Mammals in a fragmented savannah landscape in south-western Brazil

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Mammal abundance, richness, and community structure were examined in
fragments of savannah and in gallery forests of south-western Brazil in order to
assess the influence of fragment size and habitat on the communities. Five
savannah fragments and two gallery forests were sampled. Within the savannah
fragments, environmental parameters such as tree and shrub densities were
measured. Live-traps and pitfalls were used for trapping small mammals; larger
mammals were recorded from footprints and sightings. Seventeen species of
small mammal and 15 species of large mammal were recorded. Small mammals
were affected by fragment size and isolation, whereas larger mammals were not.
Communities of small mammals were better structured in the largest fragments,
and those in smaller fragments were subsets of the communities in larger
fragments. Gallery forests revealed a rather different assemblage of mammals,
but also contained species common to both gallery and large savannah
remnants. Data are discussed relating mammal community structure to area size
and vegetation structure, in an attempt to understand the present conservation
status of this fragmented landscape.

Keywords: biogeography; Cerrado; community structure; conservation;
fragmentation; isolation; species richness; matrix; nestedness subsets

Introduction

Habitat fragmentation is one of the major causes of species and population extinctions.
Fragmentation interrupts habitats and gene flow, leading to the impoverishment of
animal and plant communities (Silva and Tabarelli 2000). Populations in fragments
usually exhibit demographic problems including difficulties in maintaining the minimum
viable population size and bodily health (Chiarello 1999; Anciães and Marini 2000;
Brito and Grelle 2004). Fragmentation has also created metapopulations in which
instability is high and local extinctions are common (Hanski and Gilpin 1991).
Another important pattern that results from fragmentation is that of nested subsets
of communities. These subsets constitute parts of the entire community living in
smaller fragments with respect to continuous forests and/or larger fragments (Atmar
and Patterson 1993).

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In forest fragments and forest edges, open-area matrices are barriers for many species that avoid crossing the open areas, particularly for arboreal or habitat specialist animals (Stevens and Husband 1998; Pires et al. 2002). In addition to isolation and shape, fragment size is another important variable in determining patterns of richness and diversity of communities. Mammal species loss is usually higher in smaller fragments (Fonseca 1989; Chiarello 1999; Silva and Tabarelli 2000), but abundance can show a reverse effect, sometimes being higher in small fragments (Malcolm 1997; Pardini et al. 2005). Extinctions will usually occur in small fragments, and this has been an important question in the design of reserves: which is better, a single large reserve or several small ones (SLOSS)? (Atmar and Patterson 1993).

The Brazilian savannah (namely Cerrado) is a large biome of tropical South America. Its climate is highly seasonal. Because of the larger area occupied by open physiognomies (85%) in the Cerrado (Veloso et al. 1991; Eiten 1994), the richness of arboreal mammals is low compared with the adjacent Atlantic or Amazon forests (Fonseca et al. 1996). Nonetheless, diversity and endemicity of mammals in the Brazilian savannah are recognisable, particularly for small mammals and xenarthrans, mostly related to the open physiognomies (Fonseca et al. 1996; Carmignotto 2005).

Little is known of the general ecology and conservation status of mammals in the Brazilian savannah, especially in view of the great extent of this biome. Many studies in the biome have been carried out in its central portion, and particularly in gallery forests (Redford and Fonseca 1986; Mares and Ernest 1995; Johnson et al. 1999), but ecological studies focusing on mammals in the southern portion of the Cerrado are few or lacking. This is still more relevant in the face of deforestation, which is intense in the southern portion, leaving the landscape strongly fragmented (Machado et al. 2004).

The present study aimed to examine the patterns of community structure in mammals living in a fragmented savannah landscape in south-western Brazil, emphasizing the effects of fragmentation on the fauna. We made the following predictions: (1) as fragment size increases, mammalian richness and diversity will increase; (2) the vegetation structure will play a secondary role in the patterns of richness and diversity; (3) gallery forests will show a rather different fauna compared with woodland savannah; (4) fragmentation will have a greater effect on the smaller-bodied species (small mammals < 1 kg); and (5) mammal communities in smaller fragments will be subsets of the communities in larger fragments.

Material and methods

Description of study area

The fragments studied were located in south-western Brazil, in the state of Mato Grosso do Sul (Dois Irmãos do Buriti and Terenos municipalities), at central coordinates 20° 30′ S and 55° 18′ W. The area is located in the Paraguay River basin, ranging from 245 to 275 m above sea level (Figure 1). The climate is highly seasonal, with a marked dry and colder season (April–September) and a wet and warmer one (October–March). The minimum temperature varied from 14.0 to 21.5°C in the area during the field phases.

The region is well fragmented, but there is a mosaic of fragments forming a network, where pastures are the matrix. Cattle usually use the gallery forests,
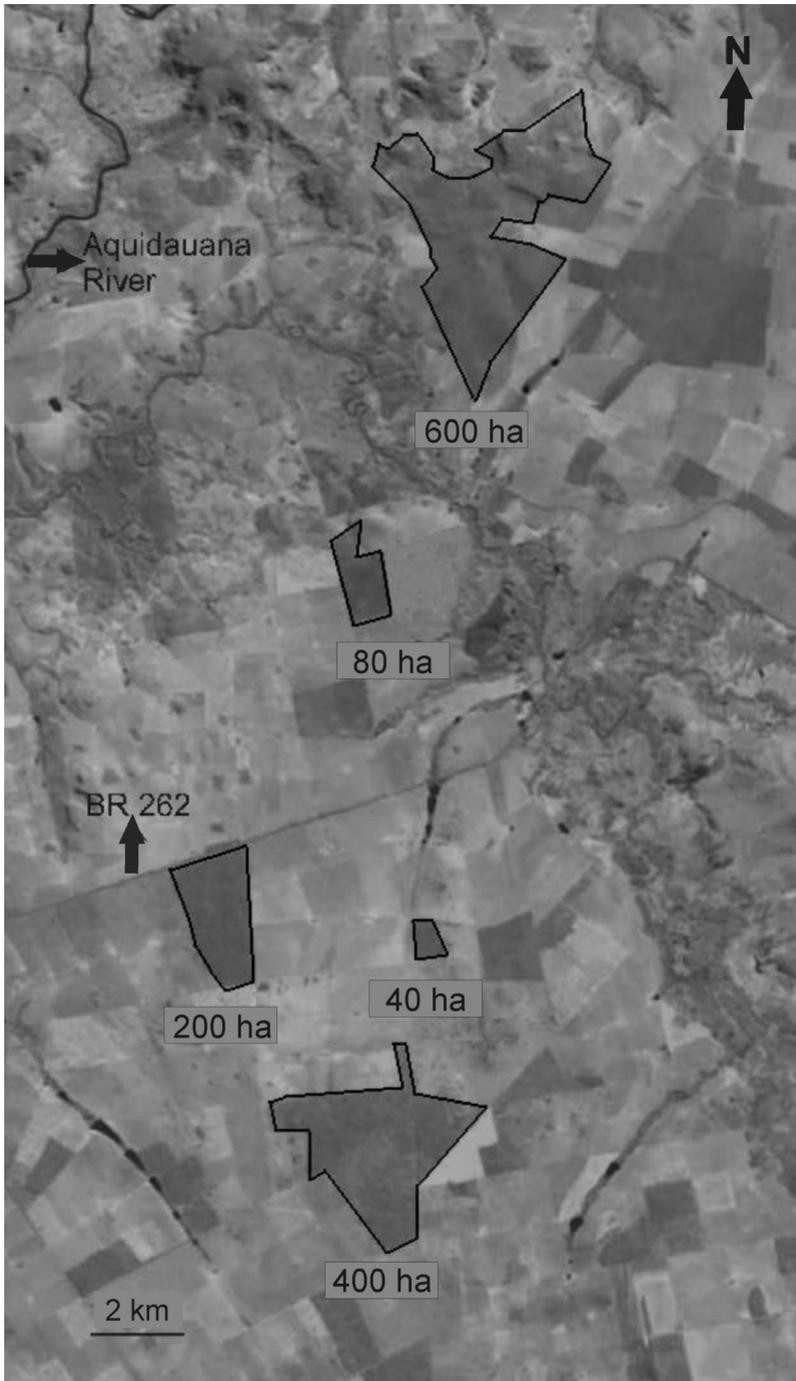
Figure 1. View of the study region in Dois Irmãos do Buriti and Terenos municipalities, state of Mato Grosso do Sul, south-western Brazil, showing the woodland savannah fragments studied and gallery forest along rivers and creeks (Cachoeirão River, crossing the landscape from right to left). Source: Embrapa Monitoramento por Satélite, Brazil.

where they find water, more than the isolated fragments of woodland savannah. Farmers closely control hunting on their properties, and so the hunting pressure is low. Five fragments of woodland savannah (Figure 2) ("cerradão") of different sizes (40–600 ha) were selected for the study (Table 1), all of them surrounded by a matrix of pasture, with two main water-courses nearby (Aquidauana and
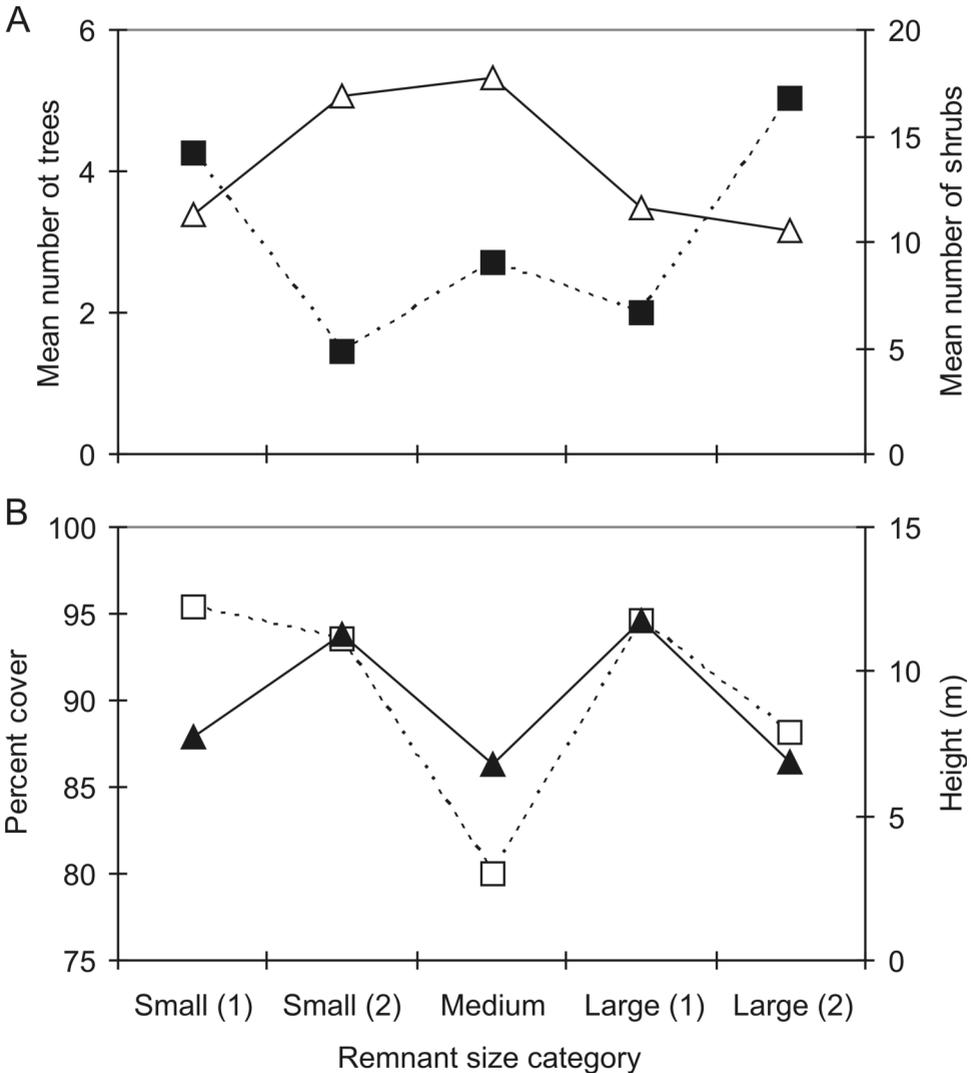
Figure 2. (A) Estimated number of trees (< 20 cm diameter breast height) and number of shrubs; (B) canopy cover and canopy height in five fragments of woodland savannah in southwestern Brazil. Notes: Black squares, trees; open triangles, shrubs; open squares, canopy cover; black triangles, canopy height; numbers in parentheses are related to smaller and larger remnant units respectively for a given size category.

Table 1. General characteristics and sampling effort of each fragment of woodland savannah and gallery forest studied in south-western Brazil from July 2002 to July 2004. Total number of sampling days in parentheses.

Size category	Size (ha)	Minimum distance from neighbouring fragments (m)	Number of field phases	Live-traps (trap-night)	Pitfalls (bucket-night)
Small$_1$	40	600	2 (15)	925	200
Small$_2$	80	1000	2 (25)	2220	500
Medium	200	1700	3 (25)	2205	500
Large$_1$	400	1000	2 (25)	2220	500
Large$_2$	600	100	3 (25)	2195	400
# 1	–	–	4 (13)	600	–
# 2	–	–	4 (14)	550	–

Notes: Subscript numbers for fragments are related to the smaller and larger units respectively for a given size category; the two gallery forests sampled are shown by different numbers: # 1, well fragmented; # 2, better conserved.

Cachoeirão rivers) (Figure 1). Fragment sizes in the region are usually no larger than 1000 ha, and small fragments of 40–150 ha are common (J. Casella, unpublished data). Isolation among fragments ranged from 0.1 to 1.7 km (Table 1), with the common distance between fragments being around 1.0 km or less. Evidence of cattle was rare in the fragments selected because these fragments were surrounded by fences and there was no evidence of cattle disturbance in the understorey. The edge effect in woodland savannah fragments is low or absent, but appears to be high in the gallery forest. The local fences do not impede the movements of the native, large mammals. All the fragments are composed of primary vegetation, but they exhibit different degrees of disturbance (fire, logging, and exotic species invasion). Some exotic grasses have invaded from the surrounding grazing lands, but this is at low level and mainly on the edges. Bamboo (*Guadua paniculata*), although a native species, is a disturbing agent in some Cerrado fragments in the region, and is sometimes found in high densities at the edges and in the interior (see Results).

Gallery forests were sampled at two sites 14 km away from each other, near the savannah fragments studied (21 km apart, and at similar altitudes), with the following central coordinates: 20º 27′ S and 55º 35′ W. Gallery forests were numbered as # 1 and # 2. Forest # 2 was best conserved, primary, and contiguous to the Aquidauana River (Piraputanga). Forest # 1 (UEMS/Aquidauana) was poorly conserved, disturbed, and not contiguous to the main river in the region, with many sites completely deforested. The area sampled for small mammals in this second gallery forest was less than 1 ha in size, but a longer stretch was surveyed for large mammals. These gallery forests, rather than being considered as sources for species in the savannah fragments, were considered as reference controls for this study, since gallery forests are the main environment occurring in the present landscape after the savannah woodlands which are the main physiognomy type.

Sampling methodology

Environment

The structure of the vegetation in the remnants was assessed by means of two transect lines (sampling stations 20 m apart) set in the fragment interior, at least 100 m from the edge and 200–400 m from each other. Centred at each station (*n* = 15) of a transect line (which follows the transect line set for pitfall traps), 10 types of measurements were taken in a 5-m radius as follows: number of bamboo plants (Bamboo), number of shrubs (Shrub), number of trees with diameter at breast height (DBH) > 20 cm (Trees > 20cm), number of trees with DBH < 20 and > 5 cm (Trees < 20cm), number of fallen logs (Logs), canopy height (Canopy height), percentage canopy cover (Canopy cover), number of termite nests (Termite), number of terrestrial bromeliads (Bromeliads), and number of live burned trees (Burned).

Small mammals

Captures of small mammals (averaging < 1 kg) occurred between August 2003 and July 2004 in the savannah fragments, with trapping extending for 5–10 days in each field phase. Remnants were sampled in pairs per field phase in a random manner. Each fragment was sampled two to three times with at least one field phase per season. Live-traps and pitfalls were active simultaneously in each pair of fragments (Table 1). In gallery forests, captures occurred from July 2002 to February 2004 and extended for three to four days in each field phase. Each of the two gallery forest areas was sampled four times, with two field phases per season, in order to equal the effort in savannah fragments.

For sampling small mammals, three types of traps and arrangements were used: (1) pitfalls; (2) wire and Sherman® traps at ground level; and (3) wire or Sherman® traps at tree level (1.5–3 m). Two grids of ground traps were installed in each fragment except for the smallest 40-ha fragment, where one grid was installed. Pitfalls were installed along three transect lines per fragment except for the smallest one, where sampling effort was two transect lines. Gallery forests were sampled by installing one transect line containing live traps along the creek at each of the two sites. The savannah fragments were sampled equally except for the smallest 40-ha fragment, where space was insufficient for setting two grids or three transect lines. We assumed that a smaller effort in this smaller fragment would give adequate results, comparable to those of larger fragments (J.L. Tellería, personal communication). Indeed, additional trapping carried out recently in this fragment has confirmed this assumption, as well as the richness and composition of the species reported here.

Ground-level grids were established, one in the interior (7 lines × 7 columns format = 49 traps) and another on the edge of each fragment (9 lines × 5 columns format = 45 traps). Grids in the interior were 200 m away from grids on the edges. The boundaries of the edges were considered to be 100 m towards the interior (Siqueira et al. 2004). Pitfalls were placed in the interior and on the edge of each fragment, following the same distance used for the grids, and at least 200 m distant from the trap grids or another pitfall transect line within a fragment. The pitfall transect lines were arranged parallel to the edge. Ten buckets (108 litres) were spaced 10 m from each other in each transect line, and were connected by a plastic fence (110 m in total length and at least 50 cm high) to drive animals to the buckets. In gallery forests, 30

(# 1) and 40 (# 2) capture stations were installed along transect lines, each station containing a ground trap.

Sherman ($40 \times 12 \times 12$ cm) and wire ($40 \times 16 \times 16$ cm) live traps (proportion 1:1) were positioned regularly at ground level in the grids of the remnants, with each station having a single trap. Live traps in lines or columns of a given grid or on a transect line were 20 m distant from each other. In addition, for trapping scansorial or arboreal mammals, about eight arboreal traps (wired or Sherman: approx. $25 \times 10 \times 10$ cm) were placed in each grid in a systematic arrangement or on transect lines in gallery forests, spaced at least 20 m from each other. The purpose of these traps was to improve sampling in each fragment or gallery forest, by supplementing the trapping effort at ground level.

The bait used was pumpkin or bacon, both mixed with codfish-liver oil and peanut butter, distributed randomly within each trap grid. After the first day of capture, the traps were rebaited daily, but in a random manner with regard to the types of bait.

Individual small mammals captured were marked by holes in the ears, and released in the same locale of capture. This marking method does not injure the animals and makes the individuals recognisable in the field (Monteiro-Filho and Graipel 2006).

Some individuals of species that are difficult to identify in the field were collected for karyological studies and identification. These individuals were prepared for skin and skull and housed in the Universidade Federal de Santa Maria zoological collection. The taxonomic arrangement followed the nomenclature utilized by Wilson and Reeder (2005) and updates (e.g., Weksler et al. 2006). Identifications were confirmed or performed by consulting specialists and by using available literature for the identification of small mammals in Brazil (Bonvicino, Otazu et al. 2002; Pessôa et al. 2002; Voss et al. 2005; Carmignotto and Monfort 2006).

Larger mammals

Large-sized mammals were recorded in fragments and in gallery forests during trapping periods by observing them directly in the field, by observing their tracks, and by captures in pitfalls for the smaller ones (e.g., armadillos). Tracks were the most important method used in both habitats, and were examined along the edges and in large trails in each fragment, which were suitable for recording them because of the presence of clear sand and absence of litter. No overlapping trails and transect lines were used for sampling small and large mammals. Although mammal species may vary in their use (in quality and intensity) of the fragments, we presumed that their simple presence in edges and trails was an indication of fragment use. Tracks of medium- and large-sized mammals in south-western Brazil can be easily recognized in the field (Borges and Tomás 2004). Tracks were identified to species level, and confirmed by the field guides of Becker and Dalponte (1999) and Borges and Tomás (2004).

Statistical procedures

A discriminant analysis (DA) was performed with structural variables, in order to determine which were responsible for the main differences among fragments. Each one of the paired variables correlated (by using Pearson correlation analyses) was excluded from the DA analysis (variables Burned and Canopy height; see Results). Each structural parameter of vegetation was tested for differences among fragments

by using analysis of variance (ANOVA) and Tukey *post-hoc* tests to examine which fragments were responsible for the main differences found.

The G-test was used to test for differences in abundance among the fragments. Spearman correlation analyses were applied to the data to investigate whether richness and species abundance vary with fragment size. The first axis of MDS ordination (reducing composition and abundance of small mammals along the fragments; see below) was also regressed against fragment area to best exploit patterns of relationships. In addition, the two main environmental variables measuring the structure of fragments plus area size were regressed on MDS axis 1, in order to indicate whether vegetation structure, fragment size, both, or neither are the major variables affecting small mammal communities.

Differences in the species composition/abundance of small mammals at different habitats and fragment sizes were assessed by ANOVA via randomization, setting one factor (fragment size and type: small fragments ($n = 2$ replicates), large ones ($n = 2$), and gallery forests ($n = 2$), against each other). Only species sampled by live traps (not pitfalls, which were not used in gallery forests) were considered. As a resemblance measure, Euclidean distance was calculated between sampling units. The number of random permutations carried out was 1000. The program used was Multiv version 2.4. This ANOVA was used because it does not assume any premises in contrast to parametric ANOVA (Pillar 2006). Large mammals were not investigated with this method because only presence/absence data were recorded for them.

The community structure of small mammals in the fragments and gallery forests was assessed by a non-metric multidimensional scaling analysis (MDS), which was performed using abundance data for the areas, in order to reduce variation in two main axes. The similarity distance measure was Bray–Curtis. The consistency of the diagram was checked by a Shepard diagram and the Stress value (Legendre and Legendre 1998). The data for all species were used in this analysis.

Beta-diversity (regional similarity) was estimated using the Sorensen index of similarity (presence/absence data) for larger mammals among forested savannah fragments, and using the Bray–Curtis index (for abundance data) for small mammals among fragments (Odegaard 2006).

The hypothesis of nestedness subsets for the savannah remnants was assessed in order to test whether there is a structural organization of species in these communities. In this particular view (randomizing columns; see later), species could be structured in depauperate communities (in small remnants) which would be subsets of rich communities (large remnants). Here we tested a nested pattern for different types of random matrices (1000 simulations) generated using the data themselves (remnants in columns and species in lines in the matrix). The results of the simulations (null hypothesis that subsets of species occur randomly in the remnants) were then compared with the structure observed in the actual communities (our database) through a histogram. The statistical software used was Aninhado version 3.0, and the metric used was the recently proposed nestedness metric based on overlap and decreasing fill (NODF) (Guimarães and Guimarães 2006; Almeida-Neto et al. 2008).

In addition to Multiv 2.4 for the ANOVA and Aninhado for nestedness, the statistical packages used were PAST version 1.74 (Hammer et al. 2001), and for correlations and G-tests, BioEstat version 3.0 statistical package (Ayres et al. 2003).

Results

Fragment characteristics

There were significant correlations between structural factors within sampling stations and across the fragments: Burned vs. Trees < 20cm ($r = 0.73$; $p < 0.0001$; $n = 150$), and Canopy height vs. Trees > 20cm ($r = 0.30$; $p < 0.001$; $n = 150$).

DA revealed the variables Trees < 20cm ($F_{(4,141)} = 22.0$, $p < 0.000001$), Shrubs ($F_{(4,141)} = 8.3$, $p < 0.00001$), and Canopy cover ($F_{(4,141)} = 6.8$, $p < 0.0001$) as the main functions to discriminate fragment structure (Wilks' Lambda: 0.371; $F_{(20, 468)} = 8.2$; $p < 0.0001$). The variables Termite and Logs were not significant ($F < 1.8$; $p > 1.19$), and the variable Trees > 20cm did not enter into the model ($F = 0.8$; $p = 0.51$).

The ANOVA resulted in similar and significant results, as did the DA, and most of the parameters had different magnitudes of differences among fragments (Table 2). *Post-hoc* Tukey tests revealed that the medium-sized fragment (200 ha) was the most dissimilar in general vegetation structure, with more burned trees, bamboos, and shrubs, and a more open canopy. The larger fragments were similar in having fewer shrubs and bamboos, whereas the smaller fragments were similar in having a close canopy cover. Fallen trunks and large trees did not vary among the fragments. Otherwise, environmental parameters were highly variable between small, medium, and large fragments, e.g. as having fewer shrubs, a higher percentage of canopy cover, and high canopy height between a small (80 ha) and a large (400 ha) fragment (Table 2; Figure 2).

Small mammals

Considering all fragments of savannah, 376 individuals were trapped in a total of 518 captures. Success in captures was 3.6% (excluding arboreal traps) for live-traps and 8.0% for pitfall traps. Marsupials (6 species) and rodents (7 species) had quite similar

Table 2. Statistical analysis of variance results on the differences in structural parameters among five remnants of different sizes in a woodland savannah (Cerrado biome) of southwestern Brazil.

ANOVA	F	P	Tukey ($p < 0.01$)	
			High score fragments	Low score fragments
Trees < 20 cm DBH*	23.0	0.0001	$Small_1 = Large_1$	$Small_2 = Medium = Large_2$
Bamboos	20.6	0.0001	$Small_2 = Medium$	$Small_1 = Large_{1, 2}$
Burned*	10.6	0.0001	$Medium = Large_2$	$Small_{1, 2} = Large_1$
Canopy height	10.5	0.0001	$Small_2 = Large_1$	$Small_1 = Medium = Large_2$
Terrestrial bromeliads	10.3	0.0001	$Small_1 = Large_2$	$Small_2 = Medium = Large_1$
Shrubs	9.7	0.0001	$Small_2 = Medium$	$Small_1 = Large_{1, 2}$
Canopy cover**	5.3	0.001	$Small_{1, 2} = Large_1$	$Medium = Large_2$
Fallen trunks	2.3	ns		
Trees > 20 cm DBH**	0.6	ns		

Notes: ns, non-significant difference; subscript numbers for fragments are related to the smaller and larger units respectively for a given size category; DBH, diameter at breast height; equal asterisks indicate variables positively correlated with each other ($p < 0.001$).

richness and abundance, with 188 individuals in each group (Table 3). In gallery forests, 75 individuals were trapped, resulting in a capture success of 6.5%. Only one individual of the Brazilian rabbit *Sylvilagus brasiliensis* (Lagomorpha) was trapped by pitfall in the savannah, and was not considered in the analyses of small mammals (but was included in the analyses of medium and large mammals).

The G-test showed significant differences in the presence and abundance of species among the savannah fragments. *Monodelphis domestica* ($p = 0.001$; df = 4; G = 18.2), *Thylamys macrurus* ($p = 0.001$; df = 4; G = 17.5), *Calomys callidus* ($p < 0.001$; df = 4; G = 27.4), and *Thrichomys pachyurus* ($p < 0.001$; df = 4; G = 24.5) differed significantly in abundance among fragments. Some of these differences showed linear patterns with fragment size: *M. domestica* ($r_s = 0.87$; $p = 0.05$) and *T. pachyurus* ($r_s = 1.00$; $p < 0.01$) showed positive and significant correlations with fragment size, whereas *Gracilinanus agilis* showed a negative relationship ($r_s = –0.90$; $p = 0.04$) with fragment size. Although *T. macrurus* and *C. callidus* showed different abundances among fragments, there were no apparent linear patterns with respect to fragment size ($p > 0.40$). *Didelphis albiventris* showed neither differences in abundances ($p = 0.40$) or a linear pattern ($p = 0.50$). Regarding *Hylaeamys megacephalus*, which was caught in both gallery forest and savannah, differences in presence and abundance were significant in these environmental units ($p = 0.01$; df = 6; G = 16.6) (Table 3; Figure 3).

The ANOVA via randomization revealed a nearly significant difference for community values (presence and abundance) among fragments and gallery forests, when spatial units were arranged by area size and physiognomy (savannah/galley forest) ($p = 0.07$; Q = 1535.8; $n = 14$ species analyzed).

There was a trend toward a positive correlation between species richness and fragment size ($r = 0.82$; $p = 0.09$). This pattern was confirmed when the gallery forests were included as large (# 2) and small (# 1) fragments (see description of the study area) in addition to the savannah fragments ($r = 0.88$; $p < 0.01$) (Figure 4).

MDS ordination using abundance of small mammals among fragments and gallery forests revealed a linear pattern in a diagram (stress = 0.043) in which axis 1 reduced the variation from smaller fragments (at right) to larger fragments and, finally, gallery forests (at left) (Figure 4). A linear relationship was seen when MDS axis 1 and savannah area sizes were counted ($p = 0.037$; $r = –0.90$). The multiple linear regression of MDS axis 1 (reduction in the composition and abundance of small mammals) and the three main important environmental variables (fragment size, small-tree density, and shrub density) in the woodland savannah resulted in a high coefficient of explanation ($R^2 = 0.96$) at a level of 0.07 for the *p*-value ($F_{(3,1)} = 105.6$). Area size contributed most to this multiple analysis ($p = 0.065$).

Regarding similarities among fragments based on abundance data (Bray–Curtis index), the medium-sized fragment was more similar to both largest fragments, whereas the smallest fragments were more similar to each other (Table 4).

The hypothesis of nestedness subsets for the actual savannah remnants was confirmed by comparing the observed arrangement of the small mammal assemblages with those generated randomly through 1000 simulations. The probability of the observed arrangement (a strongly structured pattern) differed significantly from the random pattern ($p = 0.023$), for which subsets of species occurring randomly in the remnants were expected (null hypothesis) (Figure 5). Then, a nestedness arrangement was detected, with some species occurring exclusively in the larger remnants, and other common species occurring in both larger and smaller fragments.

Table 3. Species composition and abundance of small mammals in remnants of woodland savannah and in gallery forests of the state of Mato Grosso do Sul, south-western Brazil.

Species	Gallery forests		Remnants of savannah				
	# 1	# 2	$Small_1$	$Small_2$	Medium	$Large_1$	$Large_2$
Marsupials							
Cryptonanus agricolai (Moojen, 1943)	–	–	–	–	1	–	2
Didelphis albiventris Lund, 1840	–	6	4	5	7	1	8
Gracilinanus agilis (Burmeister, 1854)	–	–	7	10	4	7	1
Monodelphis domestica (Wagner, 1842)	–	–	–	–	1	14	3
Monodelphis kunsi Pine, 1975	–	–	–	1	4	1	2
Thylamys macrurus (Olfers, 1818)	–	–	9	9	28	27	4
Rodents							
Calomys callidus [a] (Thomas, 1916)	–	–	6	30	4	24	2
Cerradomys scotti Langguth and Bonvicino, 2002	–	–	–	–	2	–	3
Hylaeamys megacephalus [b] (Fischer, 1814)	2	10	–	1	–	–	–
Necromys lasiurus (Lund, 1841)	–	–	–	1	–	–	–
Nectomys rattus [c] (Pelzeln, 1883)	1	3	–	–	–	–	–
Oecomys bicolor (Thomas, 1860)	–	1	–	–	–	–	–
Oligoryzomys chacoensis (Myers and Carleton, 1981)	–	1	–	–	–	–	–
Oligoryzomys fornesi (Massoia, 1973)	–	–	–	–	–	–	1
Rhipidomys macrurus (Gervais, 1855)	–	1	1	–	–	7	–
Proechimys longicaudatus [d] (Rengger, 1830)	–	8	–	–	–	–	–
Thrichomys pachyurus [e] (Wagner, 1845)	13	26	–	2	12	17	19
Dasyprocta azarae Lichtenstein, 1823	1	2	–	–	–	–	–
Lagomorphs							
Sylvilagus brasiliensis (Linnaeus, 1758)	–	–	–	–	–	1	–
Species richness	4	9	5	8	9	9	10

Notes: Karyotypes: [a]($2n = 48$); [b]($2n = 54$), [c]($2n = 52$),[d]($2n = 28$), [e]($2n = 34$); subscript numbers for fragments are related to the smaller and larger units respectively for a given size category; the two gallery forests sampled are shown by different numbers: # 1 is well fragmented, and # 2 is better conserved; for most analyses, *D. azarae* and *S. brasiliensis* were considered as large-sized mammals because they are easily recorded by tracks and directly recorded in the field by visual observation.
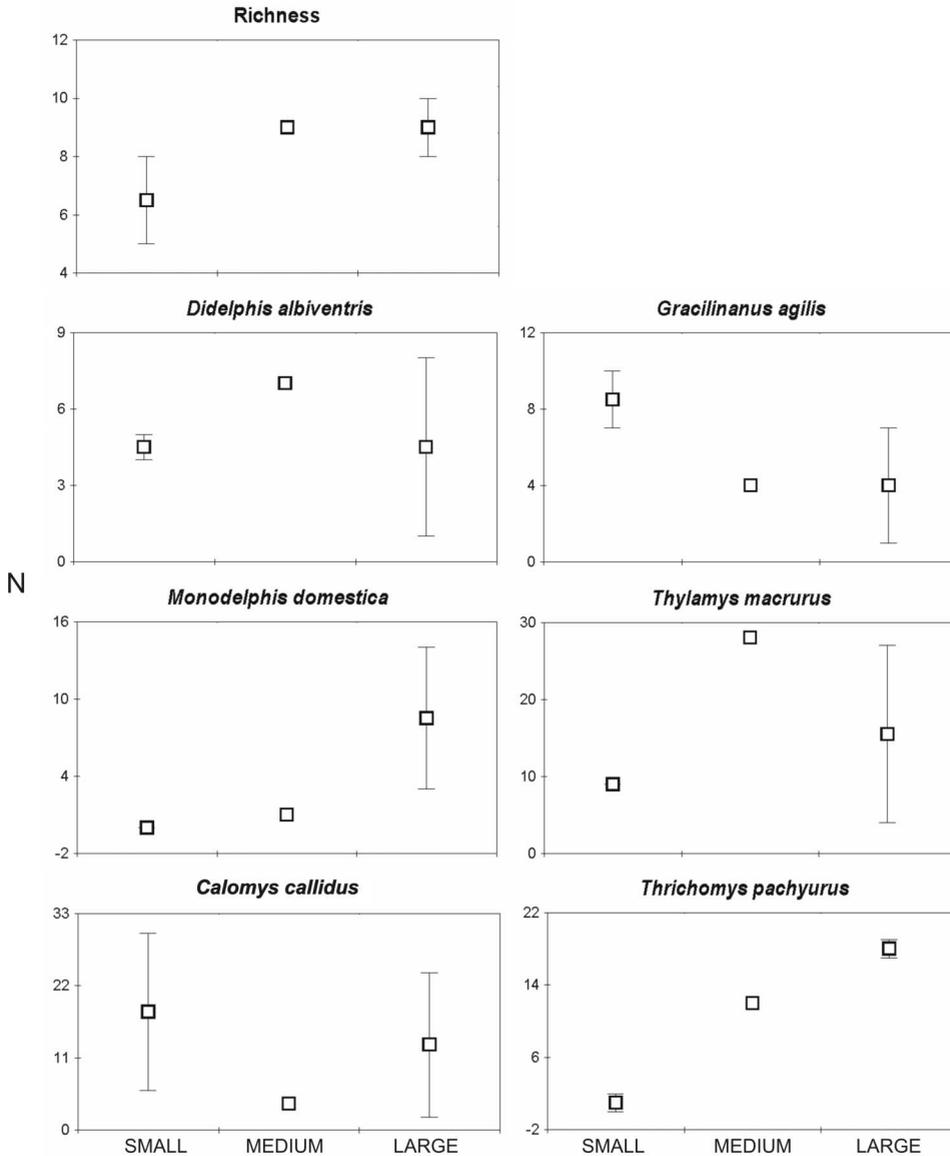
Figure 3. Species richness and abundance variation of small mammals in fragments of different sizes in a woodland savannah region of south-western Brazil. Notes: Points are mean values; bars are maximum and minimum amplitudes for the size category; all species with at least 18 individuals sampled are shown; species of *M. domestica*, *T. macrurus*, *C. callidus,* and *T. pachyurus* had significantly different abundances ($G > 17$; $p < 0.01$) among fragments, but only *G. agilis* ($r = -0.90$), *M. domestica* ($r = 0.87$), and *T. pachyurus* ($r = 1.00$) were significantly correlated with fragment size ($p \leq 0.05$).
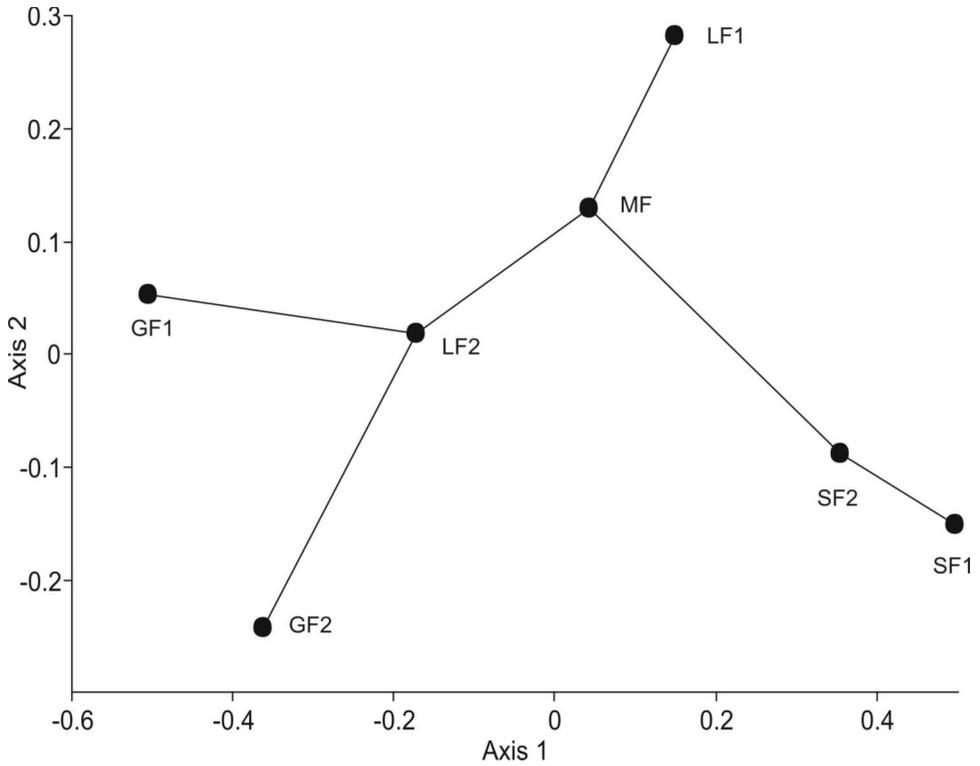
Figure 4. Diagram showing non-metric multidimensional scaling analysis (Bray-Curtis distance measure) results for composition and abundance of small mammals recorded in woodland fragments and gallery forests of south-western Brazil.

Notes: GF, gallery forest; LF, large fragment; MF, medium fragment; SF, small fragment; numbers for areas refer to smaller and larger units respectively for a given size category; stress is 0.043; minimum spanning tree is shown.

Table 4. Similarities in mammal communities in five fragments of woodland savannah in the state of Mato Grosso do Sul, south-western Brazil.

Fragments	$Small_1$	$Small_2$	Medium	$Large_1$	$Large_2$
$Small_1$	1	0.66667	**0.77778**	0.70588	**0.84211**
$Small_2$	**0.60465**	1	0.57143	0.30769	0.53333
Medium	0.46667	0.40984	1	0.46154	0.53333
$Large_1$	0.38400	0.56051	**0.62112**	1	**0.71429**
$Large_2$	0.30556	0.28846	**0.59259**	0.40559	1

Notes: Above diagonal, larger mammals using Sorensen index; below diagonal, small mammals using Bray–Curtis index; subscript numbers for fragments relate to the smaller and larger units respectively for a given size category; highest values are in bold.
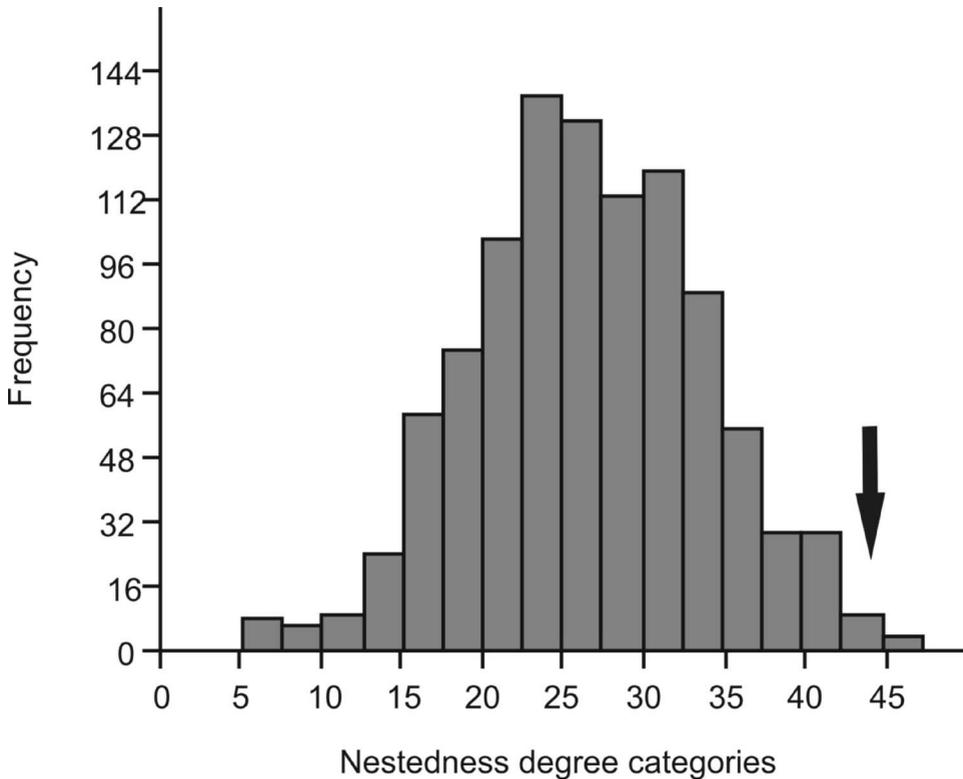
Figure 5. Histogram showing the frequency of 1000 randomly generated simulations, based on the actual matrix data for small mammals from savannah fragments of different sizes. In the simulations, groups of species were allowed to occur randomly in each fragment, generating a normal distribution. Notes: Arrow indicates the degree of nestedness observed for the actual data which was significanty higher than expected by chance ($p = 0.023$); NODF was the metric used for nestedness analysis (Guimarães and Guimarães 2006; Almeida-Neto et al. 2008).

Larger mammals

Larger mammals varied in weight from 0.9 to 240 kg (the lagomorph *S. brasiliensis* and the tapir *Tapirus terrestris*, respectively) (Fonseca et al. 1996). The most common species was *T. terrestris*, present in all fragments; followed by the giant anteater *Myrmecophaga tridactyla*, the ocelot *Leopardus pardalis* and the agouti *Dasyprocta azarae*, which were present in four of the five fragments (Table 5).

Fifteen species of larger mammals were recorded in all fragments of forested savannah during all field phases (Table 5). The mean number of species per savannah fragment was 7.8 ± 2.2 (SD). Fragments were similar to each other in patterns of fragment size or isolation regarding the presence and absence of larger mammals. For example, the smallest fragment was 84% similar to the largest fragment and 78% similar to the medium-sized fragment, whereas the two largest fragments were 71% similar (Table 4).

Table 5. Medium- and large-sized mammals occurring in gallery forests and fragments of woodland savannah in the state of Mato Grosso do Sul, south-western Brazil.

Species	Gallery forests		Fragments of savannah				
	# 1	# 2	$Small_1$	$Small_2$	Medium	$Large_1$	$Large_2$
Didelphimorphia							
Didelphis albiventris Lund, 1840	v	c					
Cingulata							
Dasypus novemcinctus Linnaeus, 1758			f	f			f
Euphractus sexcinctus (Linnaeus, 1758)	v		f	f	f		
Pillosa							
Myrmecophaga tridactyla Linnaeus, 1758			f	f		f	f
Primates							
Cebus libidinosus Spix, 1823	v	v					
Carnivora							
Cerdocyon thous (Linnaeus, 1766)			f	f	f		
Leopardus pardalis (Linnaeus, 1758)			f	f	f		f
Puma concolor (Linnaeus, 1771)			f		f		f
Perissodactyla							
Tapirus terrestris Linnaeus, 1758	f, v	f	f	f	f	f	f
Artiodactyla							
Mazama spp. Rafinesque, 1817	v		f			f	f
Pecari tajacu (Linnaeus, 1758)	v	v	f		f	f	
Rodentia							
Cavia aperea Erxleben, 1777		f					
Dasyprocta azarae Lichtenstein, 1823	v	f	f		f	f	f
Hydrochoerus hydrochaeris (Linnaeus, 1766)	v						
Lagomorpha							
Sylvilagus brasiliensis (Linnaeus, 1758)	f	f	f			f	f
Total	7	9	11	6	7	6	9

Notes: Subscript numbers for fragments are related to smaller and larger units respectively for a given size category; legends for recording methods in the field: c, carcass; f, footprint; v, visual observation.

Species richness did not differ among sites ($n = 7$) nor among savannah fragments ($n = 5$) ($p > 0.05$; G-test). *Cebus libidinosus* and *D. albiventris* occurred exclusively in the two gallery forests, as recorded by methods to survey large-sized mammals (e.g., footprints and field observation). Carnivorous or xenarthran species were commonly recorded in the woodland savannah fragments. The most frequent species considering all sites were the tapir *T. terrestris* (100%), the agouti *D. azarae* (86%), the collared peccary *Pecari tajacu* (71%), and the Brazilian rabbit *S. brasiliensis* (71%).

Discussion

By analyzing smaller and larger mammals in the study region separately, a major pattern of differentiation of these two assemblages regarding the use of landscape appeared: the community of small mammals was influenced by fragmentation, whereas larger mammals were not, but used the landscape as a whole. A second pattern was also evident regarding the use of savannah patches and gallery forest, in which both assemblages showed some differences in structure, with continuity from smaller woodland savannah fragments towards large ones and then gallery forests (Figure 4).

Small mammals in savannah fragments

Despite the inherent differences in size and structure of the fragments, the local mammal richness and community structure, particularly of small mammals, ought to be regulated by different kinds of disturbances linked to fragmentation, as seen elsewhere (Fonseca 1989; Malcolm 1997; Gascon et al. 1999; Bonvicino, Lindbergh et al. 2002; Pires et al. 2002; Pardini et al. 2005). Those factors can include type of the matrix outside the fragment, edge effect, connectivity, etc. In the present case, however, the size of remnants was the main factor determining small-mammal structure.

Therefore, our general impression was the absence of some small-mammal species in smaller fragments and their increase towards the large fragments, mostly independent of the forest structure, which was rather variable among the fragment size categories (Table 2). However, the multiple-regression analysis indicated some influence of the vegetation structure in determining small-mammal community structure, since the characteristic of a habitat appeared to affect the occurrence or abundance of a given species. In agreement with the finding of area size, a clear relationship of large fragments with small-mammal diversity and richness was reported for the Atlantic Forest (Pardini et al. 2005). Rodents were rather prominent in species composition in larger fragments here (e.g., *Cerradomys scotti*, *Oligoryzomys fornesi*, and *T. pachyurus*). Marsupials sometimes dominated in abundance or richness in the smaller fragments (see Fonseca [1989] and Malcolm [1997] for similar data), as we could see for *G. agilis* (Santos-Filho et al. 2008), but *T. macrurus* was rather generalist in habitat use (Cáceres et al. 2007).

Vegetation structure apparently determines some patterns of species occurrence in these fragments or even in gallery forest. Indeed, the open structure of the medium-sized fragment, with few trees, more shrubs, and a low canopy easily explains the absence of the arboreal *R. macrurus*, which would need high tree connectivity for arboreal movement. The high connectivity found in the best-conserved gallery forests and in the smaller remnant (see Figure 2) corroborates this hypothesis, since

this arboreal rat was found there. The occurrence of rice rats (*Cerradomys*) is a good indicator of habitat quality for the medium-sized fragment; this rat is one of the first species to disappear with disturbance and fragmentation (Malcolm 1997; Bonvicino, Lindbergh et al. 2002; Pardini et al. 2005).

Analysis of the nestedness effect indicated that the communities in the smaller fragments in the woodland savannah are subsets of the best-conserved communities of small mammals living in the larger fragments (*sensu* Atmar and Patterson 1993), and are more depauperate compared to those of larger fragments or intact woodland savannah. The increasing richness and community structure of small mammals with area size confirms this trend, in addition to the community similarities seen among the larger fragments in the study region. This means that, with fragmentation, remnants will lose vulnerable species with time, in a predictable direction (Atmar and Patterson 1993; Chiarello 1999; Pardini et al. 2005).

The limited mobility of small mammal species, together with the degree of isolation of fragments, is postulated as one of the main barriers that separate the populations in such fragments, leading to stochastic species extinctions in smaller fragments (Brito and Grelle 2004). Short distances among fragments are crucial for maintaining gene flow among sub-populations (Hanski and Gilpin 1991), and even so, small-sized species (such as arboreal ones) will have difficulty in dispersing or migrating between patches (Pires et al. 2002). In the remnants studied, the distances between fragments were usually 500 m or more, commonly around 1000 m, making it difficult for specialized, small-bodied savannah species to cross the open matrix between fragments. For Atlantic-Forest small mammals, shorter distances such as 100–300 m are enough to serve as a barrier for some species, leading to isolation or a metapopulation dynamic (Pires et al. 2002; Brito and Grelle 2004).

Fragment size affected the rodent *T. pachyurus* and the gracile mouse opossum *G. agilis* in opposite ways. This may be related to the sensitivity of the former rodent species to habitat disturbance and/or to the area-size effect. Studies elsewhere have shown that species of *Thrichomys* are rather habitat-dependent (e.g., rocky areas) (Lacher and Alho, 2001; Bonvicino, Lindbergh et al. 2002) and prefer shrubland savannah rather than grassland (Mares et al. 1986; Bonvicino et al. 2005). On the other hand, larger numbers of *G. agilis* in small remnants may be related to its adaptability to disturbed, smaller fragments of woodland savannah. This marsupial species and its congener *G. microtarsus* are versatile in their use of habitat, occupying disturbed and well-fragmented habitats, including forest edges (Mares and Ernest 1995; Bonvicino, Lindbergh et al. 2002; Cáceres, Casella et al. 2008; Santos-Filho et al. 2008).

The Short-tailed Mouse-opossum *M. domestica* is another species that may be influenced by fragmentation of savannahs. Although some studies have reported the species as a generalist, occurring in grasslands or shrublands (Lacher and Alho 2001; Bonvicino, Lindbergh et al. 2002), our data suggest that *M. domestica* may be influenced by fragmentation, such as effects of fragment size and matrix type. In other regions, *M. domestica* has been reported as a non-generalist, avoiding pasture matrix (Santos-Filho et al. 2008) or grasslands (Bonvicino et al. 2005). Open habitats with few plant substrates (e.g. pasture matrix) should function very differently from natural grasslands or shrublands in permeability and resource availability (Vieira 2003).

Larger mammals in savannah fragments

In the study region, the data for larger mammals suggested high rates of migration and dispersal between the fragments, as indicated by the similarity among the communities, independent of area size, isolation (by distance), and vegetation structure. Thus, the mosaic of remnants in this landscape maintains a structured community of large-sized mammals, with larger predators such as the cougar *Puma concolor* and medium- and large-bodied herbivores or insectivores such as the tapir *T. terrestris*, the collared peccary *P. tajacu*, and the giant anteater *M. tridactyla*, which were all present in the fragments, even in the smaller ones or in disturbed gallery forest.

However, small fragments usually harbour poorer fauna, as reported for larger mammals in the Atlantic Forest (Chiarello 1999). Such differences are most probably related to different characteristics of conservation in the different regions, such as hunting pressure, which is thought to be low in the study region (because of farmers' control and low human population density; N.C. Cáceres, personal observation) and high in the Atlantic Forest (Cullen-Jr et al. 2000). Another factor is the permeability of the pasture matrix for the large-mammal fauna, which is thought to facilitate movement between remnants (as opposed to the small-mammal fauna). The high number of large-mammal kills (mainly of *Cerdocyon thous*, *M. tridactyla*, and *Euphractus. sexcinctus*, but also including large species such as *P. concolor* and *T. terrestris*) by vehicles on the highway (BR 262) that transects the study area between the remnants (Figure 1; Cáceres et al. forthcoming) corroborates the hypothesis of a high rate of movement through the pasture matrix between remnants. Some of these large species are presently endangered or vulnerable to extinction, such as the puma *P. concolor*, giant anteater *M. tridactyla,* and tapir *T. terrestris* (IUCN 2006). These large species must use forest patches for shelter as well as feeding sites, and their use of patches will depend on the species characteristics such as dietary regime and movement rate.

Small and large mammals: a conclusion

The interactions between mammals and the fragmented landscape are complex. The size of fragments does not act solely on the determination of species composition and community structure. The vegetation structure and the degree of conservation of fragments appear to interact substantially in the determination of the animal community (Tews et al. 2004). The minimum size of fragments to support a reasonable faunal biodiversity is primarily 600 ha (Chiarello 1999), but smaller fragments (such as those between 200 and 400 ha) will also support at least a reasonable diversity (Rocha and Dalponte 2006) if isolation is weak and permeability through the matrix is facilitated. Therefore, a mosaic of woodland savannah fragments, such as the configuration of the study region, appears to be partly suitable for a conservation strategy for larger-bodied mammals in this southern Brazilian savannah, but appears unsuitable for the small-mammal fauna, in small fragments. Hence, the role of the pasture matrix as ecological corridors, particularly for small mammals, needs to be evaluated in the Cerrado biome. The apparent stability of the larger mammal fauna in the region must be supported, at least in part, by large populations of mammals living in the Pantanal biome and Maracaju Mountains (Tomas et al. 2009), which are adjacent to the study region. Otherwise, it is well known that habitat fragmentation

leads to faunal impoverishment in the long term (Silva and Tabarelli 2000; Brito and Grelle 2004), and that faunal and landscape management are necessary to diminish this problem.

Role of gallery forests

The effective presence of gallery forest in the study region (see Figure 1) is another determinant factor for mammal habitat selection and conservation in the region, since many mammal species of forested savannah use this habitat (Bonvicino et al. 1997), possibly as a corridor (sensu Pardini et al. 2005), or are even gallery forest dwellers (Redford and Fonseca 1986; Johnson et al. 1999). Gallery forest is a very different habitat than savannah in many respects, such as tree density, liana density, and humidity (Hannibal and Cáceres forthcoming). We have recorded evidence of a different community of small mammals living in gallery forests, with the exclusive presence of species such as the rodents *Proechimys longicaudatus*, *Nectomys rattus*, and *Oecomys bicolor*, and the major occurrence of *Hylaeamys megacephalus*. These occurrences agree with studies elsewhere in the Cerrado biome (Mares et al. 1986; Bonvicino, Cerqueira et al. 1996; Bonvicino, Lemos et al. 2005). Such specificity may be extended to the capuchin monkey *C. libidinosus* (=*C. cay*) which occurs exclusively in gallery forests, as observed elsewhere in the Cerrado biome (Johnson et al. 1999; Cáceres, Bornschein et al. 2008). Although gallery forests can also be used as shelter, we report here an overall use of gallery forests and savannah fragments by several mammal species, especially the tapir *T. terrestris*, the agouti *D. azarae*, and the collared peccary *P. tajacu*. This information is new for the Cerrado biome, in which most large-mammal species use gallery forests and savannah fragments of different sizes (Johnson et al. 1999; Cáceres, Bornschein et al. 2008). This indicates the relatively good conservation status of the study region in the southern Cerrado biome, as a mosaic of savannah remnants interconnected by gallery forests and pasture matrices.

Final considerations

Fragmentation of the woodland savannah and of the gallery forest influences the community structure of mammals, but particularly that of the small mammals. Large mammals appear to be less influenced by such fragmentation, but on a scale still unknown, since their population levels were not assessed. For medium- and large-sized fauna, smaller fragments exhibited similar richness and species composition to larger fragments, indicating that the large mammals can move between fragments. This should be facilitated by the matrix of pastures and the relatively short distances between these fragments, when centering on the larger mammal fauna, with higher dispersal and migration abilities. However, the regional mammal community structure is not complete because of the absence of a top predator, the jaguar *Panthera onca*, in the study area, which is thought to have been extinct from the region. The nearest jaguar population persists in the Pantanal, about 60 km away from the study region (Tomás et al. 2009). In addition, the White-lipped Peccary *Tayassu pecari* occurs only in the vicinity of the region (N.C. Cáceres, personal observation). Additional studies are necessary to understand better the community structure of mammals in this region of the Cerrado biome, with the aim of assessing the biogeographic relationships of different, adjacent landscapes and future conservation practices.

Acknowledgements

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