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Article

The Response of Bats (Mammalia: Chiroptera) to Habitat Modification in a Neotropical Savannah

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Abstract

The Brazilian savanna (Cerrado) is a biodiversity hotspot with high deforestation rates that lead to extensive habitat changes, especially around protected areas (PAs). In our study, we analyzed how bats are affected by habitat changes comparing assemblages inside and outside Cerrado PAs. We compared diversity patterns of bats in relation to species composition, number of captured bats, as well as body condition and reproductive condition in cerrado *sensu stricto* (s.s.) and gallery forests. From September 2007 to June 2008, we captured 495 bats belonging to 25 species, 4 families, and 6 foraging guilds. When comparing captured bats inside and outside PAs, we found different patterns for both habitats, but with no differences in species richness for both habitats in relation to habitat perturbation. In relation to the degree of preservation, bat assemblages tend to be dissimilar between cerrado *s.s.* and similar between gallery forests. Besides that, in cerrados *s.s.*, bats are less captured, or negatively affected, by habitat disturbance outside PAs; while in gallery forests, they are positively affected. Likewise, some bat species in gallery forests present higher body condition and more reproductive individuals outside PAs. Finally, we suggest that the intense habitat change in cerrado *s.s.* does cause negative effects on bats, while the positive effects found in degraded gallery forests may be due to the higher resource availability derived mainly from pioneer plants. Therefore, the presence of both nectarivorous bats in cerrado *s.s.* and frugivorous bats in gallery forests can be considered good indicators for habitat disturbance.

Keywords

Cerrado, deforestation, flying mammals, bioindicator, protected areas

The Brazilian Cerrado is considered the most biodiverse savanna and the third largest hotspot in the world (Myers, Mittermeier, Fonseca, & Kent, 2000), with more than 2,000,000 km^2 distributed across central Brazil and parts of Bolivia and Paraguay (Ratter, Ribeiro, & Bridgewater, 1997). Despite its important biodiversity, the Cerrado presents only 50% of its original area remaining as primary vegetation and the other half has been transformed into pasture for agricultural crops and for other uses. Unfortunately, the Cerrado's area under conservation is less than 3% of its original area (Klink & Machado, 2005). Furthermore, current estimates indicate an annual rate of loss of 0.7%, that is, 700,000 ha/year (Ministério do Meio Ambiente, 2016). The increasing rates of human population growth are adding even more pressure on wildlife populations around protected areas (PAs; Wittemyer, Elsen, Bean, Burton, & Brashares, 2008). If this pattern remains the same, the Cerrado will be only preserved within PAs surrounded by crops, livestock, and cities.

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The Cerrado hosts 251 mammal species (Paglia et al., 2012), of which 118 are bats (Aguiar, Bernard, Ribeiro, Machado, & Jones, 2016), making it the richest mammalian order in the biome. Many bat species present habitat specializations and have specific roosting sites and diets (Kunz & Lumsden, 2003; Patterson, Willig, & Stevens, 2003). Due to a high diversity of foraging strategies, bats are considered of a great importance to the maintenance of ecosystems, providing vital ecological services such as pollination, seed dispersal, and population control of insects (Kalka, Smith, & Kalko, 2008; Mello et al., 2011; Sazima, Buzato, & Sazima, 1999). Due to their species richness, importance as ecosystem services providers, and facility to sample them (Jones, Jacobs, Kunz, Willig & Racey, 2009), bats have been suggested as efficient bioindicators of environmental health (Jones et al., 2009; Medellín, Equihua, & Amin, 2000).

The flight capacity of bats enables them to travel over large distances (Aguiar, Bernard, & Machado, 2014; Arnone, Trajano, Pulcherio-Leite, & Passos, 2016; Bernard & Fenton, 2003) and to explore different phytophisiognomies as well as to explore the fragmented landscape of the Cerrado (Aguiar et al., 2014; Bernard & Fenton, 2003). Despite their high mobility, bat richness, abundance, and assembly composition may vary depending on the different types of habitat degradation (Fenton et al., 1992; Vilchis, Clarke, & Racey, 2007; Willig et al., 2007). Although it has been shown in the literature that habitat degradation caused by habitat fragmentation or other use may cause or not impact in bat species richness, abundance, and assemblage composition, the bat responses to habitat modification is still in debate, and it seems the responses are very species specific (Cunto & Bernard, 2012). Moreover, body condition may be an important factor to be considered when investigating the response of habitat modification on bats. If a shortage in food availability caused by habitat alteration leads to a low body condition in bats, these animals may also not reproduce properly (Kunz & Lumsden, 2003; Patterson et al., 2003) leading to an important population decrease as shown for the vespertilionid greater mouse-eared bat *Myotis myotis* in agricultural landscapes of temperate environments, in which prey availability is low (Zahn, Rodrigues, Rainho, & Palmeirim, 2007).

In this study, we investigated bat community and population parameters in cerrado sensu stricto (s.s.) and gallery forests located inside and outside three PAs in order to assess bat responses to habitat degradation. Cerrado *s.s.* is a savanna-like physiognomy of the Cerrado biome, and gallery forests are riparian formations with continuous canopy that surround rivers and streams (Ribeiro, Walter, Sano, & Almeida, 1998). Our objectives were threefold: (a) to compare diversity patterns between areas inside and outside PAs. To this end, we compared bat assemblages considering species composition and number of captured bats. We also compared bat diversity considering richness and number of captured bats together and separately; (b) to compare whether there are differences in bat body condition inside and outside PAs; and (c) to compare whether there are differences in the number of captured reproductive bat species inside and outside PAs. Regarding our specific objectives, we expected that (a) bat assemblages from inside PAs to be different from bat assemblages outside PAs. Since some species are more sensitive to habitat disturbance (e.g., species of the subfamily Phyllostominae), it can be expected that these species will be much less abundant or not occur in degraded sites (Cunto & Bernard, 2012; Estrada & Coates-Estrada, 2002; García-Morales, Badano, & Moreno, 2013). However, the inverse can be expected for bats that primarily feed on pioneer plants (García et al., 2013; Fenton, 1992). This expectation is based on the idea that successional plants increase their abundance in degraded areas. In accordance with this expectation, we predicted a greater diversity and species richness inside PAs; (b) we expected that bat species that depend on conserved habitats would present higher body condition inside PAs. However, we predicted the inverse pattern to occur in species that primarily feed on successional plant species; and (c) similarly to the previous expectation, while species more dependent on preserved habitat will present higher occurrence of reproductive individuals inside PAs, the inverse can be expected for species that primarily use pioneer plants as food resources.

Method

Study Area

All samplings took place in the Federal District of Brazil (Figure 1), which represents one of the priority areas for the conservation of Cerrado (Cavalcanti & Joly, 2002). This biome is formed by a vegetation mosaic that goes from open formations with sparse low trees to dense forestry formations (Ratter et al., 1997) and presents a seasonal climate with well-defined warm–wet (October to April, when about 90% of the annual precipitation of 1,100–1,600 mm occurs) and cool–dry seasons (May to September; Miranda, Miranda, & Dias, 1993). Our study was conducted in two very distinct physiognomies of Cerrado: cerrado *s.s.* and gallery forests. Cerrado *s.s.* is a xeromorphic savanna-like physiognomy that composes 70% of the Cerrado biome and is formed by spread trees and shrubs. This physiognomy presents trees ranging from 2 m to 6 m high and an arboreal cover that ranges from 20% to 50% (Ribeiro et al., 1998). On the other hand, gallery forests is a complex riparian forest encompassing 5% of Cerrado total area with trees

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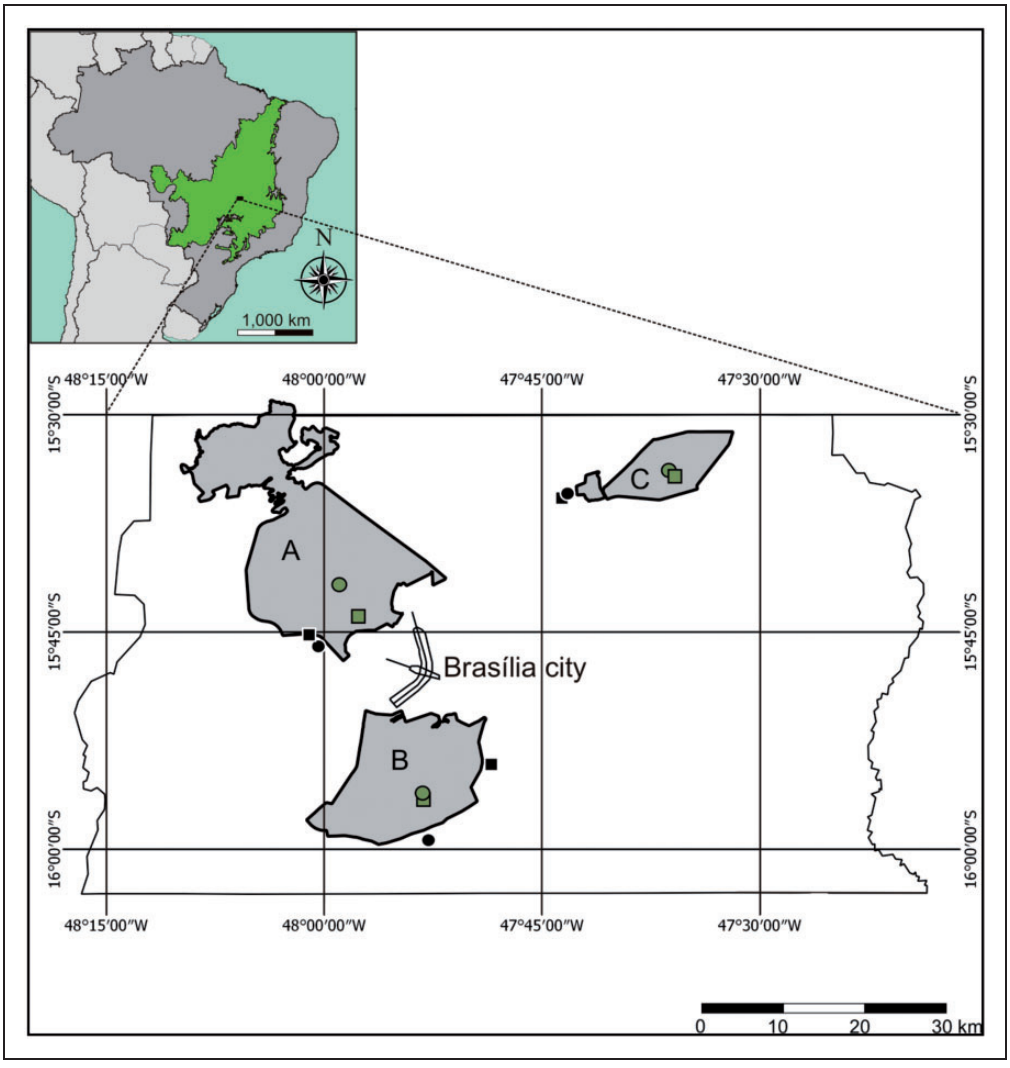


Figure 1. Map showing sites located inside (green symbols) and outside (black symbols) protected areas in the Brazilian savanna (Cerrado; green area showed in the Brazil map) where bat assemblages were sampled. A = Brasília National Park; B = Ecological Reserve of the Brazilian Institute of Geography and Statistics; C = Ecological Station of Águas Emendadas. Squares represent sites constituted of cerrado *sensu stricto* and circles represent sites constituted of gallery forests.

ranging from 20 m to 30 m high and a tree layer varying from 70% to 95% (Ribeiro et al., 1998).

Three PAs and their surroundings were sampled (Figure 1): The first is the Brasília National Park (PNB) located at 15°40′ S, 47°59′ W and containing 42,389 hectares, the second is the Ecological Station of Águas Emendadas (EEAE) located at 15°56′ S, 47°52′ W with an area of 10,547 hectares, and the last is the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE) located at 15°33′ S, 47°36′ W, with an area of 1,300 hectares. This later is part of a large legally PA that covers about 15,000 hectares together with the Brasília Botanical Garden and Fazenda Água Limpa (the ecological and agricultural field station of the University of Brasília). The PAs selected for the study were separated from each other by at least 10 km of a modified urban/agricultural matrix. Inside each PA, we choose one site composed of cerrado *s.s.* and one site composed of gallery forest. When possible, we established the sampling sites near the center of the PAs to avoid edge effects and ensure the highest level of habitat conservation. Similarly, we also choose one site of each physiognomy outside of each PA (Figure 1). Sites of cerrado *s.s.* outside PAs consisted mainly of pastures where tree coverage was highly reduced with only few pequi trees (*Caryocar brasiliensis* Cambess., 1828) no more than 5 m high and sparse shrubs remaining. Gallery forests outside PAs were characterized by a reduced width as a consequence of increased deforestation and a higher number of tree gaps. Forest clearings allowed cattle ranching, cropping, and invasion of pioneer plants. The chosen sampling sites located inside and outside considering the same PA were

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separated from each other between 1.9 km and 8.1 km in PNB, 0.6 km and 12.1 km in EEAE, and 0.6 km and 12.4 km in IBGE. Sampling sites outside of PAs were located between 0.2 km and 3.0 km from the PAs borders.

Sampling Procedures

Bats were captured from September 2007 to June 2008 along trails with the use of nine mist nets (one with 6 m × 2 m and eight with 12 m × 12 m [36 mm net mesh, Avinet Inc.]) opened 1 hr after sunset. Mist nests were left opened for 6 hr and inspected every 15 min. One gallery forest and one cerrado *s.s.* inside (representing preserved sites) and outside (representing degraded sites) a PA were sampled monthly for two consecutive days per site. The paired sampling design between inside and outside PAs of each agricultural matrix/month was designed to account for variations in body and reproductive condition due to temporal effects. As each category (protected and degraded areas) of any agricultural matrix was equally sampled across time, we assumed that the distributions of errors due to temporal effects would also be equally distributed. A total of 40 nights of sampling (1,998 net hr) were made in gallery forests and 34 nights (1,776 net hr) in cerrado *s.s.*, with the same capture effort inside and outside PAs for both vegetation categories.

All captured bats were marked with numbered plastic rings, weighed (Pesola—precision 1 g), measured for forearm length (caliper Eccofer—precision: 1 mm) and registered for their reproductive condition. Identification to the species level was done using bat identification keys (Anderson, 1997; Charles-Dominique, Brosset, & Jouard, 2001; Vizotto & Taddei, 1973). Foraging guilds were assigned to bat species according to Simmons and Voss (1998). Males were considered sexually active when their testes were evident and females when they were lactating, postlactating, or pregnant. The length of the forearm was used as an indicator of the size of the individuals in accordance to Fleming, Hooper, and Wilson (1972). Additionally, we only considered an individual adult when metacarpal epiphyseal cartilages were no longer visible (Racey, 1974). The first two males and females of each species captured were euthanatized, fixed in formaldehyde, preserved in alcohol 70%, and stored in the Bat Collection of the University of Brasília.

Data analysis

Diversity Patterns

Before conducting analyses comparing sites inside and outside PAs, we first assessed a possible spatial autocorrelation effect on the diversity and composition among all sampling sites. For that, we performed a Mantel correlogram using the paired differences in distance between localities, calculated using Google Earth (Google Inc., 2015) and the matrix of Bray–Curtis similarity. This analysis was performed in software R v.3.2.1 (R Development Core Team, 2014) using the package *ecodist* (Goslee & Urban, 2003).

To visually compare bat assemblages from inside and outside PAs, we performed a Nonmetric Multidimensional Scaling (NMDS) using Bray–Curtis similarity. For that, we conducted two separated analyses, one considering each site of cerrado *s.s.* and another considering each site of gallery forests in the software PAST 2.17c (Hammer, Harper, & Ryan, 2001). For all the subsequent analyses, we opted to group the individuals of each species captured inside and all the individuals of each species captured outside the PAs, disregarding in which PA bats were captured. Thus, we were able to compare the main patterns between preserved and degraded areas in each vegetation physiognomy (i.e., cerrado *s.s.* and gallery forests). To ensure statistical independence of samples for the analyses, we did not consider recaptures in the calculations.

To test the hypothesis whether there are differences in bat diversity considering sites located inside and outside PAs in each vegetation physiognomy, we performed a modified *t* test for the Shannon index (H′) (Poole, 1974). We also compared the Shannon equitability (EH; Krebs, 1999) using the data of bats captured inside and outside PAs for both cerrado *s.s.* and gallery forests. As a way to show the magnitude of change in bat diversity between inside and outside PAs, we used Hill numbers expressed as the exponential of H′ (Jost, 2006). This method indicates the effective number of species (ENS), that is, the number of equally abundant species that are needed to give the same value of diversity measure (Chao, Chiu, & Jost, 2014). Therefore, we were able to determine how much of the species diversity were maintained when compared inside and outside PAs. Additionally, we performed individual based rarefaction curves using the software EstimateS 9.1 (Colwell, 2013) to compare bat richness inside and outside PAs. For this analysis, we extrapolated curves based on 3 times the abundance of the smallest sample. Extrapolation above this range generates wide confidence intervals hindering statistical comparisons between samples (Colwell et al., 2012).

To investigate if there are differences in bat captures inside and outside PAs, we performed a G test (Woolf, 1957) for each species for testing the null hypothesis that these species are evenly distributed between conserved and degraded sites. Similarly, we also performed the same analysis grouping all captured bats from the frugivore and nectarivore guilds (based on Simmon and Voss's [1998] study). We choose these two guilds based on the suitable number of captured individuals for analyses (minimum of 10) and performed statistical tests in the software BioEstat 5.0 (Ayres, Ayres, Jr., Ayres, & Santos, 2007).

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Body condition. For comparing body condition between bats captured inside and outside PAs, we first performed a simple regression between forearm length (independent variable) and body mass (dependent variable) for each species. For these regressions, we excluded all the young and pregnant individuals as a way to avoid any bias related to ontogeny and the additional weight carried by females during pregnancy. After this initial analysis, we obtained the standardized residuals of each individual. These values represent the nonallometric component (i.e., the effect of body size on body mass) and, therefore, is considered a good index for body condition (Jakob, Marshall, & Uetz, 1996). While values above the regression line (positive values) also represent a body mass above the expected (i.e., good body condition), the inverse can be expected for individuals with values below the regression line (Jakob et al., 1996). After obtaining the standardized residuals (dependent variable), we performed a *t* test to compare the body condition of each species inside and outside PAs (grouping variable). When necessary, we performed Mann–Whitney tests on data sets not normalized. All the analyses regarding body condition were performed in the software BioEstat 5.0 (Ayres et al., 2007).

Reproductive Condition

For testing whether there are differences on the occurrence of reproductive bats (dependent variable) of the same species captured inside and outside PAs (independent variable), we performed a logistic regression. For this analysis, all reproductive individuals were assigned as 1 and all nonreproductive ones were assigned as 0. Similarly, individuals captured inside PAs were assigned as 1 and individuals captured outside PAs were assigned as 0. Analyses regarding reproductive condition were also performed with the software BioEstat 5.0 (Ayres et al., 2007).

Results

Diversity Patterns

There is no spatial autocorrelation in composition similarity among the sampling localities. Correlation values (r) varied from .25 to −.19 and probability values (p) varied from .073 to .927 (see Appendix for more details). With 74 sampling nights, we captured 495 bats belonging to 25 species, 4 families, and 6 foraging guilds. Among these bats, 98% are Phyllostomidae and the others are from Molossidae, Mormoopidae, and Vespertilionidae families (Table 1). The bats were distributed into six foraging guilds being 36% of the captured species frugivorous, 24% aerial insectivorous, 16% gleaning animalivorous, 16% nectarivorous, 4% hematophagous, and 4% omnivorous (Table 1).

The comparison of bat assemblages inside and outside PAs showed different patterns in cerrado *s.s.* compared to gallery forests. For the cerrado *s.s.*, the assemblages found inside PAs were very similar to each other, occupying positive regions of the graphic in both *x*- and *y*-axes (Figure 2). Although the sites outside PAs showed distinct bat assemblages, EEAE and IBGE were represented by negative values in both *x*- and *y*-axes and are more similar in comparison to PNB (positive value in *x*-axis and negative value in *y*-axis). On the other hand, only gallery forests in PNB presented a more unique assemblage considering sites inside and outside PAs (Figure 2).

There was no difference in the H′ (Shannon's diversity index) measured for the cerrado *s.s.* inside and outside PAs ($H'_{inside} = 1.420$, $H'_{outside} = 1.571$, $p = .520$) and no differences in the equitability for bats captured inside ($EH = 0.551$) and outside ($EH = 0.520$) PAs in cerrado *s.s.* However, there is higher diversity in gallery forest inside PAs ($H'_{inside} = 2.201$, $H'_{outside} = 1.922$, $p = .001$), and the gallery forests inside PAs ($EH = 0.593$) had greater equitability than outside PAs ($EH = 0.470$). For the Cerrado s.s., we found an ENS of 4.137 inside PAs; whereas outside PAs, we found an ENS of 4.811. On the other hand, gallery forests are 1.32 times more diverse inside PAs ($ENS = 9.034$) than outside PAs ($ENS = 6.834$). There are no differences for species richness between sites inside and outside PAs for both cerrado *s.s.* and gallery forests (Figure 3). Only *Carollia perspicillata* and *Glossophaga soricina* were significantly more abundant inside PAs (Table 2). Comparing abundances within the frugivorous and nectarivorous guilds, only nectarivores were more abundant inside PAs. Taking gallery forests, the flat-faced fruit-eating bat A*rtibeus planirostris* was significantly more abundant inside PAs and the white-lined bat *Platyrrhinus lineatus* outside PAs. There were no significant differences in the nectarivorous and frugivorous guilds (Table 2).

Body Condition

We compared the body condition of seven bat species (Figure 4). For the cerrado *s.s.*, we evaluated only the great fruit-eating bat *Artibeus lituratus*, and there was no significant difference (*t* test; $t_{29} = 0.358$, $p = .723$). However, in gallery forests outside PAs, *A. lituratus* ($t_{35} = 2.641$, $p = .010$) and the Gervais's fruit-eating bat *Dermanura cinerea* ($t_{37} = 2.276$, $p = .029$) presented higher body conditions. There were no differences in body condition for the nectarivorous species the Geoffroy's tailless bat *Anoura geoffroyi* (Mann–Whitney U test; $U = 35$, $p = 0.751$), the frugivorous fringed fruit-eating bat *Artibeus fimbriatus* ($U = 47$, $p = .881$), *C. perspicillata* ($t_{35} = 1.720$, $p = .094$), *P. lineatus* ($U = 75$, $p = .378$), and the little yellow-shouldered bat *Sturnira lilium* ($t_{76} = 0.471$, $p = .639$).

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Table 1. Species Composition and Total Number of Bats Captured in Cerrado *sensu strictu* (s.s.) and Gallery Forests Inside and Outside Protected Areas (PAs) in the Brazilian Savanna (Cerrado), Located in Brasília City in Three PAs (Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas).

			Cerrado s.s.		Gallery Forest		
Species by guild	Common name	Family	Inside PA	Outside PA	Inside PA	Outside PA	Total
Frugivorous							
Artibeus lituratus (Olfers, 1818)	Great fruit-eating bat	Phyl	20	18	40	41	119
Artibeus fimbriatus (Gray, 1838)	Fringed fruit-eating bat	Phyl	00	01	15	07	023
Artibeus planirostris (Spix, 1823)	Flat-faced fruit-eating bat	Phyl	02	01	15	03	021
Carollia perspicillata (Linnaeus, 1758)	Seba's short-tailed bat	Phyl	15	01	27	25	068
Chiroderma doriae (Thomas, 1891)	Brazilian big-eyed bat	Phyl	00	00	01	00	001
Chiroderma villosum (Peters, 1860)	Hairy big-eyed bat	Phyl	00	01	00	00	001
Dermanura cinerea (Gervais, 1856)	Gervais's fruit-eating bat	Phyl	00	00	21	19	040
Platyrrhinus lineatus (É. Geoffroy, 1810)	White-lined broad-nosed bat	Phyl	00	02	11	24	037
Sturnira lilium (É. Geoffroy, 1810)	Little yellow-shouldered bat	Phyl	01	06	32	75	114
Total			**38**	**30**	**162**	**194**	**424**
Nectarivorous							
Glossophaga soricina (Pallas, 1766)	Pallas's long-tongued bat	Phyl	13	03	07	05	028
Anoura caudifer (É. Geoffroy Saint-Hilaire, 1818)	Tailed tailless bat	Phyl	01	00	01	01	003
Anoura geoffroyi (Gray, 1838)	Geoffroy's tailless bat	Phyl	01	00	12	07	020
Lonchophylla dekeyseri (Taddei, Vizotto, & Sazima, 1983)	Dekeyser's nectar bat	Phyl	00	00	01	02	003
Total			**15**	**3**	**21**	**15**	**54**
Aerial insectivores							
Histiotus velatus (I. Geoffroy, 1824)	Tropical big-eared brown bat	Vesp	00	01	00	00	001
Lasiurus blossevillii (Lesson & Garnot, 1826)	Southern red bat	Vesp	00	00	01	00	001
Molossops temminckii (Burmeister, 1854)	Dwarf dog-faced bat	Molo	00	00	00	01	001
Molossus molossus (Pallas, 1766)	Pallas's mastiff Bat	Molo	00	01[a]	00	00	001
Myotis nigricans (Schinz, 1821)	Black myotis	Vesp	00	00	03	02	005
Pteronotus parnellii (Gray, 1843)	Parnell's mustached bat	Morm	00	00	00	01	001
Total			**00**	**02**	**04**	**04**	**10**
Gleaning animalivores							
Chrotopterus auritus (Peters, 1856)	Woolly false vampire bat	Phyl	00	00	01	00	001
Micronycteris megalotis (Gray, 1842)	Little big-eared bat	Phyl	00	00	00	01	001
Micronycteris minuta (Gervais, 1856)	White-bellied big-eared bat	Phyl	01	01	00	00	002
Mimon bennettii (Gray, 1838)	Southern golden bat	Phyl	00	00	00	01[a]	001
Total			**01**	**01**	**01**	**02**	**005**
Omnivorous							
Phyllostomus hastatus (Pallas, 1767)	Greater spear-nosed bat	Phyl	00	01	00	00	001
Total			**00**	**01**	**00**	**00**	**001**
Hematophagous							
Desmodus rotundus (É. Geoffroy, 1810)	Common vampire bat	Phyl	00	00	01	00	001
Total			**00**	**00**	**01**	**00**	**01**
Total abundance			**54**	**37**	**189**	**215**	**495**
Total richness			**08**	**12**	**16**	**16**	**025**

Note. Phyl = Phyllostomidae; Vesp = Vespertilionidae; Molo = Molossidae; Morm = Mormoopidae.
[a]Bats captured directly in shelters.

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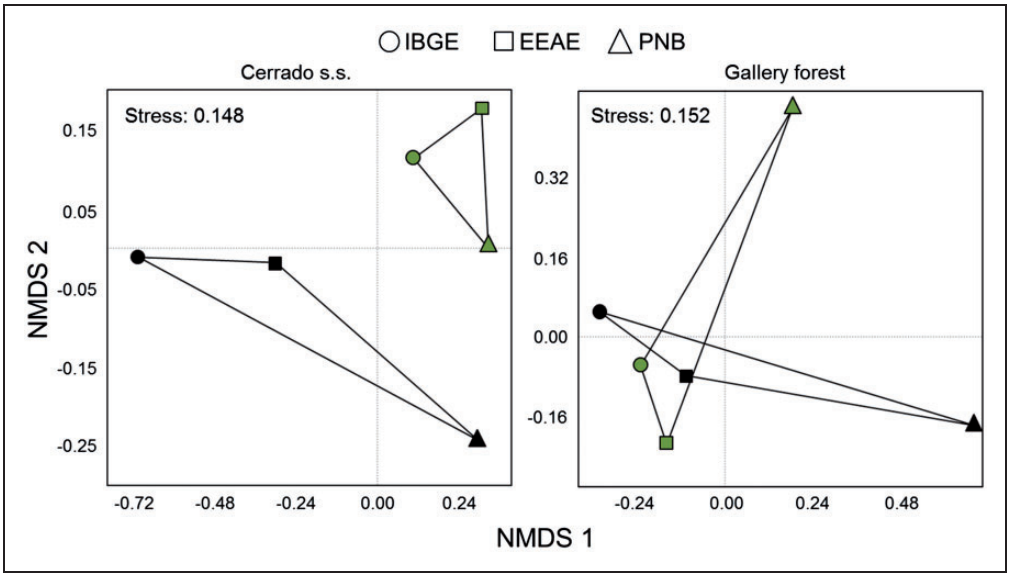


Figure 2. Results of Nonmetric Multidimensional Scaling analyses using Bray–Curtis similarity comparing bat assemblages in sites located inside (green symbols) and outside (black symbols) protected areas. Samples were made in cerrado *sensu stricto* and gallery forests of the Brazilian savanna (Cerrado) located in Brasília city. IBGE = Ecological Reserve of the Brazilian Institute of Geography and Statistics; EEAE = Ecological Station of Águas Emendadas; PNB = Brasília National Park. Stress numbers indicate the match between interobject distance (sites) and dissimilarity. The lower the stress value, the better the match.

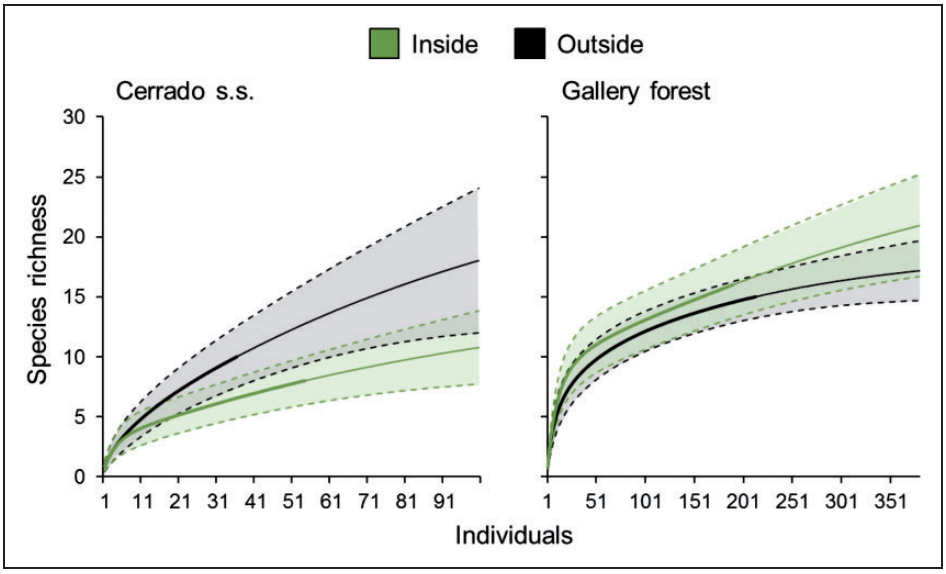


Figure 3. Individual-based rarefaction curves comparing bat richness inside (green lines) and outside (black lines) protected areas (PAs) in cerrado *sensu stricto* and gallery forests of the Brazilian savanna (Cerrado) located in Brasília city. Each curve of each vegetation type was generated grouping all captured bats from three sites located inside and three outside PAs located in three different PAs: Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas. Thick lines indicate the number of sampled individuals. Thin lines indicate the richness extrapolating 3 times the abundance of the smallest sample. Dashed lines show the 95% confidence interval.

Reproductive Condition

We compared the reproductive condition of five species captured inside and outside PAs from cerrado s.s. and gallery forests (Figure 5 and Table 3). In cerrado s.s., we found no differences for the only analyzed bat *A. lituratus*. In gallery forests, we also found no differences for the bats *A. lituratus*, *D. cinerea*, *P. lineatus*, and *S. lilium*. However, we found that the frugivorous

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Table 2. Results of G-Test Comparing the Total Number of Captured Bats From Inside and Outside Protected Areas (PAs) in Cerrado *sensu strictu* (s.s.) and Gallery Forests in the Brazilian Savanna (Cerrado), located in Brasília City.

	Number of individuals			
Species by habitat	Inside	Outside	*G* test	*p* value
Cerrado s.s.				
Artibeus lituratus	20	19	0.026	.873
Carollia perspicillata	15	01	23.213	**<.001**
Glossophaga soricina	13	03	6.738	**.009**
Frugivores	18	12	1.208	.272
Nectarivores	15	03	8.733	**.003**
Gallery forest				
Anoura geoffroyi	12	7	1.331	.249
Artibeus fimbriatus	16	7	3.618	.057
Artibeus lituratus	40	41	0.012	.911
Artibeus planirostris	15	3	8.733	**.003**
Carollia perspicillata	27	25	0.077	.781
Dermanura cinerea	21	19	0.100	.751
Glossophaga soricina	7	5	0.335	.563
Platyrrhinus lineatus	11	23	4.328	**.038**
Sturnira lilium	32	75	17.778	**<.001**
Fugivores	163	193	2.531	.112
Nectarivores	21	15	1.004	.316

Note. Captured Individuals of each species and each guild were pooled considering the three sampled PAs (Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas). Numbers in bold indicate statistically significant values ($p < .05$). Common name of each species can be seen in Table 1.

bat *C. perspicillata* presents more reproductive individuals outside PAs compared to inside (Figure 5 and Table 3).

Discussion

Diversity Patterns

Our general expectation was that some frugivorous bats would benefit in sites located outside PAs, mainly in gallery forests. Although gallery forests suffer habitat changes due to human activities (e.g., changes in the matrix for crops and pasture), these changes are less intense compared to those in cerrado *s.s.*, where almost total deforestation occurs with just few scattered trees left behind, especially the pequi tree *C. brasiliensis* (Cambess., 1828). This expectation is based on the idea that degraded gallery forests present more clearings, increasing the invasion of pioneer plants, which can be important resources for some frugivorous bats (e.g., *C. perspicillata* [Linnaeus, 1758] and *S. lilium* [É. Geoffroy, 1810]).

Our results agree that frugivorous (Stenodermatinae) and nectarivorous (Glossophaginae) bats tend to be less affected by habitat loss in riparian forests (de la Peña Cuéllar, Benítez Malvido, Ávila Cabadilla, Martínez Ramos, & Estrada, 2015) with the number of bats captured even increasing for some species in impacted areas (*S. lilium* and *P. lineatus*), probably due to the influx of pioneer fruiting plants, which provide novel feeding resources (Fleming, 1988). However, different bat species have distinct perceptions of fragmentation. Some frugivorous species, such as *P. lineatus* and *A. lituratus*, may fly up to 30 km per night in search of shelter or food (Menezes et al., 2008; Reis, Fregonezi, Peracchi, & Rossaneis, 2012), while smaller species, such as *G. soricina*, may flight within a distance of no more than 3 km from the closest PA (Aguiar et al., 2014). Nevertheless, the differences observed between bat assemblages in cerrado *s.s.*, and only one gallery forest located at the PNB may be attributed to intensity of modification in this phytophysiognomy in comparison to gallery forests. Gallery forests are protected by law, as they are responsible for the water quality of streams. Therefore, they are less impacted and more influenced by changes in the surrounding matrix, whilst cerrado *s.s.* is entirely removed and converted to crops and pastures.

On the other hand, the greater similarity between sites of gallery forests located inside and outside PAs, and the small similarity between gallery forests with their adjacent pastures outside PAs may indicate that frugivorous and nectarivorous bats use forestry formations possibly as corridors. All sampled sites in gallery forests outside PAs were, in fact, originally connected with the gallery forests inside their respective PAs. In this case, it is possible that the movement of bats among fragments resulted in the homogenization of the bat community in terms of species composition.

Other studies in the Cerrado biome indicate the importance of riparian forests as an important foraging and roosting habitat for bats (Rogers, Belk, González, & Coleman, 2006; Williams, ÓFarrel, & Riddle, 2006). Interestingly, one site of cerrado *s.s.* outside PNB presented a more distinct bat assemblage in comparison to the others outside PAs, presenting a positive value in the *x*-axis according to the NMDS analysis (as seen in sites located inside PAs). While this site was located just about 0.2 km from the PNB, the other sites were located more than 1.3 km from the nearest PA. Therefore, although there was no spatial autocorrelation between sites in assemblage composition of our study sites, this proximity might have contributed to a bat assemblage more similar to the assemblage inside the PNB, as some bat species can travel between primary and degraded areas (Bobrowiec & Gribel, 2010; Loayza & Loiselle, 2008) and site proximity might influence assemblage similarity (dos Santos, Vieira, & Faria, 2016). The evident difference on bat assemblage

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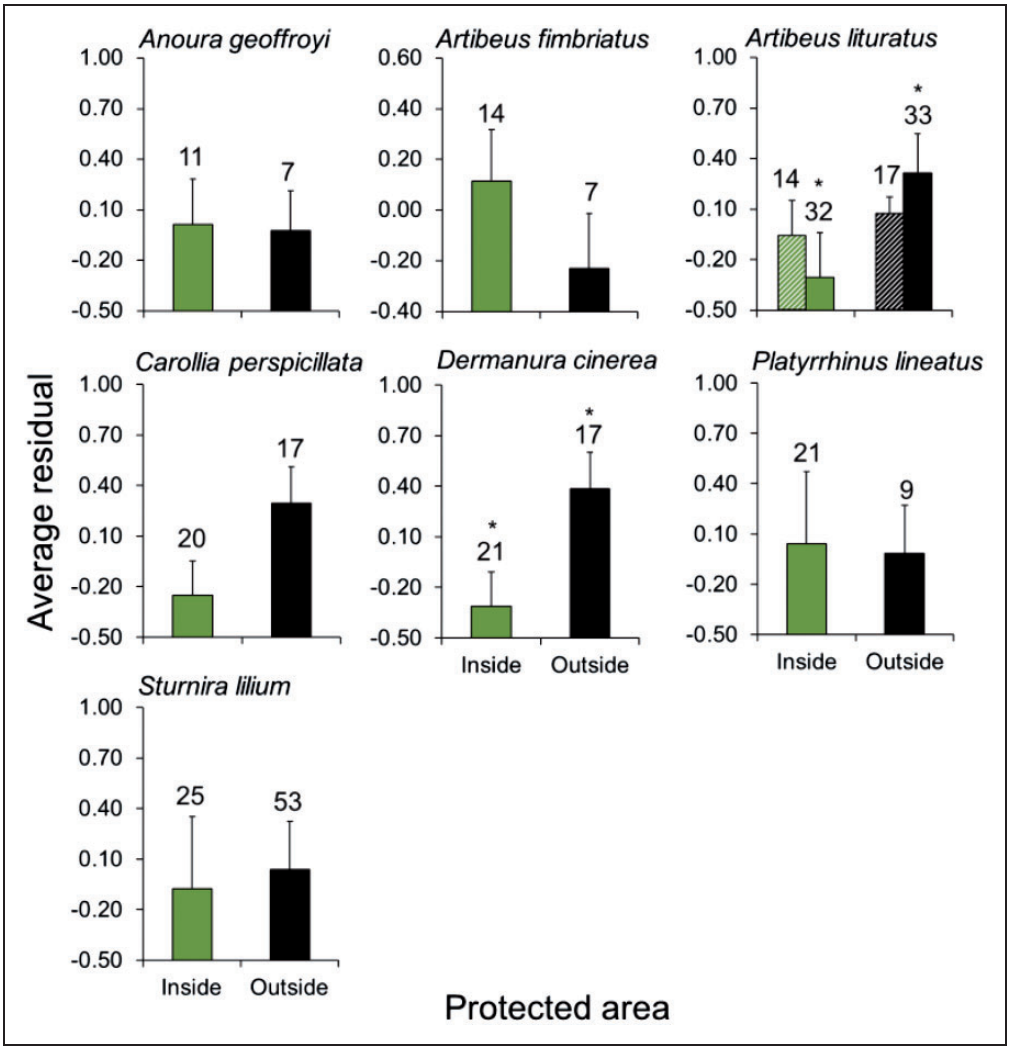


Figure 4. Average residuals representing the body condition of seven bat species captured in the Brazilian savanna (Cerrado) in cerrado *sensu stricto* (hatched bars) and gallery forests (solid bars) in sites located inside (green bars) and outside (black bars) three protected areas of Brasília city. Residuals were obtained based on simple regressions between forearm length and body mass of all bat species captured in Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas. Values above vertical bars indicate the number of analyzed individuals. Vertical bars indicate standard deviation. Asterisks indicate statistically significant values ($p < .05$) according to *t* tests or Mann–Whitney tests.

between the gallery forests inside and outside PNB can be attributed to the level of disturbance of the matrix in comparison to other sites located outside PAs. This site is immersed in a very disturbed matrix composed by contiguous cities, farming areas, and a sanitary landfill of 200 ha (Federal District, 2005). All these matrix components probably result in a great impact on the structure of this gallery forest, directly affecting the bat assemblage. In fact, in this site, we observed a much more disjuncted vegetation and a greater number of clearings in comparison to the other localities outside PAs.

While cerrado *s.s.* presented no differences in bat diversity inside and outside PAs with sites inside PAs having a diversity that is 86% of the diversity found outside PAs, gallery forests showed a higher bat diversity inside PAs, with areas outside PAs representing only 75.6% of the diversity inside PAs. Although we found a lack of differences in bat richness comparing inside and outside PAs in both phygsionomies, gallery forests inside PAs present greater equitability. Therefore, this more equal distribution of captured species in gallery forests inside PAs probably contributed to a higher diversity. The low species equitability of gallery forests outside PAs can be attributed to the increasing abundance of some frugivorous bats such as *P. lineatus* and *S. lilium*. On the other hand, the lack of differences in the diversity of cerrado *s.s.* possibly arose because of the similar species equitability. We propose that pequi trees act as an attractor for bats in pastures, contributing to the lack of difference in richness and similar equitability found for

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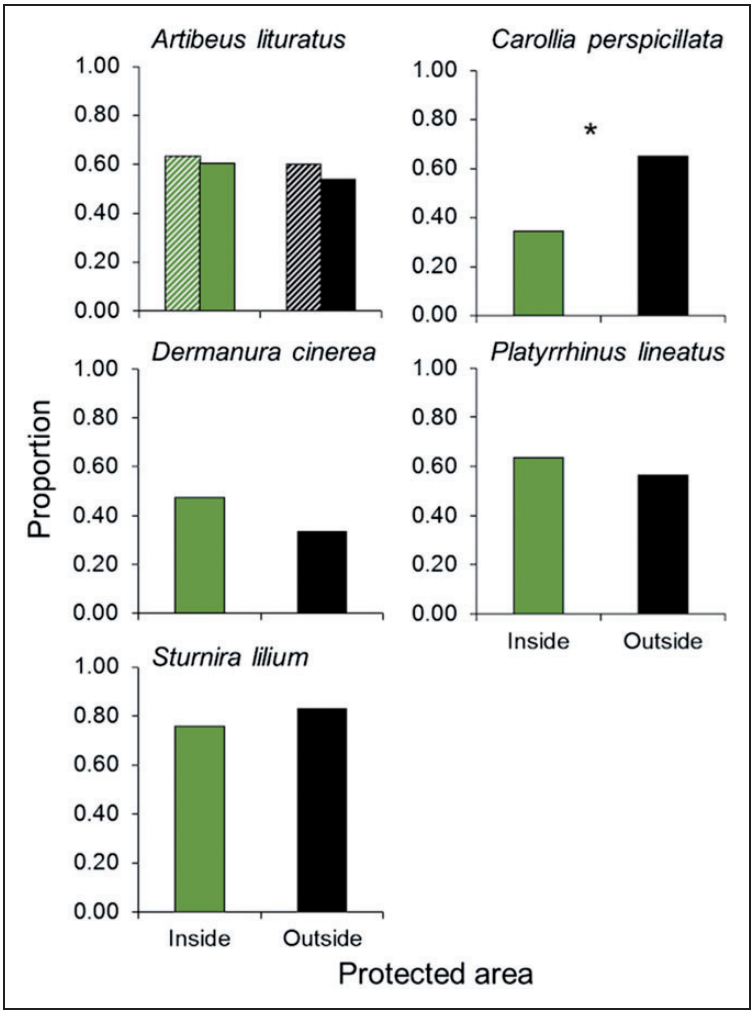


Figure 5. Proportion of reproductive individuals of five bat species captured in the Brazilian savanna (Cerrado) in cerrado *sensu stricto* (hatched bars) and gallery forests (solid bars) in sites located inside (green bars) and outside (black bars) three protected areas of Brasília city. Proportions were obtains pooling all individuals captured in Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas. The asterisk indicates statistically significant differences ($p < .05$) according to logistic regressions (see Table 3 for numerical results).

cerrados *s.s.* Approximately, 30% of the total number of bats captured and 60% of the species registered for cerrado *s.s.* outside PAs were captured in nets close to flowering and isolated individuals of pequi tree (*C. brasiliensis*). However, only 3 of the 27 nets (11%) were positioned close to these trees. Some studies found a similar pattern for other plants attracting bats (Estrada & Coates-Estrada, 2001; Galindo-González, Sosa, & Ammerman, 2003; Law & Lean, 1999; Lumsden & Bennett, 2005), such as trees of the genera *Ficus*, *Solanum*, and *Piper*. Galindo-González et al. (2003) suggest that isolated trees can be important in pastures, acting as stepping stones allowing bat movement across fragmented landscapers. Luck and Daily (2003) also comment that isolated fruiting trees are important for frugivorous birds in agricultural habitats.

According to our results in cerrado *s.s.*, we found that *C. perspicillata*, *G. soricina,* and the nectarivorous guild were more abundant inside PAs. These results suggest again that the intense removal of vegetation cover in cerrado *s.s.* can affect more intensively some bat species due to reduced shelters and food resources. Studies showed that the frugivorous bat *C. perspicillata* tend to avoid flying over pastures, being driven by localities with more food resources (Heithaus & Fleming, 1978; Trevelin, Silveira, Port-Carvalho, Homem, & Cruz-Neto, 2013). This species is one of the most common bat species of the Neotropical region and an important seed disperser of pioneer plants, which can be important for the restoration of degraded areas (Garcia, Rezende, & Aguiar, 2000). In another study conducted in the Cerrado of southeastern Brazil, a decrease in the abundance of

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Table 3. Results of Logistic Regressions Comparing the Occurrence of Reproductive Individuals Inside and Outside Protected Areas (PAs) for Five Bat Species in the Brazilian Savanna (Cerrado) in Cerrado *sensu strictu* (s.s.) and Gallery Forests.

Results by habitat	*Artibeus lituratus*	*Carollia perspicillata*	*Dermanura cinerea*	*Platyrrhinus lineatus*	*Sturnira lilium*
Cerrado s.s. (inside PAs)					
Individuals	20/19	–	–	–	–
Z value	−0.203	–	–	–	–
Odds ratio	0.875	–	–	–	–
p value	0.839	–	–	–	–
Gallery forest (inside PAs)					
Individuals	22/22	26/20	21/19	11/23	29/71
Z value	−0.566	−2.578	−0.901	0.394	0.783
Odds ratio	0.767	0.704	0.556	1.346	2.390
p value	.571	**.043**	.367	.694	.434

Note. These results are based on the total number of individuals captured in three PAs located in Brasília city: Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas. The two numbers separated by a bar in the "individuals" line represent the number of individuals used in the analyses that were capture inside and outside Pas, respectively. The *p* value in bold indicates statistically significant difference ($p < .05$). Common name of each species can be seen in Table 1.

nectarivorous bats was also observed (Muylaert, Stevens, & Ribeiro, 2016), and bats were responding positively to higher amounts of native vegetation. Probably, the decrease found in our study may be related to the high metabolism and energetic needs of nectarivorous bats (Voigt, Kelm, & Visser, 2006) that force them to narrow their activity to areas where they can find enough food resources to allow their movement. *G. soricina*, one of the main nectarivorous species in our study, has a high metabolism and needs to consume one flower every 21 s to supply its energetic requirements while hovering and flying (Winter, von Helversen, Norberg, Kunz, & Steffensen, 1993). Flowers would be hard to find in pastures, and this might possibly act as a limitation resource for the occurrence of *G. soricina* and possibly other nectarivorous species in pastures. However, in a study in an area of remnant cerrado *s.s.* surrounded by a very disturbed matrix including urban areas and monoculture of *Pinus*, in southeastern Brazil, this species was the third in number of captures (Muylaert et al., 2016). This suggests that the variation of the surrounding matrix may produce different responses on bats; and therefore, this issue should be taken into consideration in future investigations.

The increasing abundance of *P. lineatus* and *S. lilium* in gallery forests outside PAs is probably the result of a greater availability of pioneer plants. For frugivorous bats, secondary vegetation plays an important role as a food resource (Galindo-González, Guevara, & Sosa, 2000), which can explain the common pattern of a positive effect on these bats in disturbed areas. In our study, we also found a decrease in the abundance of *A. planirostris* in degraded habitats. This pattern indicates that *A. planirostris*, differently from the congeneric species *A. lituratus*, is more sensitive to habitat alteration, suggesting *A. planirostris* as a possible bioindicator species for forest disturbance.

The pattern that some frugivorous bats can benefit from secondary plants in degraded forests (Estrada & Coates-Estrada, 2001; Galindo-González et al., 2003; Garcia et al., 2000; Heithaus & Fleming, 1978; Loayza & Loiselle, 2008; Trevelin et al., 2013) was also confirmed for some species by our results regarding body condition and reproductive condition by comparing areas inside and outside PAs. In fact, these analytical approaches showed to be complementary considering species that did not show differences in abundance. For example, despite the lack of differences in abundance for *A. lituratus* and *D. cinerea* comparing inside and outside PAs in gallery forests, they presented higher body condition outside PAs. The same idea is applicable for *C. perspicillata* that presented more reproductive individuals in gallery forests outside PAs.

Implications for Conservation

Although pastures can sustain a high diversity and species richness of bats, the intensive removal of the vegetation cover for transformation into crops and pastures seems to have a large effect on assemblage composition and abundance of some bat species. Moreover, the conversion into pastures negatively affects nectarivorous bats, which possibly also affect the ecosystem services provided by these species as well as the recovery of degraded areas. One factor that can help to boost the

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species richness and abundance of bats in pastures is the maintenance of *C. brasiliensis* (pequi tree), as they can act as attractor for bats, probably representing important food sources. Therefore, it should be encouraged to keep scattered pequi trees for increasing the local richness and abundance of bats, possibly promoting the movement of these animals and connectivity of fragmented landscapes.

Our study also points out the importance of gallery forests located in unprotected areas as possible corridors for bats, since we found a general pattern of similar bat assemblages inside and outside PAs. Therefore, more attention must be given to these gallery forests near PAs, as a way to minimize the negative effects of human activities on these areas ensuring bat movement. Specially when considering that frugivorous bats, such as *Sturnina lilum* and *P. lineatus* benefit on pioneer plants and are considered good agents for regeneration of degraded areas by dispersing seeds across the landscape. Pequi trees would benefit the spreading of new seeds of pioneer plants on pasture and other open areas. Moreover, body condition and reproductive condition of bats also showed to be a complementary analytical tool for investigating how bats respond to disturbance, as we observed for *A. lituratus* and *D. cinerea* (higher body condition outside PAs) and *C. perspicillata* (more reproductive individuals outside PAs). Therefore, these analytical approaches should be taken into consideration in future studies for more reliable assessments of how habitat degradation influences different bat species.

Appendix

Table A1. Results of Mantel Correlogram Testing Spatial Autocorrelation Among 12 Bat Assemblages Sampled in Three Protected Areas (PAs) in the Brazilian Savanna (Cerrado) Located in Brasília City.

Lag distance (m)	Number of distances	Mantel *r*	*p* value
03,928	10	.182	.116
11,784	08	−.121	.282
19,640	02	−.012	.927
27,496	16	−.194	.172
35,352	07	−.118	.398
43,208	11	−.088	.464
51,064	10	.250	.073

Note. In each PA (Brasília National Park, Ecological Reserve of the Brazilian Institute of Geography, and Statistics and Ecological Station of Águas Emendadas), four sites were sampled, of which two were located inside and two outside the PA. Each site pair was composed by one site of cerrado *sensu strictu* (s.s.) and one of gallery forest.

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Authors' Note

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Declaration of Conflicting Interests

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