Community Ecology 12(1): 58-66, 2011
1585-8553/$20.00 © Akadémiai Kiadó, Budapest
DOI: 10.1556/ComEc.12.2011.1.8

Small-mammal community structure in a South American deciduous Atlantic Forest

G. L. Melo[1*], J. Sponchiado[2], A. F. Machado[3] and N. C. Cáceres[4]

[1] *Programa de Pós-Graduação em Ecologia e Conservação, CCBS, Universidade Federal do Mato Grosso do Sul, Cx.P. 549, Campo Grande, MS, 79.070-900, Brazil. E-mail: geruzalm@yahoo.com.br*
[2] *Programa de Pós-Graduação em Biodiversidade Animal, CCNE, Universidade Federal de Santa Maria, Camobi, Santa Maria, RS, 97.110-970, Brazil. E-mail: jsponchiado@yahoo.com.br*
[3, 4] *Laboratório de Ecologia e Biogeografia, Departamento de Biologia, Universidade Federal de Santa Maria, Camobi, Santa Maria, RS, 97.110-970, Brazil. E-mail: [3] ariellifm@hotmail.com, [4] niltoncaceres@gmail.com*

Keywords: Environmental complexity, Habitat selection, Heterogeneity, Species diversity, Vertical stratification.

Abstract. We investigated how the small-mammal community is structured in a deciduous forest in southern Brazil, analysing the patterns of vertical and horizontal distribution. We used 12 transect lines, with 180 live-traps distributed on the ground and in the understory, and 12 pitfall traps in total. During six field sessions, we captured 510 individuals belonging to 12 small-mammal species. The combination of different methods of capture resulted in a relative high species richness for the area, although the presence of additional species cannot be ruled out. The forest complexity plays an important role allowing the coexistence of cursorial, scansorial and some arboreal species in this community. The structural variables, liana and bamboo, were the most important ones for species richness. However, the dominant species, *Akodon montensis* was associated to sites with dense vegetation at ground level such as ferns, bamboos, and shrubs.

Abbreviation: PET–Parque Estadual do Turvo.

Nomenclature: Wilson and Reeder (2005), with the addition of Weksler et al. (2006)

Introduction

Neotropical forests have a wide diversity of small mammals, and some areas of the Atlantic Forest in Brazil may harbor more than 20 species of rodents and marsupials (Vieira and Monteiro-Filho 2003, Pardini and Umetsu 2006). The complexity, referring to the vertical strata development in forest, and the heterogeneity, referring to horizontal variations in the landscape (sensu August 1983), influence the coexistence of species with similar morphological characteristics and life habits. This differentiation in habitat use allows the spatial segregation of species, and reduces interspecific competition for overlapping niches (Dickman and Woodside 1983, Eccard and Ylölen 2003). Some studies have found a higher small-mammal species richness related with an increased complexity rather than with an increased heterogeneity of habitat (Gentile and Fernandez 1999, Grelle 2003, Lambert et al. 2005), suggesting the need for additional studies to better understand the relationship of these variables and species diversity. Studies with a three-dimensional coverage area (complexity and heterogeneity simultaneously) allow us to analyze better how these factors affect mammal communities.

In addition to differences in the use of vertical and horizontal space, small-mammal species can also use different microhabitats at a smaller scale. Locations that differ structurally can harbour important resources for certain species, and small mammals use some microhabitats more often than others, suggesting that these sites differ in quality (Simonetti 1989). Sites with greater availability of food or shelter are examples. Studies on small mammals in many regions of the world have considered microhabitat use crucial in niche segregation (Dueser and Shugart 1978, Yahner 1982, Seagle 1985, Fa et al. 1992, Brannon 2000). The genus *Akodon* present in South America, for example, has shown preferences for dense vegetation cover in Atlantic deciduous forest in Brazil (*Akodon montensis*; Lima et al., 2010); for freshwater marshes in Argentina (*Akodon azarae*; Bonaventura et al. 2003); and for temperate forest in Chile (*Akodon olivaceus*; Múrua and Gonzalez, 1982). There are many other examples in the literature demonstrating the importance of microhabitat use for small mammals in Australia (e.g., Williams et al. 2002, Vernes 2003), Asia (Shanker 2001, Wells et al. 2004) and North America (Stevens and Tello 2009).

In the seasonal Atlantic forests of South America there is a general lack of ecological mammal studies that leaves a gap in the knowledge of community diversity in these regions. It is extremely important to generate information about the fauna in these areas, because of the extensive reduction in such native forest (Myers et al. 2000). This lacuna for the seasonal forests of the interior is slowly being filled (e.g., Talamoni and Dias 1999, Lambert et al. 2005). However, small arboreal species that usually are not captured on the ground are still inadequately sampled, because studies typically emphasize the terrestrial, cursorial species. In southern Brazil, the lack of data for arboreal species is even greater, with most existing data being gathered without traps placed in the trees (Cademartori et al. 2002, Dalmagro and Vieira 2005, Lima et al. 2010).

In the present study, we investigated the community structure of small rodents and marsupials in a South American deciduous forest to evaluate the richness, composition, and abundance of species present and their relationships with the habitat. We addressed the following questions: 1) Is the species richness similar to other adjacent areas in the southern boundary of the Atlantic forest? Our hypothesis is that species richness will be lower than in communities of low latitudes, but will be higher than in communities of more fragmented and disturbed areas; 2) How does the sampling methodology influence the composition and abundance of species captured? We hypothesised that sampling methodology will be determinant for the small-mammal community composition, particularly, for the species richness evaluated in pitfall traps; 3) How are the species distributed in the vertical space (complexity) of the forest? Our hypothesis is that the small-mammal community is segregated in the three-dimensional space; 4) Is there variation in species composition over the horizontal space? We hypothesised that the heterogeneity is an important factor to the species occurrence in the two-dimensional space; and 5) How does habitat structure (microhabitat) influence species occurrence? Our hypothesis is that habitat structure influences the species distribution, with species using same microhabitat more often than others.

Materials and methods

Study area

The study was carried out in a deciduous forest in the Parque Estadual do Turvo, PET (27°00' S 27°20' S and 53° 40' W 54°10' W) located in the municipality of Derrubadas, northwestern Rio Grande do Sul, Brazil. The PET has an area of 17,491 ha, and is located on the left bank of the Uruguay River (Figure 1).

The climate is subtropical humid temperate, with hot summers (Cfa according to the Köppen classification). The mean temperatures in the warmest month (January) is above 22 °C, and in the coldest month (July) range from -3 to 18 °C.

The PET contains primary vegetation in much of its area, but suffered anthropogenic pressures before and even after its creation in 1947, being burned on two occasions in the 1940s and 1970s (Silva et al. 2005). The areas that were burned or selectively logged had dense secondary vegetation, mainly at the edges of the park and at some points along the roads that traverse it.

The PET is an area of extreme importance for biodiversity conservation, according to "Evaluation and Identification of Priority Areas and Actions for Conservation, Sustainable Use and Benefit Sharing of Biodiversity - Workshop Evaluation and Actions Priority for Conservation of Biodiversity of the Atlantic Forest and Southern Grasslands (MMA 2000).

Animal trapping

We established 12 transect lines along two dirt roads that cross the park, though all of them were at least 100 m apart from any road. Transect lines on the same road were parallel to each other and were 500 to 1,500 m apart (Mean = 760, SD = 347 m). We established eight transects in one road and four in the other (Figure 1). Each transect line contained five live-trap stations and one pitfall-trap station. The live-trap stations were 30 m from each other, and at each one, three live-traps were placed: one in the center and the others on the left and right, both 20 m from the center live-trap. The arrangement always alternated between ground and understory (height of 3 m, i.e., when the trap in the center was on the ground, the left and right ones were set in the understory, or vice versa), and the type of trap, Sherman (31 x 10 x 8 cm) or wire (45 x 16 x 16 cm). The pitfall trap was placed 100 m from the end of each transect line, where two buckets (30 liters) 12 m apart were connected by a plastic fence (36 m in

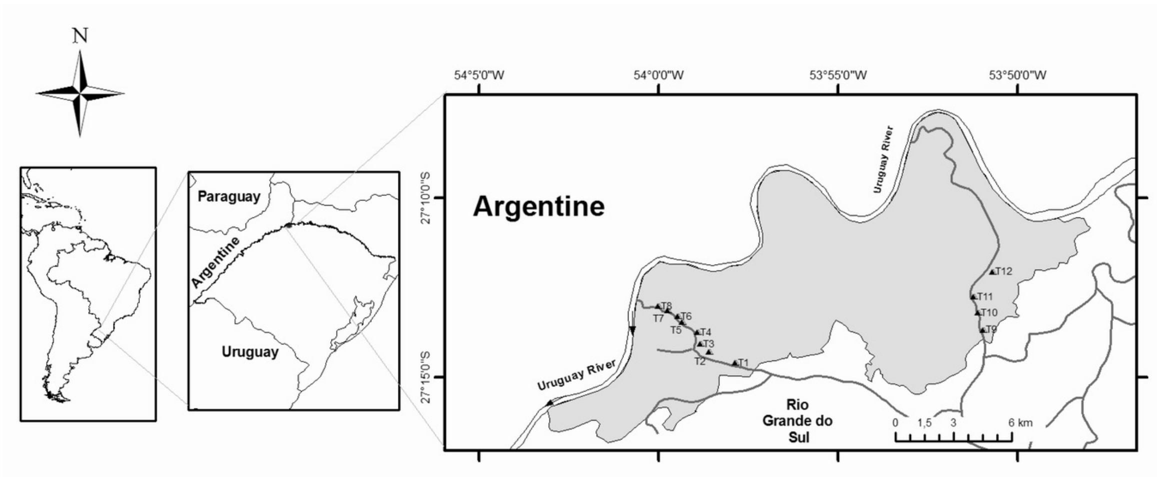

Figure 1. Location of the study area in South America, in the state of Rio Grande do Sul, Brazil, and in the Parque Estadual do Turvo, respectively, showing the arrangement of the 12 transects along two dirt roads in the reserve.

total length and 50 cm high) to guide the animals to the buckets. In total, there were 180 live-traps (90 on the ground and 90 in the understory) and 12 pitfalls trap stations (24 buckets). A mixture of bacon, squash, and peanut butter was used as bait in the Sherman and wire traps and no bait was used in the pitfalls traps.

The animals captured were marked with numbered eartags (Fish and small animal tag size 1, National Band and Tag Co., Newport, Kentucky). For each individual, the species, location of capture, and tag number were recorded. We collected only the first specimen of a species found in the study, or individuals found dead in traps due to cold or rain. Techniques were approved by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) (protocol 16095-1) and are in compliance with guidelines published by the American Society of Mammalogists for use of wild mammals in research (Gannon et al. 2007).

The fieldwork was carried out in six bimonthly phases, on eight transects (T1 to T8), starting in October 2008 and ending in September 2009; and in five bimonthly phases on the remaining four transects (T9 to T12), starting in December 2008 and ending in September 2009. Each phase lasted six consecutive nights. The total sampling effort was 6,120 trap-nights (live-traps) and 816 trap-nights (pitfall traps).

Environmental measurements

To characterize the vegetation at each point of capture on the ground, we measured nine variables that might affect the distribution of the small-mammal species captured in the study area. We counted trees with DBH (diameter at breast height) less than 10, between 10 and 30, and larger than 30 cm, counted the shrubs and lianas, and estimated the canopy height in an imaginary circle with a 4-m radius, centered on the trap. Within this space, we also noted the presence of *criciuma* (a locally common species of bamboo) and small terrestrial ferns; for these were assigned values of zero (absence) to three (high abundance). The density of seedlings was quantified by direct counting of the number of individuals on a transect line (8 m long and 1 m wide) crossing over the center of a trap.

For the pitfall traps, measurements were taken at four points 5 m from the fence in the north, south, east, and west directions. We used the mean of each variable as the final value for each pitfall-trap station.

These variables represented the degree of heterogeneity present in the area, considering a transect line as a sampling unit. On a smaller scale, it represented a measure of microhabitat, and in this case we considered each trapping station as a sampling unit.

Data analysis

The species accumulation curve was calculated by EstimateS 7.5 (Colwell 2005) based on the addition of new species as a function of sampling days, including all capture methods. The species richness was also estimated, by means of the Jackknife 1 and Jackknife 2 estimators. The difference between them is based on the number of individuals that are necessary to consider a species as rare in each sample, one or two individuals respectively. In addition to total abundance, we considered the abundance of live-traps and pitfall-traps separately, in order to assess the efficiency of each method in estimating species richness. For the same purpose, we conducted an Analysis of Variance (one-way ANOVA) via randomization (1000 interactions, Monte Carlo statistic), using the Euclidean distance as a measure of similarity between the sampling units. This ANOVA was used because it does not assume any premises in contrast to the parametric ANOVA (Pillar 2006). Each sampling unit corresponded to individuals captured in live-traps or pitfall traps (factor) on each transect line (replicates). The analysis was performed using richness, total abundance, and species abundance.

We analyzed the frequency of capture in cage traps of different strata (ground and understory) through a MANOVA via randomization, as described above. In this case, each sampling unit corresponded to the number of captures, excluding recaptures, per species on the ground and in the understory (factor) on each transect line (replicates). We performed an analysis focusing on abundance, and another emphasizing species composition (presence and absence). Assuming that there would be differences in the use of ground and understory by the small-mammal community, an ANOVA via randomization was performed for those species with a minimum of 15 captures, to examine which ones used the vertical space differently.

We calculated an index of upper-stratum utilisation through the number of captures in the understory for each species with four or more captures (the minimum number used in order to exclude rare species from the analysis). The index consisted of the number of captures in the understory divided by the total number of captures in live-traps. We took into consideration that both the ground and understory were sampled with the same trapping effort. Therefore, values that resulted in an index below 0.5 indicate a more terrestrial habit, and those giving an index above 0.5 suggest an arboreal habit; intermediate values (near 0.5) indicate a scansorial habit.

We calculated the index of upper-stratum utilisation and ANOVA via randomization (focusing on the vertical stratification) using only those records relating to live-traps. This avoids an effect of the sampling method, because the pitfalls were restricted to the ground and do not depend on the use of bait to attract animals.

We used ANOVA, via randomization, to verify the influence of environmental heterogeneity on the community, through the differences in abundance and species composition among the 12 transects. We included all records of each species at each transect line, taking as a sampling unit the sum of captures in live-traps and pitfall traps. In this analysis, we excluded the phase in which only eight transects were

Table 1. Form of locomotion and number of captures (number of individuals in parentheses when different) of small mammals in the Parque Estadual do Turvo, municipality of Derrubadas, Rio Grande do Sul, Brazil.

Species	Locomotion	Total
Order Didelphimorphia		
Family Didelphidae		
Didelphis aurita Wied-Neuwied, 1826	Scansorial[1,3,5]	24 (20)
Cryptonanus guahybae (Tate, 1931)	Scansorial[2]	7
Micoureus paraguayanus (Tate, 1931)	Arboreal[1,3,5]	4
Order Rodentia		
Family Cricetidae		
Akodon montensis Thomas, 1913	Cursorial[3,5]	539 (377)
Oligoryzomys nigripes (Olfers, 1818)	Scansorial[3,5]	38
Brucepattersonius iheringi (Thomas, 1896)	Semi-fossorial[3, 4,5]	22
Thaptomys nigrita (Lichtenstein, 1830)	Semi-fossorial[3,4,5]	15
Sooretamys angouya (Ficher, 1814)	Scansorial[4,5]	14
Oxymycterus judex Thomas, 1909	Semi-fossorial[4]	6
Euryoryzomys russatus (Wagner, 1848)	Cursorial[3,5]	4
Juliomys pictipes Osgood, 1933	Arboreal[3,5]	2
Family Echimyidae		
Kannabateomys amblyonyx (Wagner, 1845)	Arboreal[4]	1

[1] Vieira 2006, [2] Voss et al. 2005, [3] Vieira and Monteiro-Filho 2003, [4] Reis et al. 2006, [5]present study

sampled, in order to use an equal sampling effort along replicates.

The ANOVA via randomization was performed for each environmental parameter, to evaluate the degree of heterogeneity of environmental variables along the 12 transects. In this case, each transect line was considered as a sampling unit, with the ground traps considered as replicates. We used data for both live-traps and pitfall traps because of each transect line had the same number of samples.

The relationship between the abundance of more terrestrial species and the environmental variables measured at each point of capture on the ground was evaluated using the Mantel test. First, environmental variables were correlated with each other to detect the presence of redundancy. We used Euclidean distance as a measure of dissimilarity between environmental variables, and Bray-Curtis for the species-abundance matrix. Next, we used a Multiple Linear Regression Analysis to assess the effect of each structural variable on the abundance of the dominant species and on the small-mammal community. In the latter case, we reduced the data in a single dependent variable through Principal Coordinates Analysis (PCoA), using the first axis generated as a measure of community structure. Finally, we used a Spearman Correlation Analysis to associate each structural variable with species richness. Again, we excluded the data for the phase in which we sampled only eight transects, in both the Mantel test and Multiple Linear Regression, to avoid a different trapping effort between transect lines. It is worth to point out that macro and microhabitats have different concepts in the literature (Jorgensen 2004). Here we used the same measurement variables for both, heterogeneity (in a macro scale) and microhabitat (in a fine scale), but we considered the first one in regard to transect-line (landscape) variation and the second one to sampling unit (trap) variation.

The ANOVA, MANOVA and Correlation analyses were performed through Multiv software version 2.4 (Pillar 2006); the Multiple Linear Regression analysis using the Biostat software (Ayres et al. 2005); and the Mantel test and PCoA using the software PAST (Hammer et al. 2001).

Results

Overall community structure

We obtained 676 captures (510 individuals) of 12 small-mammals species belonging to nine of rodents and three of marsupials. For live-traps, capture success was 16% for traps on the ground and 1% for traps in the understory, whereas pitfalls had a 19% capture success. Overall, *Akodon montensis* was the dominant species in the PET with 76.6% of total captures, followed by *Oligoryzomys nigripes* with 5.6%, and 17.8% for all other species (Table 1).

The species-accumulation curve, though it tended to stabilize, showed a small change toward the end of sampling, and a slight increase in richness cannot be discarded if a further sampling effort was performed. Likewise, the estimators Jack 1 and Jack 2 calculated higher, expected species richness for the study area (Figure 2).

Community structure by sampling method

The collector curve shows that the rate of species accumulation, as well as the estimated richness was greater for pitfall traps than for live-traps. There was a trend toward stabilization of the curve represented by live-traps, and with a smaller standard deviation. However, the curve based on pitfall traps was still rising and seemed far from reaching the asymptote (Figure 3). Eight species were captured in live-traps and 10 in pitfall traps, with only three captured solely in pitfall and two in live-traps. When we compared only the ground samples, *A. montensis* and *Sooretamys angouya* were caught significantly more often in live-traps, whereas *O. nigripes* was captured predominantly in pitfalls. Although the general abundance was higher in live-traps, pitfalls had significant higher species richness (Table 2).

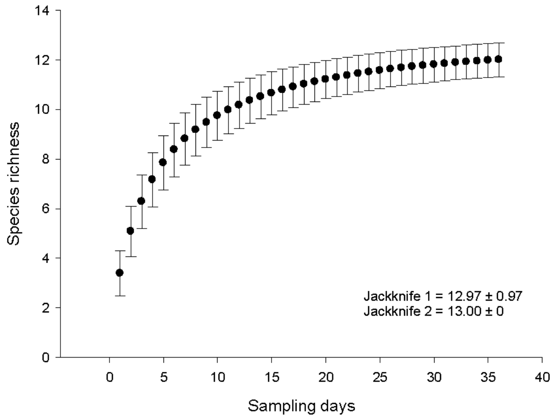

Figure 2. Richness estimators and species accumulation curve (collector curve) as a function of a 36-d sampling effort in the Parque Estadual do Turvo, during six phases of fieldwork between October 2008 and September 2009 in the municipality of Derrubadas, Rio Grande do Sul, Brazil. Data from live-traps and pitfall traps were combined.

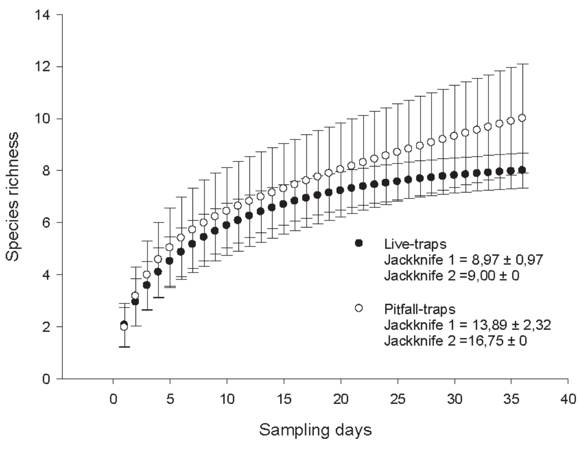

Figure 3. Richness estimators and species accumulation curves (collector curve) as a function of a 36-d sampling effort in the Parque Estadual do Turvo, during six phases of fieldwork between October 2008 and September 2009 in the municipality of Derrubadas, Rio Grande do Sul, Brazil. Data from live-traps and pitfall traps were analyzed separately.

Vertical space use

Among the species captured in live-traps, *Didelphis aurita*, *A. montensis*, *Euryzomys russatus*, *Oxymycterus judex,* and *O. nigripes* mostly used the ground. *Sooretamys angouya* was captured both on the ground and in the understory. *Micoureus paraguayanus* and *Juliomys pictipes* seemed to be the most arboreal species.

There were significant differences in the use of vertical space by the small-mammal community, in relation to both composition and abundance. This difference was significant for *A. montensis* and *D. aurita*, which used more the ground. *Sooretamys angouya* showed no preference for strata, and was captured equally on the ground and in the understory. The other species were not analysed statistically with respect to vertical stratification, because of the small number of records (Table 3). However, the index of understory utilisation shows that the majority of species captured in the PET have a more cursorial or scansorial habit. *Micoureus paraguayanus* can be considered the most arboreal species, with the highest rate of understory use (Table 1, Figure 4).

Heterogeneity analysis in the PET

Among predictor variables, there were significant correlations between the number of seedlings and number of ferns ($r = -0.33$, $p \leq 0.001$) and trees with DBH <10 ($r = 0.34$, $p \leq 0.001$), so we decided to exclude the "seedling" variable from the analysis.

The small-mammal community showed a homogeneous distribution in the PET: no differences in the assemblage were detected ($Q = 391.75$, $p = 1.00$). However, most environmental variables differed among the transect lines, mostly with respect to small trees, ferns, bamboos, and shrubs, based on the p value (Table 4).

Relationships with environmental variables

There was no association between terrestrial small-mammal community and environmental parameters, which indi-

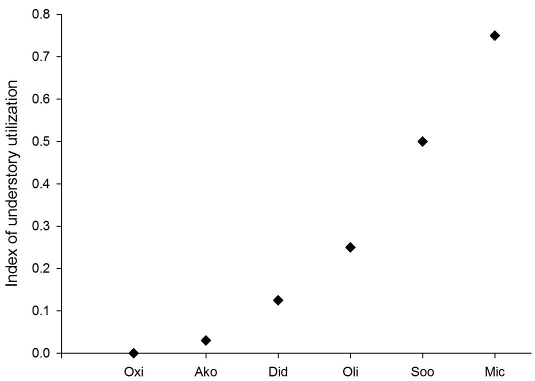

Figure 4. Index of understory utilization for species captured in live-traps in a Deciduous Forest in the Parque Estadual do Turvo, southern Brazil. Oxi = *O. judex*, Ako = *A. montensis*, Did = *D. aurita*, Oli = *O. nigripes*, Soo = *S. angouya*, Mic = *M. paraguayanus*.

Table 2. Richness, abundance, and number of individuals (total, mean number per area, and standard deviation) of rodents and marsupials, and results of ANOVA comparing numbers of individuals captured in pitfall traps and live-traps (Sherman and wire) on 12 transects in the Parque Estadual do Turvo, Brazil. * P ≤ 0.05.

Species	Pitfall trap			Live-trap			ANOVA	
	Total	Mean	SD	Total	Mean	SD	Q	P
Richness	10	4.50	1.09	8	2.75	1.14	18.38	0.002*
Abundance	157	13.08	4.25	353	29.42	10.37	1247.00	0.001*
Akodon montensis	73	6.08	2.70	304	25.33	10.40	2053.50	0.001*
Oligoryzomys nigripes	34	2.83	2.41	4	0.33	0.45	40.04	0.002*
Brucepattersonius iheringi	22	1.83	1.27	-				
Thaptomys nigrita	15	1.25	1.22	-				
Cryptonanus guahybae	7	0.58	0.67	-				
Oxymycterus judex	2	0.17	0.39	4	0.33	0.77	0.16	0.737
Sooretamys angouya	1	0.08	0.29	13	1.08	1.08	6.00	0.009*
Euryoryzomys russatus	1	0.08	0.29	3	0.25	0.45	0.16	0.588
Juliomys pictipes	1	0.08	0.29	1				
Kannabateomys amblyonyx	1	0.08	0.29	-				
Didelphis aurita	-			20	1.67	1.37		
Micoureus paraguayanus	-			4	0.33	0.49		

Table 3. Richness, abundance, and number of individuals (total, average per unit area, and standard deviation) of rodents and marsupials, and results of ANOVA comparing the numbers of individuals captured in live-traps (Sherman and wire) on the ground and in the understory on 12 transects in the Parque Estadual do Turvo, Brazil. * P ≤ 0.05.

Species	Ground			Understory			ANOVA	
	Total	Mean	SD	Total	Mean	SD	Q	P
Richness	7	2.75	1.14	6	1.42	1.08	4.0	0.003*
Abundance	332	27.67	10.25	21	1.75	1.60	8081.6	0.001*
Akodon montensis	296	24.66	10.30	8	0.66	0.98	8066.7	0.001*
Didelphis aurita	18	1.5	182	2	0.17	0.45	13.5	0.016*
Sooretamys angouya	7	0.58	090	7	0.58	0.90	0.0	1
Oxymycterus judex	4	0.34	078	0				
Oligoryzomys nigripes	3	0.25	0.45	1	0.08	0.29		
Euryoryzomys russatus	3	0.25	0.45	0				
Micoureus paraguayanus	1	0.08	0.29	3	0.25	0.45		
Juliomys pictipes	0		.	1	0.08	0.29		

cates that the characteristics of habitat measured do not influence the community structure of small mammals (Mantel, R = 0.017, p = 0.36). In the same way, we did not find any relationship between the structural variables and the community structure measured through the PCoA first axis (F= 1.03, r^2 = 0.03, p = 0.414). However, when considered just the species richness we found a positive correlation with liana (r = 0.32, n = 90, p = 0.001) and a negative correlation with bamboo (r = -0.34, n = 90, p < 0.001). The dominant species *Akodon montensis* was selective in microhabitat use (F = 2.9, r^2= 3.4, p = 0.024), mainly for sites with higher density of small plants on the ground level. Ferns (p = 0.001) had the highest explanation in the model, followed by trends for shrubs (p = 0.062) and bamboos (p = 0.078) for that species.

Discussion

The PET has a high species richness compared to other areas in the southern limit of the Atlantic Forest. The number of small-mammal species reported for the Atlantic Forest in southern Brazil ranges mostly from four to eight (Cáceres 2004, Cademartori et al. 2004, Cherem 2005, Dalmagro and Vieira 2005, Lima et al. 2010), with one case of 11 species in a coastal rainforest (Graipel et al. 2006). The larger number found here is apparently due to a combination of sampling methods used, and the large size of the PET area, with 17,000 ha, as discussed later. Despite of the high species richness, the community was dominated by *A. montensis* and *O. nigripes*, which are abundant in disturbed habitats of the Atlantic Forest (Pardini 2004). However, when comparing our result with those observed in other large-sized, best-conserved reserves northward in the Atlantic Forest, we highlight that there is some effect of species lost with latitude (Lyons and Willig 2002), provided that those studies have reported small-mammal richness around 20 species (Bonvicino et al. 2002, Vieira and Monteiro-Filho 2003, Pardini 2004, Pardini and Umetsu 2006).

The combination of sampling methods using pitfalls and live-traps proved to be adequate to record small-mammal species with differences in morphology and ecology, as also observed in other studies elsewhere (Nicolas and Colyn 2006, Gambalemoke et al. 2008, Umetsu et al. 2006, Fontúrbel 2010, Cáceres et al. in press). This is more important due to the fact that each method sampled exclusive species. The overall collector curve involving both methods showed a high tendency to stabilize, highlighting the effective combination of methods. The abundance was higher in live-traps than in pitfall traps, which would be expected due to the dominance of *A. montensis*, which is easily captured by this trap type (Lima et al. 2010). Taking into account that the live-traps were used in larger number and over a larger area than

Table 4. Number of significant results in the ANOVA via randomization and the contrasts between pairs of transects sampled to evaluate the difference between the measured environmental variables on 12 transects in the Parque Estadual do Turvo, Brazil.

P-value	Tree DBH			Can	Lia	Shr	Fer	Bam
	<10	10 to 30	>30					
0.01 < p < 0.05	15	8	2	9	10	8	11	7
p < 0.01	8	8	0	2	2	7	22	3
The most different transect lines	9 and 10	4 and 10	11	9	6 and 7	3 and 5	10 and 12	2 and 12
Total	0.001	0.002	0.546	0.045	0.024	0.006	0.001	0.005

Can = canopy height, Lia = lianas, Shr = Shrubs, Fer = ferns, Bam = Bamboo

the pitfall traps, a higher number of individuals captured by this method was expected, though capture success was greater in pitfalls.

Considering live-traps, the richness estimators, estimated adequately the number of species, since eight species were captured and nine was expected. The collector curve for live-traps showed a tendency to stabilize, confirming the observed richness. Furthermore, we used a mixture of different kinds of bait in all live-traps in order to attract a wide range of species with different food habits. The use of alternative baits is an important strategy to improve captures of different groups of small mammals (e.g., marsupials and rodents) as demonstrated in temperate forest of Chile (Fontúrbel 2010).

Contrarily, the richness estimators using the pitfall-trap data estimated a maximum of 16.75 species for the area, and the collector curve continued to rise. Other studies have emphasized the importance of using pitfall traps to sample the species composition of small mammals in South America (Lyra-Jorge and Pivello 2001, Umetsu et al. 2006, Cáceres et al. in press). This method is less selective because it does not depend on the animal attraction to bait, provided that fences drive them to buckets, performing captures of species improbable to be caught in live-trap with traditional bait, such as those lighter ones (Voss and Emmons 1996, Lyra-Jorge and Pivello 2001 Umetsu et al. 2006, Cáceres et al. in press, Table 2). Despite differences regarding the latitudinal gradient and inherent species substitution, our results for community composition were similar to other studies that have used pitfalls as sampling method (Pardini et al. 2005, Pardini and Umetsu 2006).

Trapping in the upper forest strata has been effective for sampling arboreal small-mammal species (Malcolm 1991, Vieira and Monteiro-Filho 2003, Wells et al. 2004, Lambert et al. 2005, Fontúrbel 2010, Hannibal and Cáceres 2010). However, for the small mammals in the PET, despite the equivalent capture effort on the ground and in the understory, no species were exclusively recorded in traps placed in trees, and capture success was low compared to that obtained by ground traps. One possible explanation is that the PET has a dense understory and a well-discontinuous canopy, disfavoring the occurrence of strictly arboreal species (Malcolm 1995). In contrast, cursorial and scansorial species, which are limited to the ground and/or the understory, were common in the study area. The capture effort in the understory would be enough to sample even strictly arboreal species, because most of these species often descend to the understory (Malcolm 1991, Vieira and Monteiro-Filho 2003, Hannibal and Cáceres 2010). As examples, *Caluromys lanatus* (Olfers, 1818) and *M. paraguayanus* were not captured, or rarely captured, respectively, in the PET, provided that both species are strictly arboreal (Vieira and Monteiro-Filho 2003, Cáceres and Carmignotto 2006), which highlight the unfavorable canopy condition of the study area. Nevertheless, although we did not find any strictly arboreal species, we did catch six species with different degrees of vertical strata use, which shows the importance of environmental complexity in the community structure of the PET.

The spatial heterogeneity of the environment in the PET was not so important, provided that the species distribution was uniform along the transect lines. However, it should be taken into account that the sampling methods did not cover the park uniformly, being restricted to vicinities of two dirt roads, which cross the PET, for logistical reasons. Therefore, although there were differences among environmental variables across the transect lines, we may not have sampled sites that contain high quality resources for those rare species we have captured. The great extent of the park area (~17 000 ha) supports this hypothesis, in which there should be sites where rarer species we have found are in fact more abundant (e.g., sites with more continuous canopy, and riparian ones).

Most small-mammal species of the Atlantic Forest are adapted to secondary or altered habitats (Bonvicino et al. 2002). As mentioned earlier, species characteristics of these sites are prevalent in the PET community, as confirmed by the relationship found between species richness and lianas. Therefore, the dense understory provided by such lianas, which are characteristic of disturbed habitats in the region, provides a suitable habitat for these more generalist species, as was the case of the dominant species, *A. montensis*. Bamboos, however, were correlated negatively with species richness, additionally suggesting the disturbance in the interior of park (Cáceres et al. 2010). *Akodon montensis* is abundant in the park, being favoured by fern, shrub and bamboo densities (Lima et al. 2010). However, the PET is connected to continuous, Argentinean best-conserved forests across the Uruguay River, which indicates its potential for uncover other not sampled small-mammal species, and the importance of the park for wildlife conservation in the southern limit of the Atlantic Forest.

In conclusion, the PET harbors a rich community of small mammals compared to other areas at the southern limit of the Atlantic Forest, even in detriment of its apparently disturbed physiognomy. The combination of different sampling methods was important to assess species diversity, as well as the exclusive use of live-traps underestimated the species diversity when compared to pitfall efficiency. Moreover, environmental complexity seems to play an important role allowing the coexistence of cursorial, scansorial and some arboreal species in this community. Heterogeneity does not seem to affect the distribution of species in the park, but we acknowledge that not all habitats have been sampled, such as those following water courses.

Acknowledgements. Our thanks to colleagues of the Laboratório de Ecologia e Biogeografia of the Universidade Federal de Santa Maria: B. Peres, C. Marks, D. Pathek, and F. Della Flora, and our friends E. Grotto, M. Rocha, and L. Milani for help in the fieldwork essential to this study. To C. Saydelles, G. Wallau, and L. Becker for helping in karyotyping. To the staff of the PET for logistical support. To Capes for a scholarship to the first author, and to CNPq for financial support to NCC (Edital 06/2008 - Jovem Pesquisador, Processo 569182/2008-5). NCC is a CNPq research fellow.

References

August, P. V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64: 1495-1513.

Ayres, M., M. J. Ayres, D. L. Ayres and A. S. Santos. 2005. *BioEstat 4.0: Aplicações estatísticas nas áreas das Ciências Biológicas e Biomédicas*. 4th ed. Sociedade Civil Mamirauá/CNPq, MCT, Imprensa Oficial do Estado do Pará, Belém.

Bonaventura, S. M., V. Pancotto, N. Madanes and R. Vicari. 2003. Microhabitat use and density of sigmodontine rodents in *Spartina densiflora* freshwater marshes, Argentina. *Mammalia* 67:367-377.

Bonvicino, C. R., S. M. Lindbergh and L. S. Maroja. 2002. Small non-flying mammals from conserved and altered areas of Atlantic Forest and Cerrado: comments on their potential use for monitoring environment. *Braz. J. Biol.* 62: 1-12.

Brannon, M. P. 2000. Niche relationships of two syntopic species of shrews, *Sorex fumeus* and *S. cinereus*, in the southern Appalachian mountains. *J. Mammal.* 81: 1053-1061

Cáceres, N. C. 2004. Occurrence of *Conepatus chinga* (Molina) (Mammalia, Carnivora, Mustelidae) and other terrestrial mammals in the Serra do Mar, Parana, Brazil. *Revista Brasileira de Zoologia* 21: 577-579.

Cáceres, N. C. and A. P. Carmignotto. 2006. *Caluromys lanatus*. *Mammalian Species* 803: 1-6.

Cáceres, N. C., R. P. Napoli, J. Casella and W. Hannibal. 2010. Mammals in a fragmented savannah landscape in south-western Brazil. *J. Nat. Hist.* 44: 491-512.

Cáceres, N. C., R. P. Napoli and W. Hannibal. 2011. Differential trapping success for small mammals using pitfall and standard cage traps in a woodland savannah region of south-western Brazil. *Mammalia* 75: 45-52.

Cademartori, C. V., M. E. Fabián and J. O. Menegheti. 2004. Variações na abundância de roedores (Rodentia, Sigmodontinae) em duas áreas de Floresta Ombrófila Mista, Rio Grande do Sul, Brasil. *Revista Brasileira de Zoociências* 6: 147-167.

Cademartori, C. V., R. V. Marques, S. M. Pacheco, L. R. M. Baptista and M. Garcia. 2002. Roedores ocorrentes em Floresta Ombrófila Mista (São Francisco de Paula, Rio Grande do Sul) e a caracterização do seu habitat. *Comunicações do Museu de Ciências e Tecnologia - PUCRS - Série Zoologia* 15: 61-86.

Cherem, J. J. 2005. Registros de mamíferos não voadores em estudos de avaliação ambiental no sul do Brasil. *Biotemas* 18: 169-202.

Colwell, R. K. 2005. *EstimateS: Statistical estimation of species richness and shared species from samples*. Version 7.5. Available at: http://viceroy.eeb.unconn.edu/estimates.

Dalmagro, A. D. and E. M. Vieira. 2005. Patterns of habitat utilization of small rodents in an area of Araucaria forest in Southern Brazil. *Austr. Ecol.* 30: 353-362.

Dickman, C. R. and D. P. Woodside. 1983. A test of a competition model with reference to three species of small mammals in south-eastern Australia. *Oecologia* 60: 127-134

Dueser, R. D. and H. H Shugart, Jr. 1978. Microhabitats in a Forest-Floor Small Mammal Fauna. *Ecology* 59: 89-98.

Eccard, J. A. and H. Ylölen. 2003. Interspecific competition in small rodents: from populations to individuals. *Evol. Ecol.* 17: 423-440.

Fa, J. E., F. J. Romero and J. Lopez-Paniagua. 1992. Habitat use by Parapatric Rabbits in a Mexican High-Altitude Grassland System. *J. Appl. Ecol.* 29: 357-370.

Fontúrbel, F. E. 2010. A methodological approach to assess the small mammal community diversity in the temperate rainforest of Patagonia. *Mammal. Biol.* 75: 294-301.

Gambalemoke, M., I. Mukinzi, D. Amundala, G. Katuala, J. Kennis, A. Dudu, R. Hutterer, P. Barrière, H. Leirs and E. Verheyen. 2008. Shrew trap efficiency: experience from primary forest, secondary fallow land and old palm plantation in the Congo River basin Democratic Republic of Congo. *Mammalia* 72: 203-212.

Gannon, W. L., R. S. Sikes and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* 88: 809–823.

Gentile, R. and F. A. S. Fernandez. 1999. Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. *Mammalia* 63: 29-40.

Graipel, M. E., J. J. Cherem, E. E. Monteiro-Filho and L. Glock. 2006. Dinâmica populacional de marsupiais e roedores no Parque Municipal da Lagoa do Peri, Ilha de Santa Catarina, sul do Brasil. *Mastozoología Neotropical* 13: 31-49.

Grelle, C. E. V. 2003. Forest structure and vertical stratification of small mammals in a secondary Atlantic Forest, South-eastern Brazil. *Studies on Neotropical Fauna and Environment* 38: 81-85.

Hammer, Ø., D. A. T. Harper and P. D. Ryan. 2001. *PAST: Paleontological Statistics Software Package for Education and Data Analysis*. Palaeontologia Electronica 4:9 p.

Hannibal, W. and N. C., Cáceres. 2010. Use of vertical space by small mammals in gallery forest and woodland savannah in south-western Brazil. *Mammalia* 74: 247–255.

Jorgensen, E. E. 2004. Small mammal use of microhabitat reviewed. *J. Mammal.* 85: 531-539.

Lambert, T. D., J. R. Malcolm and B. L. Zimmerman. 2005. Variation in small mammal species richness by trap height and trap type in southeastern Amazonia. *J. Mammal.* 86: 982-990.

Lima, D. O., B. O. Azambuja, V. L. Camilotti and N. C. Cáceres. 2010. Small mammal community structure and microhabitat use in the austral boundary of the Atlantic Forest, Brazil. *Zoologia* 27: 99-105.

Lyons, S. K. and M. R. Willig. 2002. Species richness, latitude, and scale-sensitivity. *Ecology* 83: 47–58.

Lyra-Jorge, M. C. and V. R. Pivello. 2001. Combining live trap and pitfall to survey terrestrial small mammals in savanna and forest habitats, in Brazil. *Mammalia* 65: 524-530.

Malcolm, J. R. 1991. Comparative abundances of Neotropical small mammals by trap height. *J. Mammal.* 72: 188-192.

Malcolm, J. R. 1995. Forest structure and the abundance and diversity of Neotropical small mammals. In: M. D. Lowman and N. M. Nadkarni (eds.), *Forest Canopies*. Academic Press, San Diego. pp. 179-197.

MMA (Ministério do Meio Ambiente). 2000. *Avaliação e ações prioritárias para a conservação da biodiversidade da Mata Atlântica e Campos sulinos*. Secretaria de Biodiversidade e Florestas (SBF), Ministério do Meio Ambiente (MMA), Brasília.

Murúa, R., R. A. González. 1982. Microhabitat selection in two Chilean cricetid rodents. *Oecologia* 52: 12-15.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

Nicolas, V. and M. Colyn. 2006. Relative efficiency of three types of small mammal traps in an African rainforest. *Belg. J. Zool.* 136: 107-111.

Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodivers. Conserv.* 13: 2567-2586.

Pardini, R. and F. Umetsu. 2006. Pequenos mamíferos não-voadores da Reserva Florestal do Morro Grande – distribuição das espécies e da diversidade em uma área de Mata Atlântica. *Biota Neotropica* 6: 1-22.

Pardini, R., S. M. Souza, R. Braga-Neto and J.P. Metzger. 2005. The role of forest structure, fragments size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biol. Conserv.* 124: 253-266.

Pillar, V. P. 2006. *MULTIV, Multivariate exploratory analysis, randomization testing and bootstrap resampling*. User's guide v. 24. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Reis, N. R., A. L. Peracchi, W. A. Pedro and I. P. Lima. 2006. *Mamíferos do Brasil*. Universidade Estadual de Londrina, Londrina.

Seagle, W. 1985. Competition and Coexistence of Small Mammals in an East Tennessee Pine Plantation. *Amer. Midland Nat.* 114: 272-282.

Shanker, K. 2001. The role of competition and habitat in structuring small mammal communities in a tropical montane ecosystem in southern India. *J. Zool.* 253: 15-24.

Silva, C. P., J. K. F. Mähler Jr., S. B. Marcuzzo and S. Ferreira. 2005. *Plano de Manejo do Parque Estadual do Turvo*. Secretaria do Meio Ambiente, Porto Alegre.

Simonetti, J. A. 1989. Microhabitat use by small mammals in central Chile. *Oikos* 56: 309-318.

Stevens, R. D. and J. S. Tello 2009. Micro- and macrohabitat associations in Mojave desert rodent communities. *J. Mammal.* 90: 388–403

Talamoni, S. A. and M. M. Dias. 1999. Population and community ecology of small mammals in southeastern Brazil. *Mammalia* 63: 167-181.

Umetsu, F., L. Nashara and R. Pardini. 2006. Evaluating the efficiency of pitfall traps for sampling small mammals in the Neotropics. *J. Mammal.* 4: 757-765.

Vernes, K. 2003. Fine-scale habitat preferences and habitat partitioning by three mycophagous mammals in tropical wet sclerophyll forest, North-Eastern Australia. *Austr. Ecol.* 28: 471–479.

Vieira, E. M. and E. L. A. Monteiro-Filho. 2003. Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil. *J. Trop. Ecol.* 19: 501-507.

Voss, R. S. and L. H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforest: a preliminary assessment. *Bull. Amer. Mus. Nat. Hist.* 230: 1-115.

Voss, R. S., D. P. Lunde and S. A. Jansa, 2005. On the contents of *Gracilinanus* Gardner & Creighton, 1989, with the description of a previously unrecognized clade of small didelphid marsupials. *American Museum Novitates* 3482: 1-34.

Weksler, M., A. R. Percequillo and R. S. Voss. 2006. Ten new genera of Oryzomyine rodents (Cricetidae: Sigmodontinae). *American Museum Novitates* 3537: 1-29.

Wells, K., M. Pfeiffer, M. B. Lakim and K. E. Linsenmair. 2004. Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia*.* *J. Biogeogr.* 31: 641-652.

Williams, S. E., H. Marsh and J. Winter. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 83: 1317-1329

Wilson, D. E. and D. M. Reeder. 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference*. 3rd ed. Johns Hopkins University. Press, Baltimore.

Yahner, R. H. 1982. Microhabitat use by small mammals in farmstead shelterbelts. *J. Mammal.* 63: 440-445

Received July 21, 2010
Revised November 2, 2010
Accepted February 4, 2011