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ORIGINAL ARTICLE

Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes

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Abstract Despite major advances in mammal research, there are knowledge gaps regarding distribution, composition, and the functional role of mammal species within agricultural and fragmented landscapes. Also, there is a lack of knowledge about which factors influence mammal assemblages within agricultural ecosystems. Therefore, this study aimed to estimate the contribution of forest cover, functional connectivity, drainage, and amount of sugar cane toward explaining the functional diversity of terrestrial mammals. We made an inventory of terrestrial mammals in an agricultural and fragmented landscape in an Atlantic Forest-Cerrado ecotone in southeastern Brazil, assessed the functional diversity of mammal assemblages, and proposed conservation strategies at the landscape level. Data collection occurred from September/2011 to August/2012 through a combination of complementary methods: active search; trapping stations; collection of fecal samples, which were identified by hair cuticle and fecal DNA analysis; and data from the literature. Functional diversity (FD) was calculated using a set of ecological traits including body mass, locomotion form, behavioral and dietary traits, and the environmental sensitivity of species. Akaike information criterion was used to compare generalized linear models between FD values and landscape metrics. Our results reveal a surprising insight about the role exerted by agricultural and fragmented landscapes, which still sustain impressively high biodiversity levels and a meaningful

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amount of ecological functions, indicating some resistance of species to pressure from the agricultural matrix and advancing urbanization. The amount of ecological functions performed by mammal species within agricultural and fragmented landscapes was similar to pristine areas and more preserved landscapes. Functional connectivity (amount of area assessed for species able to cross 200 m of matrix) was the most plausible model (wAICc = 0.873). Thus, we concluded that improving functional connectivity guarantees high FD values, and we demonstrate the importance of maintaining and restoring structural connections between fragment patches within these landscapes for species conservation and the maintenance of populations over time.

Keyword Functional diversity · Connectivity · Tracks · Fecal DNA analysis · Hair cuticle analysis · Live-traps

Introduction

Among the factors that drive declines in biodiversity worldwide, habitat loss and fragmentation are known to have severe impacts on vertebrate communities (Gascon et al. 1999; Pardini et al. 2010; Ferraz et al. 2012), particularly on mammals. These processes trigger a selective effect on communities, which tends to eliminate sensitive species in favor of generalist ones (Ceballos and Ehrlich 2002; Fahrig 2003; Ferraz et al. 2010), resulting in wildlife assemblages that are impoverished in terms of species diversity (Silva and Pontes 2008; Tabarelli et al. 2010) and ecological functions (Flynn et al. 2009; Magioli et al. 2015). This selective effect can be observed in distinct ecosystems, including the Brazilian Atlantic Forest and Cerrado biomes, two of the most threatened biodiversity hotspots in the world (Mittermeier et al. 2011). Nowadays, both biomes present high levels of fragmentation and several areas that are surrounded by monocultures, forestry or cities (Klink and Machado 2005; Ribeiro et al. 2009).

Despite all modifications caused by human activity, these agricultural and fragmented landscapes still retain high levels of biodiversity (Galetti et al. 2009) and species that perform a significant amount of ecological functions (Magioli et al. 2015). These environments represent not only essential refuges for the fauna but also important providers of ecosystem services at the landscape level. Studies conducted over the last 15 years in agricultural and fragmented landscapes in the Atlantic Forest and Cerrado show evidence of the presence of important and threatened mammal species (Chiarello 2000a; Rocha and Dalponte 2006; Dotta and Verdade 2007; Silva and Pontes 2008; Eduardo and Passamani 2009; Bruna et al. 2010; Lessa et al. 2012; Hannibal 2014; Magioli et al. 2014a; Reale et al. 2014; Estrela et al. 2015) such as large predators (*Puma concolor*, *Leopardus pardalis*, and *Chrysocyon brachyurus*), large herbivores (*Mazama* sp.), and seed dispersers (*Dasyprocta* sp., *Cuniculus paca*, *Pecari tajacu*). Recent evidence also indicates that some species (such as *P. concolor*, *Cuniculus paca*, *Coendou spinosus*, *Dasypus novemcinctus*, *Hydrochoerus hydrochaeris*, and small mammals) use the modified landscape matrix (i.e., the agricultural matrix) as habitat and a food source (Magioli et al. 2014b).

Although agricultural and fragmented landscapes apparently maintain high biodiversity levels, it is possible that some important functional traits have been lost. Species such as the jaguar (*Panthera onca*)—a top predator—the southern muriqui (*Brachyteles arachnoides*), the tapir (*Tapirus terrestris*), and the white-lipped peccary (*Tayassu pecari*)—large seed dispersers—are possibly extinct in these landscapes (Galetti et al. 2013; Jorge et al. 2013), and the functional roles they play in the ecosystem are consequently being lost. Thus, we require information on the remaining functional traits in these landscapes to assess which ecological functions still occur.

Functional diversity measurements gained prominence in several ecology fields and with different taxonomic groups over the last decade (Cianciaruso et al. 2009). These measurements use values and ranges of biodiversity traits to assess how they influence ecosystem functioning (Tilman 2001); they also provide insights about the ecological functions performed by each species (Petchey and Gaston 2002). Functional diversity can determine the amount of ecological functions remaining in agricultural and fragmented landscapes in comparison to pristine areas, allowing the proposal of novel conservation planning strategies (Magioli et al. 2015; Ribeiro et al. 2016).

When working at the landscape scale, several factors can influence biodiversity and the ecological functions it performs, because landscape structure affects the distribution and abundance of organisms (Fahrig 2005). Recent mammal studies incorporate landscape metrics as explanatory variables for traditional measures (e.g., species richness and diversity), such as habitat amount, fragmentation levels, and impacts caused by the landscape matrix and urbanized areas (Andrén 1994; Fahrig 2003; Pardini et al. 2005; Umetsu and Pardini 2007; Lyra-Jorge et al. 2010; Dotta and Verdade 2011; Thornton et al. 2011; Bogoni et al. 2016). Nevertheless, there is little information about the influence of landscape metrics on ecological functions and species functional traits.

Thus, the present study aimed to estimate the contribution of forest cover, functional connectivity, drainage, and the amount of sugar cane plantations toward explaining the functional diversity of terrestrial mammals. Since knowledge on species occurrence is essential to calculate functional diversity indices, we conducted an inventory of terrestrial mammals (small-, medium- and large-sized) within an agricultural and fragmented landscape to increase knowledge of the species that persist therein. Studies that use a single inventory method possibly underestimate species richness and diversity, because each method is selective with respect to the species it can record (e.g., sand plots, camera trapping, active search).

Consequently, those studies may also underestimate the importance and conservation value of a specific area. Therefore, we proposed the use of multiple inventory methods with the intention of creating a more realistic picture of the mammal assemblages in our studied landscape. We assessed the functional diversity of the recorded mammal assemblages and compared them to assemblages in more preserved landscapes and pristine areas. Finally, we propose conservation strategies with a landscape perspective.

Material and methods

Landscape of study

The landscape of study is located at Campinas Metropolitan Region (CMR), São Paulo State, Brazil, which comprises 20 municipalities and represents the third largest industrial center in the country (AGEMCAMP–Agência Metropolitana de Campinas 2014). The CMR landscape is mainly composed of urbanized areas (23.3 %), sugarcane plantations (19.2 %) and an extensive road network, with only 9.3 % of forest cover, and low percentages of other land uses (Matias et al. 2012); such a landscape mosaic is commonly found in southeastern Brazil (Silva and Tabarelli 2000). This region is located in an ecotone between Atlantic Forest and Cerrado biomes (IBGE – Instituto Brasileiro de Geografia e Estatística 2004a), where the predominant vegetation is semi-deciduous forests (IBGE – Instituto Brasileiro de Geografia e Estatística 2004b). In the northern area of the CMR (665 km^2), we selected eight forest fragments (Fig. 1) with areas ranging from 44.9 to 234.1 ha. The fragments F6 and F8 are federally protected areas, Area of Ecological Interest "Matão de Cosmópolis" and Area of Ecological Interest "Mata de Santa Genebra," respectively.

Medium and large-sized mammal survey

To produce the most comprehensive list of mammalian species in this landscape, and to address the lack of published studies regarding species distribution in São Paulo State (Vivo et al. 2011), we employed two complementary methods: (1) active search for direct and indirect evidence, and (2) the identification of fecal samples by hair cuticle and DNA analysis.

Active search

In this study, we classified cursorial mammals weighing between 1 and 7 kg as medium-sized (Chiarello 2000b) and those weighing over 7 kg as large-sized (Emmons and Feer 1997). We collected data through an active search method

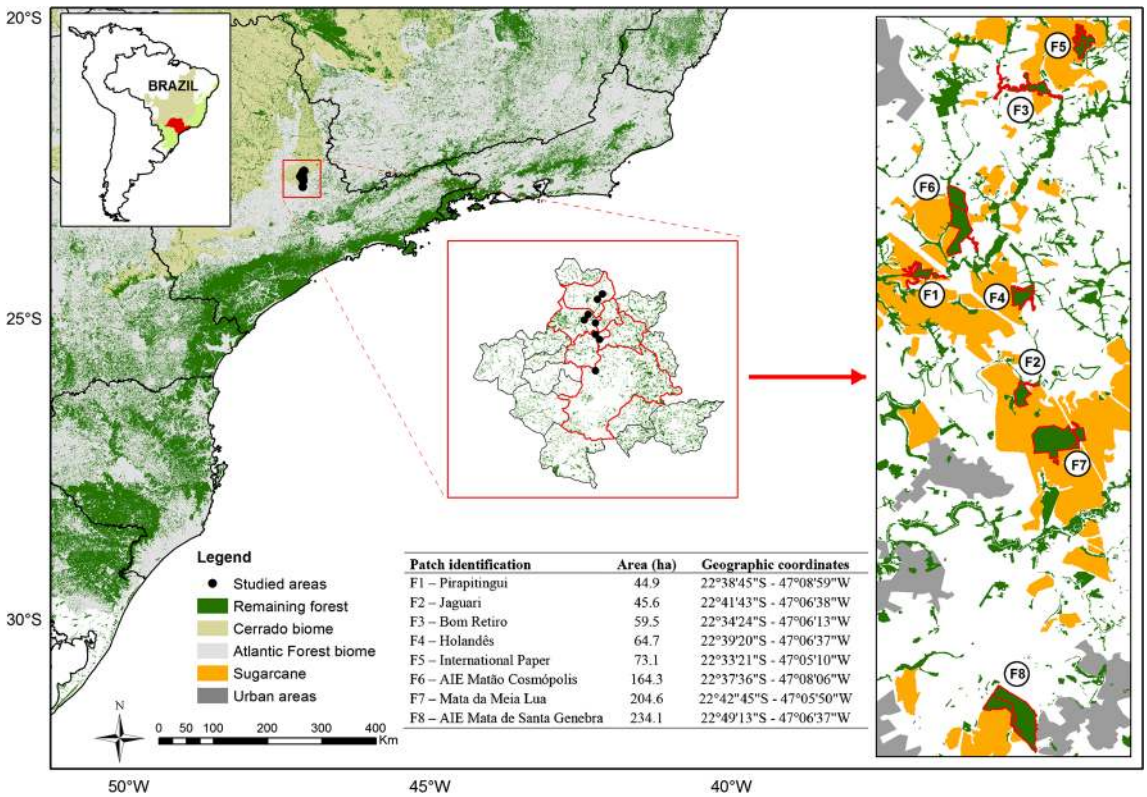

Fig. 1 Study landscape located at the northern area of the Campinas Metropolitan Region (CMR), São Paulo, Brazil. The studied forest fragments are highlighted

(Voss and Emmons 1996), which consisted of walking on dirt roads and trails, at an average speed of 1 km/h, on the edges of all studied forest fragments while searching for direct (i.e., sightings, vocalizations) and indirect (i.e., tracks, feces, carcasses, burrows, food leftovers) evidence of mammalian activity. This method also allowed for the identification of small-sized species (<1 kg) and the composition of the small mammal species list. During the active search, we collected fecal samples of felids and canids; this complementary method improved species identification by using hair cuticle and fecal DNA analysis. Both methods are described below. When possible, we also collected hair and blood samples from road-killed mammals within the study area.

Each individual sampling campaign consisted of five consecutive days. Sampling always started at 8 am and lasted three to five hours per fragment, depending on the amount of animal signs and fecal samples found. Fifteen sampling campaigns were conducted between September 2011 and August 2012. The minimum time interval between sampling of individual fragments was 2 weeks (e.g., the sampling campaigns were often, but not always, conducted every other week). Rainy days and sugarcane harvesting were obstacles to sampling on some days, since the sampling methods depended on observation of tracks and other vestiges that can be obscured by rain or crop management activities. In the end, we achieved 67 days of survey for all sites, which accounted for 678.5 km of cumulative sampling.

During sampling, we carefully measured and photographed all visible tracks and compared them with guidebooks (Becker and Dalponte 1999; Oliveira and Cassaro 2006; Borges and Tomás 2008). We also measured and photographed all fecal samples, bagging and labelling them with information about the site and the geographic coordinates. Fecal and hair samples collected for DNA analysis were stored in sterile preservative-free plastic tubes. For blood samples, we used tubes containing EDTA. All this material was maintained at −22 °C in the laboratory until DNA extraction. To identify other medium- and large-sized mammal evidence (e.g., vestiges, sightings, vocalizations), we used the support of specialized literature (Emmons and Feer 1997; Chame 2003; Borges and Tomás 2008).

Hair cuticle analysis

Following Korschgen (1980), we fragmented and soaked the collected fecal samples in soapy water for a day, subsequently washed them in running water with the aid of a 1 × 1 mm mesh sieve, and then screened the moist matter. The resulting material was dried in an oven at 50 °C and placed in plastic bags for later identification of food items and predator guard-hairs. The samples were identified using the hair cuticle analysis described in Quadros (2002). The predator guard-hairs were cleaned with 70 % alcohol and dried with absorbent paper, deposited on a slide containing a thin layer of partially dried nail polish, and finally covered by another slide wrapped in transparent tape. This set of slides was fixed, pressed, and left to rest for a day. Then, the hair was removed from the slide, and its imprint was photographed in a microscope at ×150 magnification. We identified the species through comparisons of the hair imprint with photos from Quadros (2002) and with reference collections from museum species.

DNA analysis

We extracted the DNA from fecal samples with the commercial silica-binding extraction kit "QIAmp® DNA Stool Mini Kit, Qiagen" following the manufacturer's instructions. All DNA extractions occurred in a UV-sterilized laminar flow hood in an isolated laboratory area dedicated to noninvasive samples. We treated the equipment, including trays, spatulas, and forceps, in a 20 % sodium-hypochlorite bath for at least 10 min to avoid contamination. Each batch of extractions ($n = 12$ to 15) included one negative control (sterile water). These negative controls were included in all PCR reactions to monitor possible contaminations. For blood and hair DNA extractions, we followed a phenol/chloroform/isoamylic ethanol protocol (Sambrook et al. 1989). The species identification process used two short fragments of the mtDNA ATP synthase subunit 6 (ATP6, 126pb) and cytochrome oxidase I (COI, 187 pb) genes, as described in Chaves et al. (2012). Products were visualized on a 1 % agarose gel stained with GelRed (Biotium), purified using the enzymes ExoSAP-IT (Affymetrix), sequenced using BigDye Terminator sequencing kit (Applied Biosystems), and analyzed in ABI PRISM 3130 Genetic Analyzer. We aligned all of the DNA sequences with the CLUSTALW algorithm, implemented in Geneious pro software (Drummond et al. 2011), and compared them with reference sequences from multiple Neotropical carnivore species (Chaves et al. 2012) available on http://dna-surveillance.fos.auckland.ac.nz:23060/page/carnivora/title. We used the neighbor-joining algorithm (Saitou and Nei 1987) to assess species identity as inferred by reliable clustering with reference sequences, which we measured by 1000 bootstrap replications.

Small mammal survey

To sample small mammals, we selected six forest fragments in the study area, five of smaller size (fragments F1, F2, F3, F4, and F5) and one larger area as reference (fragment F7, Fig. 1), as the larger area may support higher species diversity and greater vegetation complexity and structure (August 1983; Robinson and Redford 1986). We employed two methods: (1) trapping stations composed of Sherman and Young traps and (2) an active search for direct and indirect evidence (as described for medium- and large-sized mammals). Data was

available for fragment F8 (see MMA – Ministério do Meio Ambiente 2010); fragment F6 was sampled only by the active search method due to time constrains for captures.

Trapping stations

In each sampling site, we placed 40 trap stations at 10-m intervals along one transect. Each station contained two Sherman traps (one on the ground and another in the understory). Additionally, every other station included Young traps, which were placed on the ground. We installed a total of 80 Sherman traps and 20 Young traps at each sampling site and recorded the geographic coordinates of their locations. The traps remained open for four consecutive nights, and the surveys were conducted in the morning. We avoided sampling during full moons, because they may have a selective effect on the capture of nocturnal species (e.g., Beltran and Delibes 1994; Upham and Hafner 2013).

We baited the traps with a mass composed of ripe banana, corn meal, fish liver oil, vanilla extract, and peanut butter. The captured specimens were measured (head-body length, tail, foot, and ear), weighed (Pesola® dynamometers), and individually marked with small cuts on their ears to check for recaptures. We recorded data on sex, age (young or old), station number, trap position (ground or understory), and reproductive condition of collected specimens. After these procedures, we released the animals at the same capture site. Specimens that we were unable to identify in the field were euthanized and collected following the ethical standards recommended by Brazilian Society of Mammalogy (Resolution n. 1000/2012). We conducted 12 sampling campaigns between August 2011 and August 2012—two in each forest fragment (one in the rainy season and the other in the dry season)—resulting in a sampling effort of 4800 trap-nights.

Data analysis

We estimated mammal species richness using 1st order Jackknife and Bootstrap. For small mammals, we considered the capture success in each forest fragment and for the whole sample as the relative frequency of captures by the total sampling effort (total trap-nights). Threat categories (i.e., vulnerable, endangered, critically endangered) were identified according to Percequillo and Kierulff (2009), Portaria MMA n. 444 (2014) and IUCN – International Union for Conservation of Nature and Natural Resources (2015). The nomenclature we used followed Paglia et al. (2012), Trigo et al. (2013), and Vivo and Carmignoto (2015). In order to produce the most comprehensive mammalian list, we also considered records of additional species found in studies (i.e., papers, theses and technical reports) conducted previously (1997–2014) in our study sites and in other forest fragments of CMR.

Functional diversity analysis

For the functional diversity calculation of medium and large-sized mammal assemblages, we also included some small-sized species that are commonly recorded in medium- and large-sized mammal inventories (e.g., *Cavia* sp., *Callithrix* sp., *Guerlinguetus* sp.; see Magioli et al. 2015). We used the functional diversity measure (FD) proposed by Petchey and Gaston (2002, 2006) for the calculation. The analysis consists of (i) building a trait matrix for each assemblage, (ii) converting the trait matrix into a distance matrix, (iii) grouping species to produce a functional dendrogram, and (iv) calculating a FD value for each assemblage by summing the total branch length of the dendrogram. We used the modified Gower's distance (Pavoine et al. 2009) for the distance matrix construction with UPGMA clustering.

To modify the assemblage created by Magioli et al. (2015) for all the medium and large-sized mammals of the Atlantic Forest biome ($N = 88$), we used current literature on mammal nomenclature and distribution ($N = 83$) and standardized the FD values for each assemblage, ranging from 0 to 1. We selected species traits including those based on resource use, such as physical (body mass and form of locomotion) and dietary data (trophic guild, foraging substrate, and food type), a behavioral trait (social behavior) and an environmental sensitivity trait (species sensitivity), which relates the tolerance of species to habitat modification, resource availability, and anthropogenic pressure. Species classification can be seen in Electronic supplementary material (ESM) 1 Table S1. We calculated FD values for each mammal assemblage in the studied sites and for the whole mammal assemblage recorded in the landscape. These values were then compared to assemblages in areas with similar size and landscape configuration (e.g., inserted in agricultural matrices, similar connectivity degree, and disturbance regime) and to assemblages in large preserved areas (ESM 1 Table S2). From assemblages used for comparison, only the species lists were compiled for FD calculation. All analyses were performed in R 3.2.2 (R Core Team 2015).

We used the Akaike information criterion corrected (AICc) for small samples (Burnham and Anderson 2002) to compare generalized linear models between FD values (response variable) and landscape metrics (explanatory variables), aiming to determine which model best explains the variation in FD values. For the explanatory variables, we created one buffer of 250-m radius and another of 1000-m radius from the center of each forest fragment. We then calculate the variables for both buffers, including the percentage of forest cover, percentage of sugar cane plantations and drainage density; we also calculated and included as variables the amount of forest that can be assessed by species that have the ability of cross 200 and 500 m of open areas (i.e., pasture and sugarcane)—henceforth called the area connected at 200 and 500 m. As species richness is closely related to FD (Petchey and Gaston 2002),

and as a significant positive relationship has been observed between FD and patch size for medium- and large-sized mammals in the Atlantic Forest (Magioli et al. 2015), our models excluded these variables (i.e., species richness and patch size). We considered the best models as those that presented a ΔAICc ≤2 and a high Akaike weight (wAIC). We conducted AICc analysis using the 'bbmle' package (Bolker 2008) available in R 3.2.2.

Results

Medium- and large-sized mammals

Active search

We recorded 29 species of medium- and large-sized mammals, including 26 native and 3 exotic species (Table 1, ESM 2 Fig. S1). The order Carnivora showed the highest number of species, with 12 recorded species, belonging to four families: Canidae, Felidae, Mustelidae and Procyonidae. *Lycalopex gymnocercus* represents a new record for São Paulo State. Of all medium- and large-sized species, seven are listed under some threat category in São Paulo State: *Myrmecophaga tridactyla*, *Chrysocyon brachyurus*, *Leopardus pardalis*, *Leopardus wiedii*, *Leopardus guttulus*, *Puma concolor*, and *Mazama americana* (Percequillo and Kierulff 2009). These species—with the exception of *M. americana* and *L. pardalis*, but including *Puma yagouaroundi* and *Alouatta guariba*—are also listed nationally as being under some threat (Portaria MMA n. 444 2014). At the global scale, only two species are listed as being under some threat: *M. tridactyla* and *L. guttulus* (IUCN 2015). *Cabassous tatouay*, *Galictis cuja*, and *L. wiedii* are considered data deficient species for São Paulo State (Percequillo and Kierulff 2009; Vivo et al. 2011). The recorded species richness was similar to that presented by 1st order Jackknife (27.93 ± 0.93) and Bootstrap (27.63) estimators, which suggests that sampling sufficiency was achieved for the study area.

Hair cuticle analysis and DNA identification

We collected 652 fecal samples for hair cuticle analysis and initially identified these samples in the field as deposited by felids ($N = 539$) and canids ($N = 113$; Fig. 2a). Site F7 provided the highest number of samples ($N = 171$), for both felids and canids (Fig. 2a). We randomly selected 251 fecal samples for screening and identified 115 of them to species level, resulting in a record of eight species (*Cerdocyon thous*, *C. brachyurus*, *Eira barbara*, *L. pardalis*, *L. guttulus*, *L. wiedii*, *P. concolor*, and *P. yagouaroundi;* Fig 2b) and complementing the lists for each studied site. In addition, we collected 39 fresh fecal samples exclusively for DNA analysis and successful recovered the DNA of 17 (43.6 %) of them, leading to the identification of five species (*C. thous*, *C. brachyurus*, *L. gymnocercus*, *L. pardalis*, and *P. concolor*). We identified two road-killed individuals as *L. wiedii* through DNA analysis of both hair and blood samples of each individual.

Small mammals

We recorded 14 small mammal species: 5 by live-traps, 5 by active search, and 4 from data in the literature (Table 1, ESM 2 Fig. S2). Families Cricetidae and Didelphidae were the most representative in number of recorded species ($N = 6$ in each family). None of the recorded species were listed in any threat category.

Trapping stations

We performed 145 capture events—85 in the dry season and 60 in the rainy season—corresponding to 3 % efficiency per trap-night, which resulted in a record of five species (Table 1). Most capture events (41 %) occurred in F7, followed by 22 % in F2 and 15 % in F1, which are the smaller forest fragments, while those of intermediate size (F3, F4, and F5) represent 6 to 8 % of the events (Table 1). The estimated species richness for all sampled sites was 5.00 ± 0.00 for 1st order Jackknife and 5.00 for Bootstrap. Species richness ranged from two to four species, with higher richness and a lower capture rate in F3. *Akodon montensis* (36 % of captures) and *Oligorizomys nigripes* (21 %) were predominant among rodents (Table 1). *Cerradomys subflavus* was recorded only in F2 and F3. For marsupials, *Didelphis aurita* had the highest number of captures (19 %) and was virtually restricted to F7, while *Didelphis albiventris* (18 %) appeared in all sampled sites, except in F7; both species occurred in sympatry in F3 (Table 1). Studies previously conducted in F8 recorded 12 small mammal species in this fragment [Table 1, see MMA (2010) and Siviero and Setz (2011)].

Active search

We recorded five small mammal species through tracks, sightings and vocalizations (Table 1). The genus *Callithrix* was recorded only through vocalization in F7; however, three species of this genus have been recorded in CMR (Table 1), compromising the identification at species level through vocalization data alone. Through tracks, we identified *Lutreolina crassicaudata* in F3 and F6, and *Nectomys squamipes* in F3; *Cavia aperea* was sighted in F1. On a post-survey visit in F3, we sighted *C. penicillata* and *Guerlinguetus brasiliensis*, and the records from this non-survey sighting were included in our species list.

Table 1 Mammal species recorded in each forest fragment and at Metropolitan Region of Campinas (CMR), São Paulo, Brazil, including record type, total number of captures, and total number of species per fragment

Taxon	Studied forest remnants									
	F1	F2	F3	F4	F5	F6	F7	F8	CMR	Record
Didelphimorphia										
Didelphidae										
Caluromys philander Linnaeus, 1758								x[d]	x	R
Chironectes minimus (Zimmermann, 1780)									x[g]	R
Didelphis albiventris Lund, 1840	x (2)	x (11)	x (2)	x (9)	x (2)	x		x[d]	x	T,C (26)
Didelphis aurita (Wied-Neuwied, 1826)			x (1)				x (26)	x[e]	x	T,C (27)
Gracilinanus microtarsus Wagner, 1842								x[d]	x	R
Lutreolina crassicaudata (Desmarest, 1804)			x			x		x[d]	x	T,R
Pilosa										
Myrmecophagidae										
Myrmecophaga tridactyla Linnaeus, 1758							x		x	T
Cingulata										
Dasypodidae										
Cabassous tatouay (Desmarest, 1804)	x	x	x	x	x	x	x		x	T
Dasypus novemcinctus Linnaeus, 1758	x	x	x	x	x	x	x	x	x	T,O
Dasypus septemcinctus Linnaeus, 1758			x			x[f]	x	x	x	T
Euphractus sexcinctus (Linnaeus, 1758)			x		x	x[f]	x	x[d]	x	T
Artiodactyla										
Cervidae										
Mazama americana (Erxleben, 1777)			x		x		x	x[d]	x	S,T,R
Mazama gouazoubira (G. Fischer [v on Waldheim], 1814)					x	x	x	x[d]	x	T,R
Suidae										
Sus scrofa (Linnaeus, 1758)[a]					x				x	T
Primates										
Atelidae										
Alouatta guariba (Humboldt, 1812)							x	x	x	S,V
Callitrichidae										
Callithrix Erxleben, 1777							x			V
Callithrix aurita (É. Geoffroy in Hum boldt, 1812)									x[h]	R
Callithrix jacchus (Linnaeus, 1758)									x[b]	R
Callithrix penicillata (É. Geoffroy, 1812)			x						x	S,V,R
Cebidae										
Sapajus nigritus Goldfuss, 1809						x	x	x	x	S,V
Pitheciidae										
Callicebus nigrifrons (Spix, 1823)									x[b]	R
Carnivora										
Canidae										
Canis familiaris (Linnaeus, 1758)[a]	x	x	x	x	x	x	x	x	x	S,T,F
Cerdocyon thous (Linnaeus, 1766)	x	x	x	x	x	x	x	x	x	S,T,H,M
Chrysocyon brachyurus (Illiger, 1815)	x	x	x		x	x	x		x	T,H,M
Lycalopex gymnocercus (G. Fischer, 1814)	x				x				x	F,M
Felidae										
Leopardus pardalis (Linnaeus, 1758)	x	x	x	x	x	x	x	x	x	T,H,M
Leopardus guttulus (Schreber, 1775)	x	x	x	x	x	x	x	x	x	T,H
Leopardus wiedii (Schinz, 1821)	x	x	x	x	x	x	x	x	x	T,H,M
Puma concolor (Linnaeus, 1771)	x	x	x	x	x	x	x	x[d]	x	T,H,R,M

Table 1 (continued)

Taxon	Studied forest remnants									
	F1	F2	F3	F4	F5	F6	F7	F8	CMR	Record
Puma yagouaroundi (É. Geoffroy Saint-Hilare, 1803)	x	x	x	x	x	x	x	x	x	T,H
Mustelidae										
Eira barbara (Linnaeus, 1758)						x[f]	x	x	x	T,R,H
Galictis cuja (Molina, 1782)		x	x	x	x	x	x	x[d]	x	S,T,R
Lontra longicaudis (Olfers, 1818)		x	x			x	x[c]	x	x	T,F,R
Procionidae										
Procyon cancrivorus (G. [Baron] Cuvier, 1798)	x	x	x	x	x	x	x	x	x	F
Lagomorpha										
Leporidae										
Lepus europaeus Pallas, 1778[a]	x	x	x	x	x	x	x	x	x	S,T
Sylvilagus brasiliensis (Linnaeus 1778)	x			x		x	x	x[d]	x	S,T,F,R
Rodentia										
Caviidae										
Cavia aperea Erxleben, 1777	x							x[d]	x	S,R
Hydrochoerus hydrochaeris (Linnaeus, 1766)	x	x	x	x		x	x	x	x	S,T,F
Cricetidae										
Akodon montensis Thomas, 1913	x (9)	x (13)		x (1)			x (28)	x[d]	x	C (51)
Calomys cf. *callosus* (G. Fischer, 1814)								x[e]	x	R
Cerradomys subflavus (Wagner, 1842)		x (8)	x (1)						x	C (9)
Necromys lasiurus (Lund, 1840)								x[e]	x	R,C (1)
Nectomys squamipes (Brants, 1827)			x						x	T,R
Oligoryzomys nigripes (Olfers, 1818)	x (11)		x (5)	x (2)	x (8)		x (4)	x[e]	x	R,C (30)
Cuniculidae										
Cuniculus paca (Linnaeus, 1758)		x		x		x[f]	x	x[d]	x	F,R
Echimyidae										
Myocastor coypus (Molina, 1782)			x				x	x[d]	x	T
Erethizonthidae										
Coendou spinosus (F. Cuvier, 1823)	x				x	x[f]	x	x	x	T,O
Sciuridae										
Guerlinguetus brasiliensis (Gmelin, 1788)			x			x[f]		x[d]	x	S,R
Species richness (except exotic species)	18	17	25	16	18	24	29	33	44	–
Total of captures	22	32	9	12	10	–	58	–	–	–

The number of captures in live-traps is displayed in parentheses in front of each captured species

C captures, *R* reference, *S* sighting, *V* vocalization, *T* tracks, *F* feces, *H* hair cuticle analysis, *M* DNA identification, *O* other vestiges (burrows, carcasses, food leftovers)

[a] Exotic species

[b] Gaspar 1997

[c] Rodrigues 2009

[d] Monteiro-Filho 1995

[e] (MMA – Ministério do Meio Ambiente 2010)

[f] Magioli et al. 2014a

[g] Siviero and Setz 2011

[h] Fabiana Umetsu (pers. comm.)

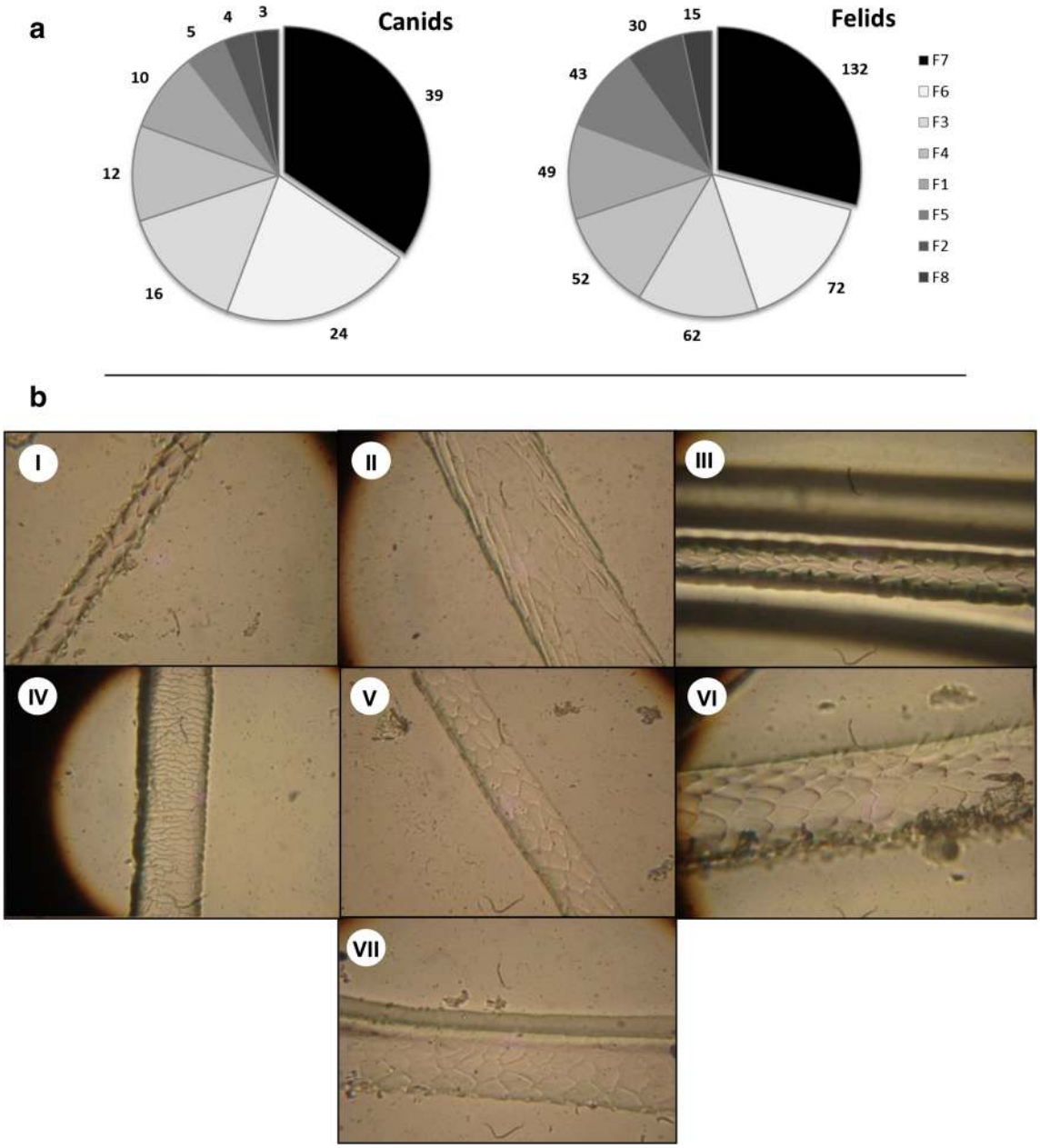

Fig. 2 **a** Distribution of the collected fecal samples in each forest fragment at Campinas Metropolitan Region (*CMR*), São Paulo, Brazil. **b** Pictures of the guard-hairs identified by optical microscope with a ×150 magnification. (*I*) *Leopardus pardalis*, (*II*) *Leopardus guttulus*, (*III*) *Leopardus wiedii*, (*IV*) *Puma concolor*, (*V*) *Puma yagouaroundi*, (*VII*) *Cerdocyon thous*, (*VIII*) *Chrysocyon brachyurus*

Species richness at CMR

Four species (*Callicebus nigrifrons*, *Callithrix jacchus*, *Callithrix aurita*, and *Chironectes minimus*), which were not detected in our survey, were detected in previous studies in Campinas-SP (Gaspar 1997, Fabiana Umetsu, pers. comm., Siviero and Setz 2011). Including *C. aurita*, the number of threatened species increased to eight (of mammals of all sizes) for São Paulo State (Percequillo and Kierulff 2009). Through the addition of these species records, species richness increased from 40 to 44 species (Table 1) for all mammals. Considering each mammal group, richness increased to 17 small mammal species, and to 27 species of medium- and large-sized mammal species, corresponding to approximately 60 % of the medium- and large-sized mammal species known to occur in São Paulo State ($N = 45$, Vivo et al. 2011).

Functional diversity analysis

The recorded mammal assemblages showed a wide range of FD values (0.31–0.54) similar to other mammal assemblages in areas with similar characteristics, which also presented a

wide range of values (0.29–0.48; Fig. 3a). The larger forest fragments (>150 ha) in these agricultural and fragmented landscapes showed the highest FD values. As expected, assemblages in pristine areas presented high FD values with low variation between them (0.62–0.67; Fig. 3a).

In a landscape perspective, the whole mammal assemblage recorded in our study presented a higher FD value (0.63) than values obtained for assemblages in similar landscapes (Fig 3b), such as those studied by Martin (2007), Silva and Pontes (2008) and Dotta and Verdade (2011). When comparing the FD value of the whole assemblage to that of an assemblage in a landscape with higher forest cover and larger preserved forest fragments, such as the one studied by Chiarello (1999; 0.65), values were similar (Fig. 3b). We observed the same response when FD values were compared to large pristine areas, such as those studied by Brocardo et al. (2012), Kasper et al. (2007) and Faria (2006)—0.67, 0.62, and 0.62 respectively.

Landscape metrics, such as the area connected at 200 m and the percentage of forest cover at 250 and 1000 m, showed a significant positive relationship with FD values (Table 2, ESM 3 Fig. S3). However, when we compare the models between FD values and landscape metrics, the model between FD and the area connected at 200 m best explained the variation in FD values (Table 2).

Discussion

Species richness for both mammal groups was similar to assemblages found in larger preserved areas (e.g., Chiarello 1999; Brocardo et al. 2012; Carmignotto 2004), but lacks species such as the largest top predator *Panthera onca*, large seed dispersers *Tapirus terrestris*, *Tayassu pecari*, and *Brachyteles arachnoides*, and the more sensitive species *Speothos venaticus*. Almost half of all recorded species are considered generalists from a habitat and/or resource use perspective; these species are favored by the highly fragmented and agricultural landscape (Bonecker et al. 2009; Dotta and Verdade 2011; Magioli et al. 2014b). Surprisingly, we did not

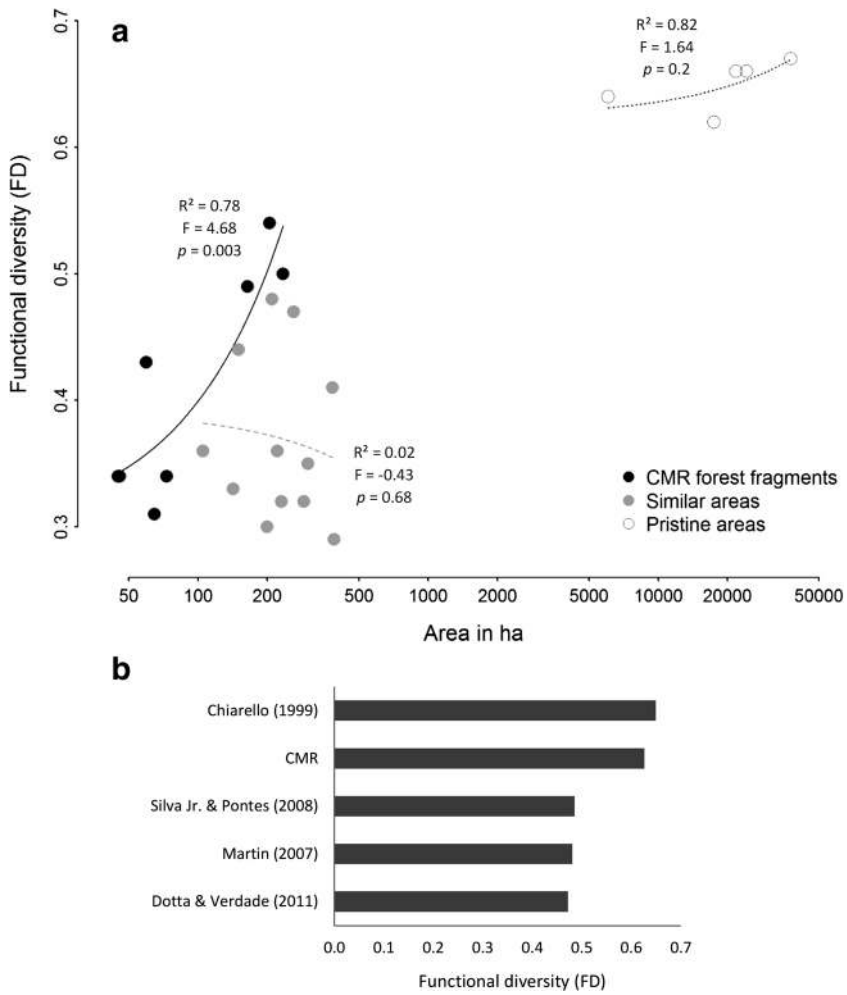

Fig. 3 **a** Comparison of functional diversity (*FD*) values of medium- and large-sized mammal assemblages between the studied sites at Campinas Metropolitan Region (*CMR*), São Paulo, Brazil, with similar and pristine areas. **b** Comparison between the FD values obtained for the whole mammal assemblage recorded at CMR to assemblages in similar and preserved landscapes

Table 2 Relationships and results of model comparisons between FD values and landscape metrics for mammal assemblages in the Campinas Metropolitan Region, São Paulo, Brazil [R^2 (coefficient of determination); F and p (significance of regression coefficients)]

FD~explanatory variable	R^2	F	p	ΔAICc	wAICc
Area connected at 200 m	0.785	4.66	0.003	0.0	0.873
Percentage of forest cover at 1000 m	0.603	3.01	0.024	4.9	0.075
Percentage of forest cover at 250 m	0.517	2.53	0.045	6.4	0.035
Drainage density at 250 m	0.227	−1.36	0.221	10.1	0.006
Area connected at 500 m	0.161	1.07	0.326	10.9	0.004
Drainage density at 1000 m	0.145	−1.04	0.339	10.9	0.004
Percentage of sugarcane at 250 m	0.035	−0.49	0.640	11.9	0.002
Percentage of sugarcane at 1000 m	0.003	−0.15	0.886	12.2	0.002

detect some of the common species that are usually found in Atlantic Forest and Cerrado fragments, such as *Nasua nasua*, *Dasyprocta azarae*, and *Tamandua tetradactyla* (Rocha and Dalponte 2006; Bruna et al. 2010; Dotta and Verdade 2011; Penido and Zanzini 2012); these absences may be related to poaching, small species populations or their extinction in the studied area. Nonetheless, the CMR still maintains threatened species that exhibit habitat and feeding specializations, such as *M. tridactyla* (Medri and Mourão 2005), *M. americana* (Varela et al. 2010) and *L. wiedii* (Oliveira and Cassaro 2006), as well as other extremely rare species such *L. crassicaudata* and *C. minimus*, increasing the conservation value of the region. Furthermore, the records of *Cabassous tatouay*, *Galictis cuja* and *L. wiedii*, species considered data deficient in São Paulo State (Percequillo and Kierulff 2009; Vivo et al. 2011), contribute important information on their distribution.

Only two recorded species, *C. brachyurus* and *D. albiventris*, are characteristic of the Cerrado biome and were expected to occur given that the study area is an Atlantic Forest-Cerrado ecotone. That these species were also recorded in Atlantic Forest fragments (Prado et al. 2008; Cantor et al. 2010, 2013; Dotta and Verdade 2011; Penido and Zanzini 2012; Reale et al. 2014) indicate that they are adapted to survive in these areas. In addition, although not exclusive to the Cerrado biome, some species such as *Calomys* sp., *C. subflavus*, *Necromys lasiurus*, *M. tridactyla* and *L. gymnocercus* are favored by open areas (Braga 2004; Jiménez et al. 2008; Percequillo et al. 2008; Vivo and Carmignoto 2015). Until now, *L. gymnocercus* had not been officially recorded in São Paulo State (Vivo et al. 2011), and it is noteworthy that this record extends the known distribution of the species by approximately 430 km, according to the IUCN distribution map (Jiménez et al. 2008).

The three exotic invasive species we recorded in CMR landscape—*Canis familiaris*, *Lepus europaeus and Sus scrofa*—are known to negatively affect environments by preying on wild animals, introducing diseases, competing with native species for resources, and causing damage to cultivated areas and forest fragments (Campos et al. 2007; Oliveira et al. 2008; Deberdt and Scherer 2007; Zanon and Reis 2010; Pedrosa et al. 2015). Among the recorded species of genus *Callithrix*, C. *jacchus* can be considered a native exotic because its known original distribution is in the north/northeast portion of the Atlantic Forest and Cerrado biomes (Rylands et al. 2008b), while *C. aurita* and *C. penicillata* are expected to occur in the region (Rylands and Mendes 2008; Rylands et al. 2008a).

The large amount of fecal samples we collected indicates an intense use of the landscape by carnivore mammals, as Lyra-Jorge et al. (2008) also observed in a agricultural and fragmented landscape in northeastern São Paulo State. This intensive use may be related mainly to high prey availability, especially of generalist rodent species such as *A. montesis* and *O. nigripies* (Talamoni and Dias 1999; Pardini et al. 2005, 2009; Umetsu and Pardini 2007). These species are common in agricultural landscapes dominated by sugarcane (Gheler-Costa et al. 2012; Martin et al. 2012), and prey to most mammal carnivores that occur in the CMR.

Species identification by hair cuticle and fecal DNA analysis for medium- and large-sized mammals proved to be efficient and reliable complementary tools, increasing species richness and diversity. Fecal DNA analysis is rarely used in Brazil, but the method proved to be an important tool for correct species identification, as in the case of *L. gymnocercus* in our study. The active search method for small mammals resulted in the record of five species (Didelphimorphia, Primates and Rodentia), which indicates that this is also an important complementary method for increasing species richness in inventory studies. Therefore, the use of multiple methods for species identification, such as the methods employed in our study, highlights that inventories based on lesser efforts or on a single method may underestimate species richness and diversity and, consequently, the importance of several areas.

In a landscape perspective, it was evident that the CMR still supports a high amount of ecological functions performed by medium- and large-sized mammals, similar to more preserved landscapes and large pristine areas. Analyzing each studied site individually, the larger ones (>150 ha) presented higher FD values when compared to small similar areas, and their values approached those of pristine areas. Thus, despite the poor conditions this landscape offers (i.e., small forest

patches, low connectivity, high levels of isolation, pressure from the agricultural matrix and the presence of an extensive road network), it still maintains a set of species with important ecological functions. However, the wide range of values within the CMR landscape highlights a scenario common to agricultural and fragmented landscapes, in which they may not be suitable for the maintenance of mammal populations over the long term (Galetti et al. 2009). Flynn et al. (2009) observed that agriculture intensification tends to reduce FD values for mammal assemblages.

The strong relationship between FD values and the area connected at 200 m stresses that connectivity between spatially close forest fragments and riparian vegetation is important, and restoring structural connection can increase the functional diversity of mammal assemblages. Over recent years, the number of studies that include connectivity as a conservation strategy to maintain biodiversity has risen substantially worldwide (Ayram et al. 2015). Several studies with mammals and other taxonomic groups recommend increasing connectivity as an essential measure to maintain wildlife populations (Dixo et al. 2009; Pardini et al. 2010; Martensen et al. 2012; Ferraz et al. 2012; Tambosi et al. 2014; Banks-Leite et al. 2014; Magioli et al. 2015). Connectivity not only augments habitat amount, it also enables species movement and genetic flow across the landscape. Currently, the riparian forests are the only structural connection remaining between forest fragments in the CMR and most fragments in agricultural and fragmented landscapes. However, most of these riparian forest are very degraded (i.e., not exerting their functional role) or even nonexistent at several locations. Therefore, these results stress the urgency of conservation planning actions in a regional context to maintain the species that inhabit the region and their essential functional roles.

Implications for conservation

As presented above, improving connectivity between spatially close forest fragments is an important strategy for species conservation within agricultural and fragmented landscapes. Magioli et al. (2015) recommended compliance with the Brazilian Forest Code (Federal Law No. 12,651/2012) for small forest fragments. This nationwide legislation presents an important set of conservation guidelines for Brazilian forests, in particular the protection of riparian forest ecosystems ('areas of permanent preservation') and the establishment of 'legal reserves', which correspond to a percentage of the land in private farmlands that must be occupied by native forests, acting as stepping stones. In other words, these measures improve connectivity within landscapes (Banks-Leite et al. 2014) and augment their permeability for the fauna. Thus, we recommend that riparian forests should be the target of actions that promote biological restoration in agricultural and fragmented landscapes, which will improve mammal populations' persistence and increase the genetic flow on a regional scale.

In addition to compliance with the Brazilian Forest Code, our recommendations for larger forest fragments (>150 ha)—the most functionally enriched areas—include investments that promote the recovery of the fragments' quality, the increase of their effective area, a reduction of pressure on edges and the control of invasive species (Rodrigues and Gandolfi 2007). Moreover, for a more effective conservation framework, we also recommend the establishment of vegetation corridors through riparian forests linking these larger forest fragments to smaller fragments in the landscape to increase wildlife movement, functional diversity, and genetic flow.

The extensive road network present in São Paulo State, and in the CMR landscape specifically, can act as a barrier for the fauna, blocking the movement of species and the genetic flow across the landscape (Miotto et al. 2011, 2012; Abra 2012; Huijser et al. 2013). There are several records of road-killed mammals in the Atlantic Forest and Cerrado biomes (Coelho et al. 2008; Cáceres et al. 2010; Freitas et al. 2014; Huijser et al. 2013; Bueno et al. 2015), most of which occurr in the CMR landscape and include threatened species such as *P. concolor*, *P. yagouaroundi*, *L. pardalis*, *L. guttulus*, *C. brachyurus*, *M. tridactyla*, and *L. wiedii* (species we address in this study). Therefore, we also recommend investments in mitigation measures such as safe crossing opportunities for wildlife, which may reduce animal-vehicle collisions and road mortality and improve wildlife movement across the landscape (Huijser et al. 2013), especially of abundant large-bodied species such as *Hydrochoerus hydrochaeris*, responsible for accidents with fatal injuries in roads in São Paulo State (Bovo et al. 2016).

Final considerations

Our results reveal a surprising insight about the importance of agricultural and fragmented landscapes, which still sustain impressively high biodiversity levels and a meaningful amount of ecological functions, indicating some resistance to pressure from species to the agricultural matrix and advancing urbanization. Assessing functional diversity in a landscape scale generated more robust information than analyzing each mammal assemblage separately, giving a more comprehensive insight on the amount of ecological functions still occurring. Also, these results offer opportunities to study which ecological services are performed by the remaining species and their impact on ecosystem dynamics. The forest fragments are the last refuges for the fauna in human-dominated landscapes, but are fragile in the context of the landscape structure. The influence exerted by connectivity over functional diversity values highlights the need for actions toward the restoration of functional connectivity on a large scale, aiming at species conservation and the maintenance of populations over time. In

addition, the combination of inventory methods used in our study proved an effective framework for producing the most comprehensive picture of the mammalian species present in a determined area, reducing the odds of underestimating species richness and diversity and, by extension, the importance of an area. There are still gaps of information on how biodiversity persists within agricultural and fragmented landscapes, and future research should focus on themes such as resource and habitat use by species, how they move through the landscape matrix, the ecosystem services they perform and the genetic diversity of wildlife populations, increasing our knowledge of these areas and of species conservation.

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