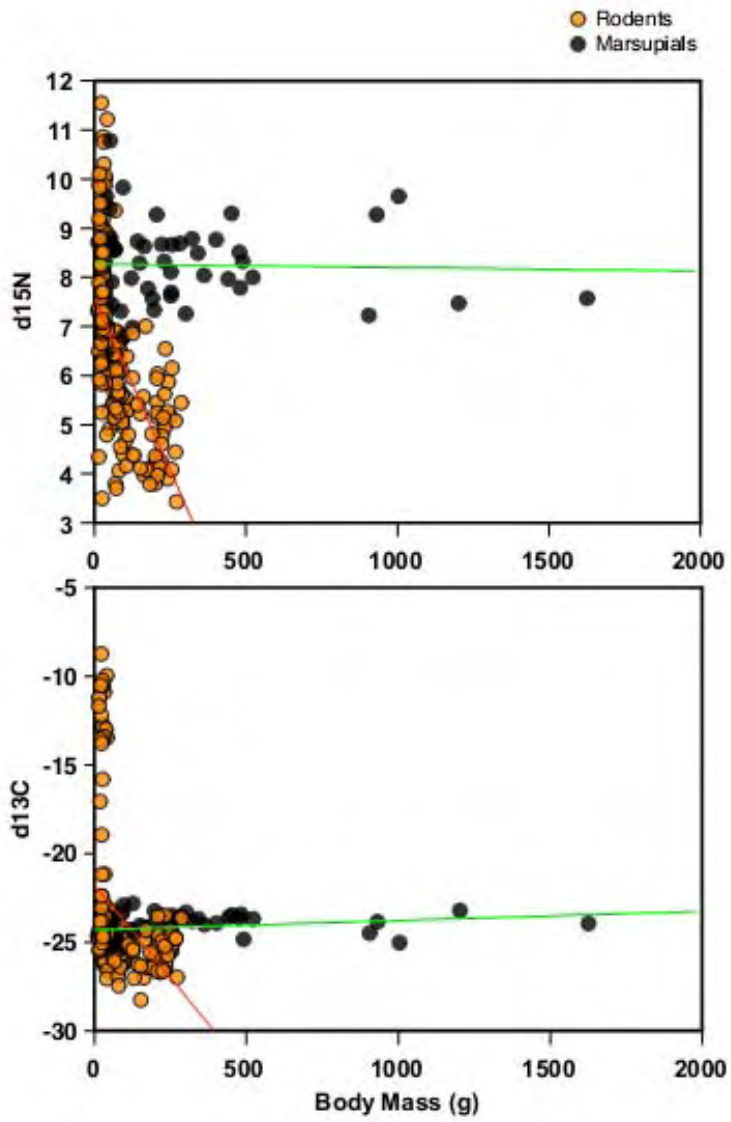

Figure 3. Linear regression between individual values of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) and their body mass (g) for marsupials (black color) and rodents (orange color) collected at the Atlantic rainforests.

DISCUSSION

The use of carbon and nitrogen stable isotope ratios from hair samples revealed distinct diet patterns among small mammal species that inhabit the largest remnant of continuous Atlantic forest in Brazil. For marsupials, we found that ecological segregation is determined neither by species' trophic niches nor by body size, rather is likely due to differences in vertical habitat use (Vieira and Monteiro-Filho 2003). On the other hand, for rodents, the diet together with body size was sufficient to elucidate the high number of coexisting species once the community was organized into different guilds. In a similar way, Hyodo et al. (2011) studying the structure of a food web in a Malaysian rain forest obtained clear differentiation in both $\delta^{13}C$ and $\delta^{15}N$ for birds and volant and non-volant mammal species.

Assuming an enrichment of 3 ‰ per trophic level (Vanderklift and Ponsard 2003) we demonstrated a strong correlation between $\delta^{15}N$ values and consumers' trophic position. Overall, the small mammal community studied comprises up to three trophic levels with insectivorous and omnivorous species being more enriched in ^{15}N-isotope than frugivorous-granivorous ones. A recent study conducted in a montane forest in Madagascar also reported a small mammal community structured in three trophic levels with insectivorous Tenrecidae presenting higher $\delta^{15}N$ values than the omnivorous Tenrecidae and rodents (Dammhahn et al 2013).

In our community all marsupials were concentrated at a high position on the food chain relying mostly on invertebrates as a food source, probably fungi, and fruit. In general the didelphid marsupials are known to be omnivorous (Cáceres 2004, Casella and Cáceres 2006) with a diet composed of invertebrates, fruits, small vertebrates, and occasionally flowers, fungi, nectar, gum trees and carrion (Santori et al 1995, 1997, Vieira and Astúa de Moraes 2003, Aléssio et al 2005). It was suggested that small didelphid marsupials have insectivory tendencies while the larger didelphids tend to be frugivores-omnivores (Santori et al 1995). Our findings were consistent with these marsupials' dietary habits with an exception of the low fruit consumption. All but one species analyzed in this study were classified as insectivore-omnivores; *Didelphis aurita* is considered a frugivore-omnivore (Paglia et al 2012). However it had previously been classified as insectivore-omnivore due to a diet consisting primarily of insects, with fruits being consumed only during the wet season (Cáceres and Monteiro-Filho 2001).

Differential fractionation of stable carbon isotopes during photosynthesis causes C3 and C4 plants to have distinct carbon-isotope signatures (Bender 1971, Kelly 1999). Carbon fixed by terrestrial C3 plants end up with average $\delta^{13}C$ values of -27 ‰ (ranging from -35 ‰ to -21 ‰) in tropical forests, while C4 plants average -12 ‰ (varying from -14 ‰ to -10 ‰) in open areas (Boutton 1991, Ehleringer 1991). Marsupials markedly consume C3 plants thus presenting low $\delta^{13}C$ values. Given that the carbon isotope may also indicates habitat use (Ambrose and DeNiro 1986, Cerling et al 2005), these low values show that all marsupials are forest restricted.

Diet was not a good parameter to explain coexistence among marsupials since all species share the same trophic niche probably sharing similar food. Body size differences between species in the same guild may be an important component in resource partitioning. In our study scale, the species *D. aurita* was separated from the others marsupials by body size (mean body weight of about 1.078 g). However, the others two pairs of species (*M. nudicaudatus* x *P. frenatus* and *Marmosops incanus* x *Monodelphis scalops*) had similar body sizes and trophic niches, suggesting possible inter-specific competition. But according niche-complementarity hypothesis, two or more species are able to coexist when their niches present large overlap in one dimension but are substantially distinct in others (Schoener 1974), for example in use of space. The species *M. nudicaudatus* and *M. scalops* are exclusively terrestrial (Vieira and Monteiro-Filho 2003, Paglia et al 2012) while *M. incanus* and *P. frenatus* have scansorial habits (Cunha and Vieira 2002). These differences in vertical habitat use among pairs of species with similar body size and from the same guild may be important in promoting species coexistence in these communities. This pattern has been already observed in a study on mammal species in French Guiana (Charles-Dominique et al 1981) where species with similar diet and body size used different forest layers.

In contrast, rodents were more plastic in their use of resources showing a broad trophic niche with species distributed in three trophic levels and using distinct carbon primary sources. The first trophic level of our community comprises two terrestrial frugivore-granivore species which differ notably in body mass; *Euryoryzomys russatus* with an average body mass of 72 g and *Trinomys iheringi* of 204 g. Species of strikingly-different body sizes are able to explore and select preys of varied sizes and types, as already demonstrated for birds (Hespenheide 1975). *Brucepattersonius soricinus* occupy the third trophic level of the community. This species is more enriched in ^{15}N than marsupials and can be considered an insectivore specialist. Pinotti et al.

(2011) found that the stomach contents of *B. soricinus* included primarily arthropods. Using stable isotope analysis of hair samples from this species, our results were consistent with previous findings (Pinotti et al 2011).

At the second trophic level there are four rodent species, all classified as omnivores but divided into two pairs of species due to differential consumption of ^{13}C-isotope. Two species are extremely enriched in ^{13}C (*N. lasiurus* and *O. nigripes*), whereas the others are ^{13}C depleted *(A. montensis* and *T. nigrita*). The latter pair of species share ecological characteristics regarding diet and vertical use of space (Pinotti et al 2011, Finotti et al 2012, Paglia et al 2012), have similar body size, but differ in their period of activity. The activity period is an important dimension in resource partitioning among sympatric species mainly if they overlap in other niche axis and occur in high abundance within a community (Graipel et al 2003). *Thaptomys nigrita* has diurnal habits (Davis 1947), while *A. montensis* has peaks of activity during the twilight (Graipel et al 2003).

The occurrence of *N. lasiurus* at PECB (Brocardo et al 2012) was unexpected because this species is commonly found in open areas and grasslands in Cerrado or among Atlantic forest fragments (Bonvicino et al 2008, Pires et al 2010), occurring mainly in microhabitats with elevated grass height and fruit availability (Vieira et al 2005). *Necromys lasiurus* and *Oligoryzomys nigripes* are considered omnivorous rodents, with plant matter as the main food resource for *O. nigripes* (Pinotti et al 2011), fruits for *N. lasiurus* (Vieira et al 2005) and insects presents in low proportions for both (Oliveira and Bonvicino 2011). Hence they are omnivores that incorporate a greater amount of fruits to the diet. Our results revealed trophic niche overlap between them but through niche complementarity they are able to coexist due to differences in body mass, period of activity (Vieira and Baumgarten 1995, Graipel et al 2003) and vertical use of space (Bueno 2003, Vieira et al 2005).

Both species are separated from the rest of the small mammal community due to the high $\delta^{13}C$ values that are characteristic of C4 plants typically found in open areas and grasslands (Ehleringer 1991). However, our study sites are within the largest remnant of continuous Atlantic rainforest (Ribeiro et al 2009), thus we did not expect to find these isotopic signals in both species. Godman et al. (2000) suggested that species often found foraging in forest edges can have elevated $\delta^{13}C$ values. However, there were no forest edges near our capture stations,

furthermore these species are not capable of moving long distances in the Atlantic forest (Pires et al 2002, 2010, Püttker et al 2006). We therefore believe that these species may be feeding on invertebrates that consume mostly C4 plants found inside or near clearings or feeding directly on C4 plants, in the form of fruits. To confirm this it is necessary to collect more food resources, identify them and map the distribution of plants of different photosynthetic pathways in the areas because our food sources pool may not represent all food items available there for the animals.

Body size had no correlation with any of the isotopes for marsupials, except for a slightly positive correlation in $\delta^{13}C$ values of *M. nudicaudatus* which indicates that individuals with higher body mass are consuming food items more enriched in ^{13}C. This pattern was also observed for the rodent *Trinomys iheringi*. This enrichment can be explained by the canopy effect (Medina and Minchin 1980) that states that the $\delta^{13}C$ values of leaves and fruits in the canopy are higher than those in the gaps/clearings and understory. As both species are exclusively terrestrial (Vieira and Monteiro-Filho 2003), eat fruits and were captured in high abundances in Carlos Botelho State Park, more specifically at the grids localized under primates routes, we believe they are consuming food from the top of canopy in the form of fallen fruits. This was also observed in Ituri Forest, where six duiker species (*Cephalophus* spp.) that inhabit the subcanopy also had higher $\delta^{13}C$ values with most of their diet derived from fallen canopy fruits (Cerling et al 2004).

Identifying the mechanisms that are crucial to determine the structure and composition of a community is the first step to understanding interspecific relations in an assemblage. The factors that promote or facilitate species coexistence for tropical forest-dwelling species are poorly known, especially among rodents and marsupials, the most diverse ecological group in the Atlantic rainforest (Pardini and Umetsu 2006). We realized that species coexistence is a complex phenomenon and one sole characteristic (diet or body size) is not sufficient to explain the high number of species living in the same area. Stable isotopes analyses allow us to identify the food resources that species incorporate during their lifetime (Ambrose and DeNiro 1986) and elucidate several ecological attributes of cryptic nocturnal species. We hope that our results, which were obtained in continuous areas, will be valuable as a baseline in future studies on species coexistence within small mammal communities in fragmented or defaunated forests.

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SUPPLEMENTAL MATERIAL

Appendix I. Details on the small mammals sampling protocol.

In each area we set up three grids with live-traps and six transects of pitfalls. Each grid covered an area of 0.6 ha and had live-traps of two types and four sizes, Sherman (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) and Tomahawk (45 x 16 x 16 cm). In each grid, there were 24 capture stations. Each station had one Sherman trap (a small, a medium or a large, randomly chosen). Furthermore, six stations also had a Tomahawk trap. In total, there were 90 live-traps (30 traps per grid). Every two pitfall-trap transects were placed parallel to each other and 30-m apart from each other. Each line had four plastic buckets (60 liters, with 40 cm of top diameter, 35 cm of bottom diameter, and 56-cm deep), buried with the rim at the ground level. In each line, buckets were buried every 10 m and connected to each other with 0.5-m tall drift fence that extended an additional 10 m at each end, totaling 50 m of fence. In total, we used 24 buckets. To minimize pseudo-replication at the grid level we spaced all grids and transects in each site at least 100 m from each other based on distances moved per night by Atlantic Forest small mammals (Mendel and Vieira 2003, Püttker et al 2006).

We baited all traps including pitfall-traps with a mixture of bacon, corn meal, peanut butter and mashed bananas, checked them each morning and rebaited if necessary. We used bait in buckets in order to minimize starvation of the animals caught, which could spend more than 12 hours inside the buckets before released. Furthermore we used igloos of styrofoam in the buckets so the animals could use it as shelter against rain and cold weather. All individuals captured at first time were marked with a numbered ear tag (Ear Tags, National Band and Tag Co, Newport, Kentucky, USA). Every individual was identified, weighted and had its biometric data measured. In case of identification's uncertainty, the animal was collected and carried to Instituto Butantã for cytogenetic analysis. The animals were deposited as reference material in vertebrate scientific collection of Laboratório de Mastozoologia e Biogeografia, Universidade Federal do Espírito Santo, ES, Brazil.

Table 1S. Mean body mass (g), species richness, abundance and trophic categories of the 25 small mammal species (nine marsupials and 16 rodents) identified in each of the Atlantic forest areas.

Order/Family/Species	Mean body mass (g)	Abundance (Nº indiv. captured)				Trophic categorie*
		ITA	VG	CB	n	
Didelphimorphia						
Didelphidae						
Didelphis aurita	1079	3	6	2	11	Omnivore
Gracilinanus microtarsus	18			2	2	Insectivore
Marmosops incanus	51	13	18	4	35	Insectivore
Metachirus nudicaudatus	320			7	7	Insectivore
Monodelphis sp. n.	21	4	1		5	Insectivore
Monodelphis americana	10			1	1	Insectivore
Monodelphis iheringi	20	13	17		30	Insectivore
Monodelphis scalops	36	2	6	7	15	Insectivore
Philander frenatus	247	8	1	21	30	Insectivore
Rodentia						
Cricetidae						
Akodon cursor	32			5	5	Insectivore
Akodon montensis	29	23	67	7	97	Insectivore
Blarinomys breviceps	23	1	5		6	Insectivore
Brucepattersonius soricinus	32	7	10	2	19	Insectivore
Calomys tener	10		1		1	Granivore
Delomys sublineatus	54			4	4	Granivore
Euryoryzomys russatus	72	86	84	60	230	Granivore
Juliomys pictipes	13	10	2	4	16	Frugivore
Oecomys catherinae	54	2			2	Frugivore
Oligoryzomys nigripes	18	21	42	5	68	Frugivore
Necromys lasiurus	31			6	6	Frugivore
Nectomys squamipes	196	1			1	Omnivore
Rhipidomys mastacalis	51	1			1	Granivore
Sooretamys angouya	138	4			4	Granivore
Thaptomys nigrita	23	45	106	16	167	Insectivore
Echimyidae						
Trinomys iheringi	204	9	1	37	47	Granivore
TOTAL		253	367	190	810	

***** From Vieira and Baumgarten 1995, Cáceres 2004, Reis et al 2011 and Paglia et al 2012

Table 2S. Mean and standard deviation (in parenthesis) of $\delta^{13}C$ and $\delta^{15}N$ values from each of four categories of food sources collected at the Atlantic forests. The isotopic data were defined in delta notation (δ) and reported in parts per mil (‰).

	Mean and SD of $\delta^{13}C$ and $\delta^{15}N$ values (‰)								
	ITA			**VG**			**Carlos Botelho**		
	Mean$\delta^{13}C$	Mean$\delta^{15}N$	n	Mean$\delta^{13}C$	Mean$\delta^{15}N$	n	Mean$\delta^{13}C$	Mean$\delta^{15}N$	n
Food sources									
Invertebrates	-27.20 (± 2.27)	6.08 (± 1.7)	31	-29.43 (± 3.75)	7.64 (± 3.54)	4	-26.72 (± 1.76)	5.19 (± 2.69)	11
Fungi	-25.38 (± 1.55)	7.93 (± 3.58)	3	-24.49 (± 1.51)	6.37 (± 4.47)	11	-25.87 (± 2.27)	4.97 (± 5.80)	19
Fruit	-27.39 (± 0.46)	2.56 (± 0.38)	3	-30.97 (± 2.81)	0.65 (± 2.33)	15	-29.62 (± 2.79)	1.93 (± 1.83)	12
Leaves	-34.71 (± 2.11)	1.12 (± 0.75)	3	-28.89 (± 6.28)	-0.53 (± 2.27)	21	-29.78 (± 5.33)	-1.70 (± 2.43)	13

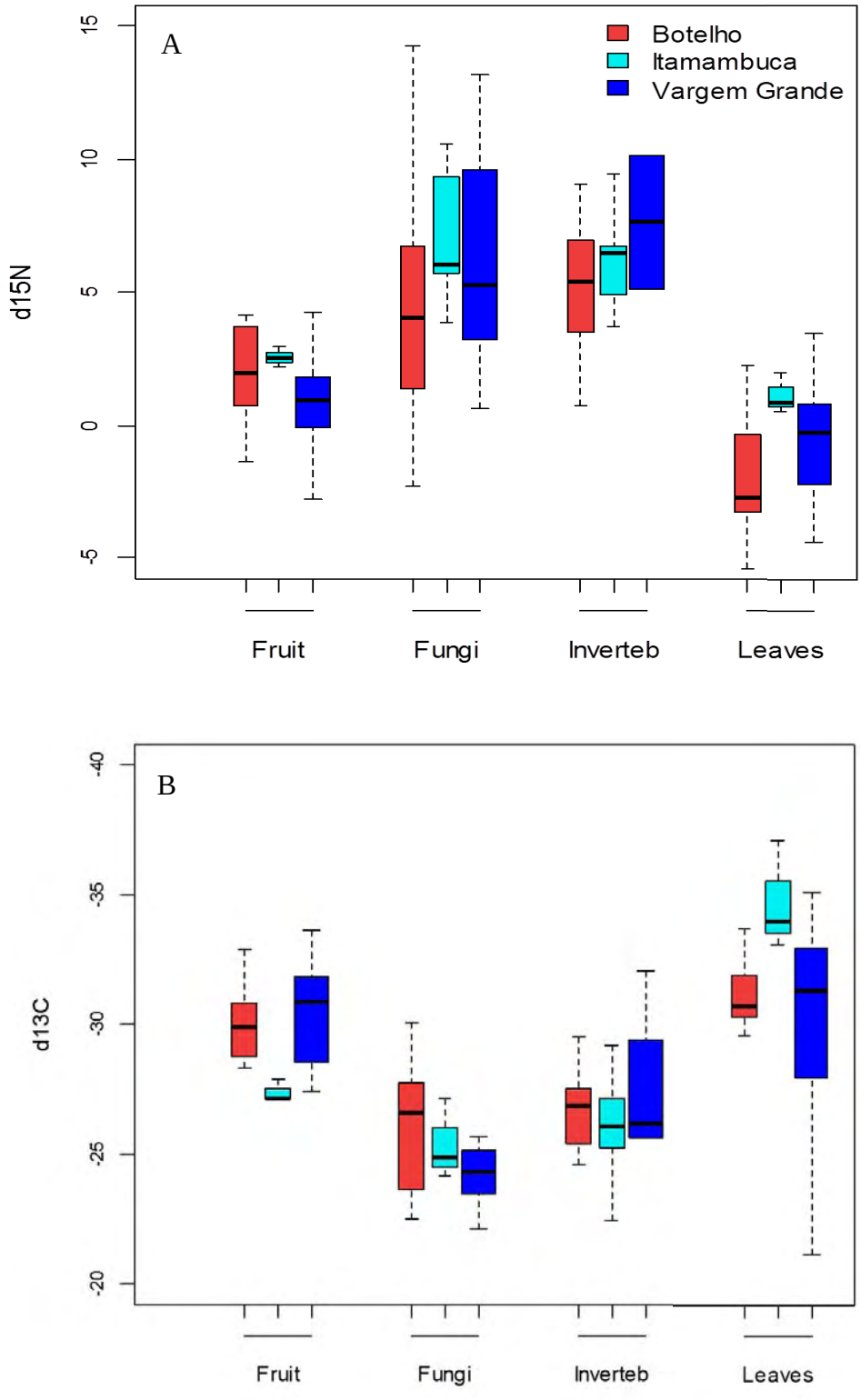

Figure 1S. Box-plot showing median and quartis of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values of food sources sampled in the Atlantic forests. The colors refer to each area.

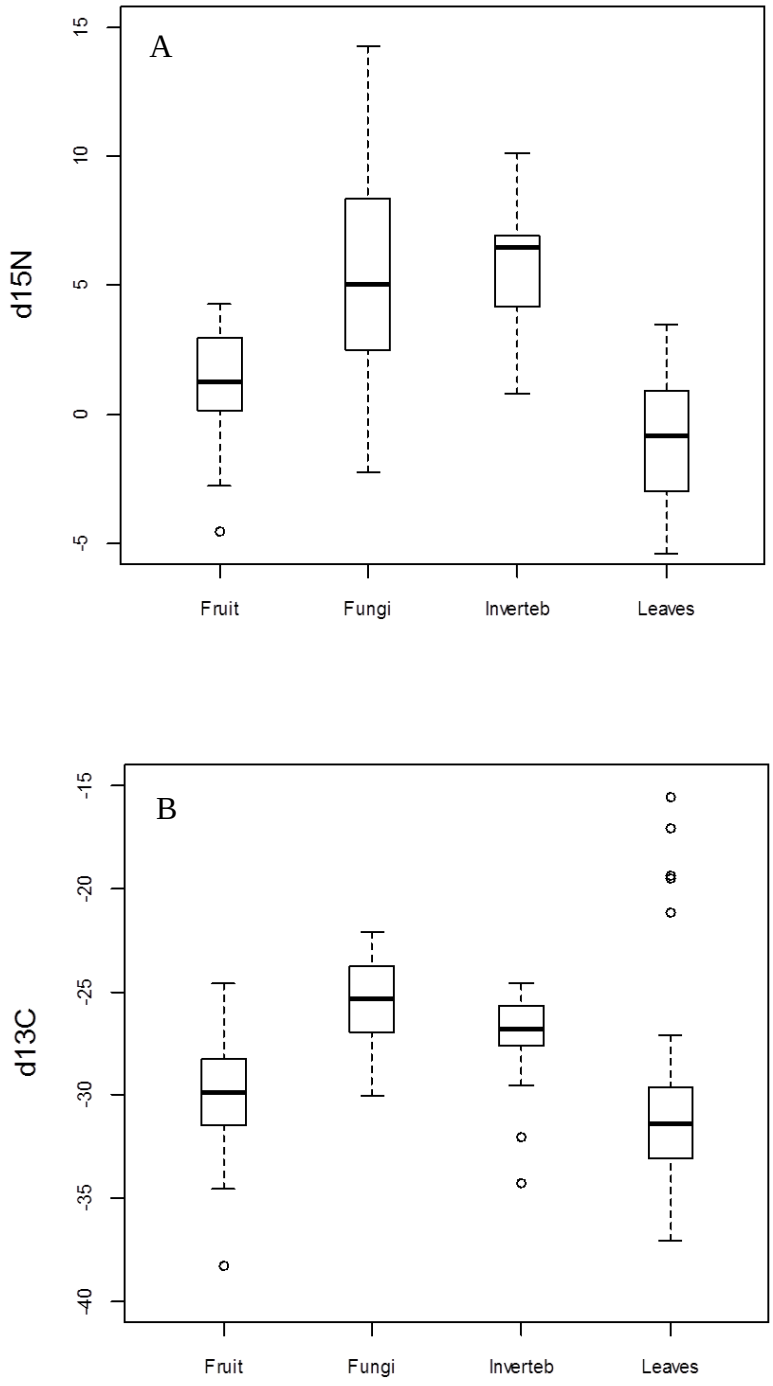

Figure 2S. Median values of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) of each category of food sources collected at the Atlantic rainforests. The word "Inverteb" refers to invertebrates.

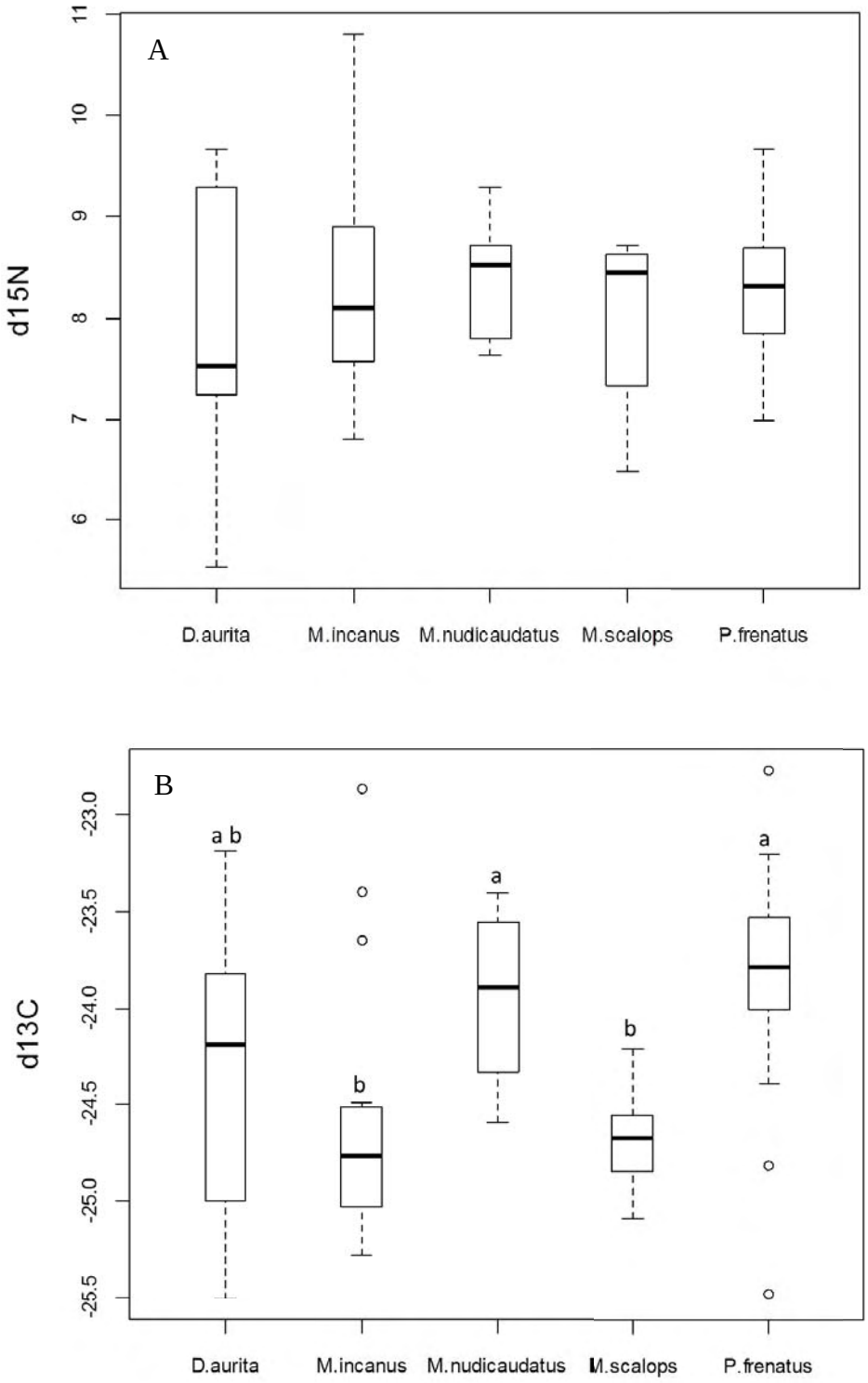

Figure 3S. Median values of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) from hair samples of five marsupial species collected at the Atlantic rainforests. Mann Whitney's pairwise comparison post-hoc groups membership are indicated by a and b.

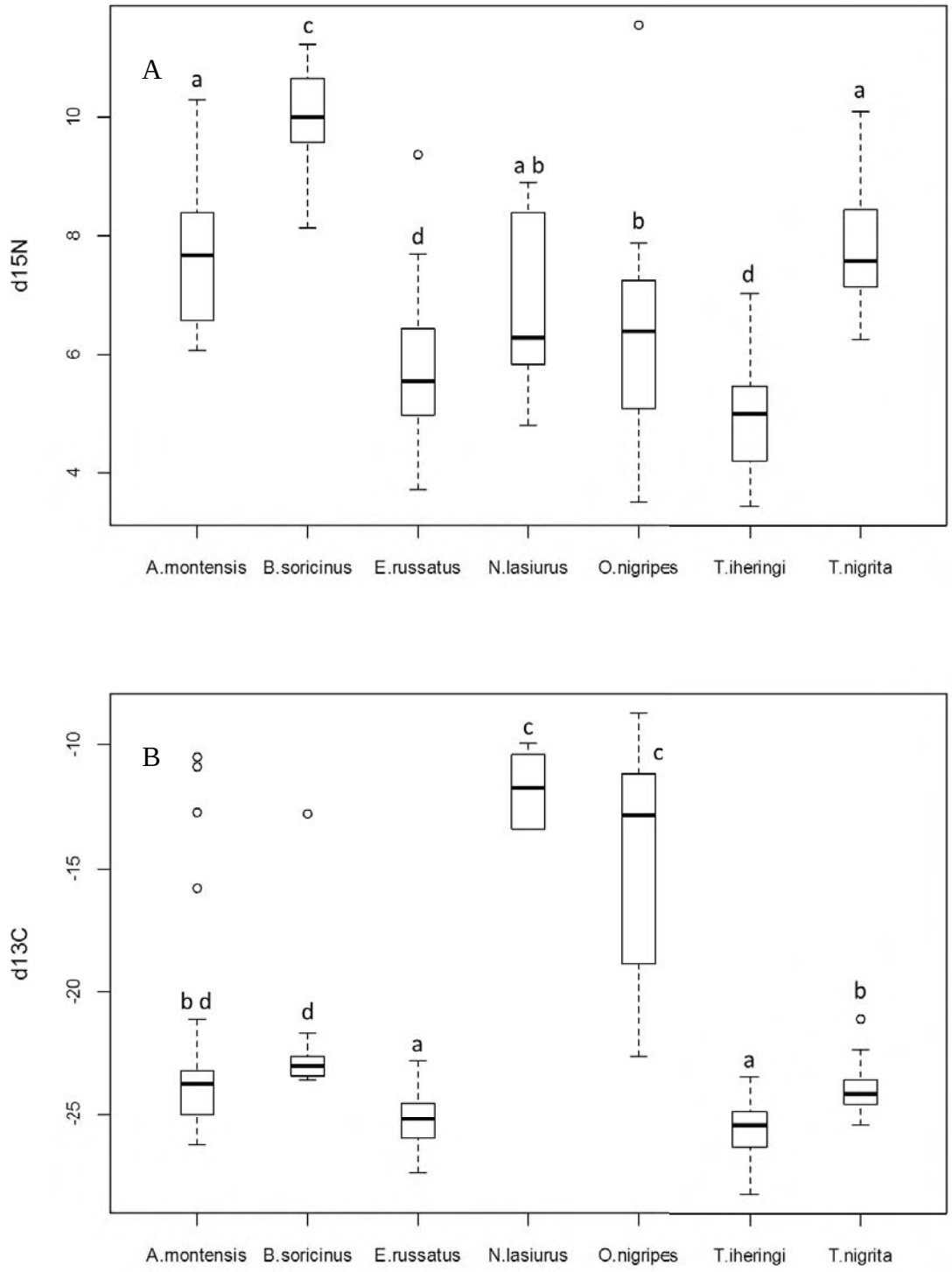

Figure 4S. Median values of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) from hair samples of seven rodent species collected at the Atlantic rainforests. Mann Whitney's pairwise comparison post-hoc groups membership are indicated by a, b, c and d.

Table 3S. Linear regression results (R^2 and p-values) between isotopes (^{15}N and ^{13}C) and body mass of the 12 small mammal species (five marsupials and seven rodents) in the Atlantic rainforest.

	Regression results (body mass X isotopes)				
Order/Family/Species	R^2	$\delta^{15}N$ (p-value)	R^2	$\delta^{13}C$ (p-value)	n
Didelphimorphia					
Didelphidae					
Didelphis aurita	0.00	NS	0.28	NS	6
Marmosops incanus	0.00	NS	0.22	NS	15
Metachirus nudicaudatus	0.00	NS	0.56	0.05*	7
Monodelphis scalops	0.07	NS	0.03	NS	6
Philander frenatus	0.00	NS	0.00	NS	23
Rodentia					
Cricetidae					
Akodon montensis	0.21	NS	0.01	NS	18
Brucepattersonius soricinus	0.33	NS	0.39	NS	8
Euryoryzomys russatus	0.28	<0.0001**	0.00	NS	80
Oligoryzomys nigripes	0.00	NS	0.01	NS	11
Necromys lasiurus	0.01	NS	0.19	NS	6
Thaptomys nigrita	0.27	0.0009**	0.04	NS	37
Echimyidae					
Trinomys iheringi	0.01	NS	0.12	0.02*	44

* Positive correlations

** Negative correlations