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Research Article

Loss of multiple dimensions of bat diversity under land-use intensification in the Brazilian Cerrado

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Abstract

The Brazilian Cerrado is a Neotropical savanna extremely threatened by human-driven habitat changes while simultaneously one of the formations with the highest degree of floristic endemism in the world. In the last decades, more than half of the Cerrado area has been converted by agriculture and livestock production, leading to a significant loss of its natural vegetation. Here we evaluated changes in bat diversity between varying agricultural land use intensity levels and phytophysiognomies of the Cerrado. Because processes behind the patterns of community assembly act on ecological redundancies and complementarities of organisms and not only, or necessarily, on the number of species present in a certain region, we focused on taxonomic, functional and phylogenetic diversity of bats. We predicted that all three dimensions of bat diversity were negatively correlated with increasing levels of land-use intensity in the Cerrado, and that this pattern was mirrored in distinct phytophysiognomies of the domain. We sampled bats in the central Brazilian Cerrado using a comprehensive sampling scheme of mist-nets and automated real-time ultrasound-recording units in 27 sampling points covering different physiognomies and levels of land-use modification for two consecutive years. To our knowledge our sampling was unique in combining these two techniques, returning information on close-, edge- and open-space foraging guilds, rarely all sampled in Neotropical bat studies. A remarkable total of 64 species of six families were registered in the study area. In general no statistical differences were found in any of the diversity metrics between the sampled physiognomies, but a decrease in taxonomic, functional and phylogenetic diversity was observed in all physiognomies associated with land use intensification and this was consistent across guilds. This demonstrates the potential negative impact of land use intensification in ecosystem services provided by bats, including pollination, seed dispersal and insect control.

Introduction

The Cerrado biome is one of the world's biodiversity hotspots and the second largest biome of South America (Myers et al., 2000). Harbouring more than 10000 plant species, of which 44% are endemic (Myers et al., 2000), it originally occupied an area of about 2 million km^2, representing almost 23% of the Brazilian territory (Ratter, 1997; Klink and Machado, 2005). Presently, the Cerrado is one of the biomes most threatened by anthropogenic changes, with annual net loss of up to 1.2% in some regions (Espírito-Santo et al., 2016). Indeed, in the last decades, more than half of the area originally occupied by the biome has been converted by agriculture – in particular by intensive soya plantations – and livestock production, resulting in significant loss of its natural vegetation and associated impacts in diversity as a whole (Klink and Machado, 2005). Recently the Cerrado has also started to be threatened by monoculture afforestation, the expansion of soybean cultivation, of which Brazil is the world's second major producer, and the construction of large dams (Fearnside, 2001; Stickler et al., 2009; Pielke et al., 2011). Mining activities also pose a serious threat to the biome not only due to the direct impact of soil erosion, sinkhole formation, and contamination of soil, ground and surface water by chemicals from mining processes, but also because several active mine-tailing dams subsist and may be at risk of collapsing, as occurred with the Rio Doce dam in 2015 (Garcia et al., 2017). Recent studies indicate that if there is no reversal in this trend, from 2030 there will no longer be any natural areas of Cerrado except those inside strictly protected areas, which represent only up to 6% of the area currently occupied by this biome (Machado et al., 2004; Klink and Machado, 2005).

Whilst the floristic value of the Cerrado has long been recognized, its fauna was once considered poor (Redford and Fonseca, 1986; Vitt and Caldwell, 1993). However, in the last decade many studies have shown that the Cerrado actually holds much richer animal communities associated to its highly diverse flora than previously thought (Nogueira et al., 2009, 2011; Bernard et al., 2011; Laranjeiras et al., 2012; Valdujo et al., 2012; Azevedo et al., 2016). Dominated by savanna-type vegetation, the Cerrado presents several phytophysiognomies, from grassy to forest formations (Oliveira-Filho and Ratter, 2002; Aguiar et al., 2010). Because floristic structure and composition play an important role in structuring animal communities, both at the local and landscape scales (Hutchinson, 1959; MacArthur and Macarthur, 1961; Williams et al., 2002; Tews et al., 2004; Qian and Kissling et al., 2010), the structure of animal communities in the Cerrado seems to be constrained by the environmental differences existing between distinct phytophysiognomies (Nogueira et al., 2009; Laranjeiras et al., 2012).

Bats are one of the most diverse vertebrate groups in the Neotropics (Brosset and Charles-Dominique, 1990; Simmons and Voss, 1998), and a model taxa to study patterns and processes of community as-

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sembly (Kalko, 1998; Stevens et al., 2007). Neotropical bats are not only taxonomic diverse but also extremely varied in ecological terms, comprising all trophic levels known in mammals (Kalko et al., 1996; Kalko, 1997; Simmons and Voss, 1998), from nectarivory and frugivory, to insectivory, carnivory and sanguinivory (Findley, 1993; Petterson et al., 2003; Kunz et al., 2011; Rojas et al., 2012). Due to this, they provide essential ecosystem services in Neotropical regions controlling insect populations, dispersing seeds and pollinating several plants (Fleming, 1982; Fleming et al., 2001; Petterson et al., 2003; Kalka et al., 2008; Kunz et al., 2011), and gaining a special relevance in more arid habitats where they are the main pollinators of several plant species (Bustamante et al., 2010); in the Cerrado they add up to over 118 species (Nogueira et al., 2014; Aguiar et al., 2016).

Sensitive to environmental changes such as habitat fragmentation, habitat loss and deforestation (Gorresen and Willig, 2004; Estrada-Villegas et al., 2010; Farneda et al., 2015; Rocha et al., 2017) bats are a model group for studies on the impact of landscape changes. In Neotropical forests, where bat ecological research and conservation efforts were mainly focused, especially at the Amazonian and Central American rainforests, land-use changes, habitat loss and fragmentation have been shown to result in changes in bat population dynamics and diversity (Medellín et al., 2000; Bernard and Fenton, 2002; Meyer and Kalko, 2008a; Estrada-Villegas et al., 2012; Peña-Cuéllar et al., 2012). Few studies, however, have emphasized the impact of human-driven habitat changes in savanna-like environments. Specifically in the Cerrado there are also no studies evaluating the effects of distinct phytophysiognomies as underlying processes of bat assemblage structuring patterns (but see Willig, 1983; Aguirre, 2002; Bernard and Fenton, 2007; Zortéa and Alho, 2008).

Given the widespread threat to the conservation of the Brazilian Cerrado represented by intensive soya cultivation and grazing from livestock, the assessment of the effects of anthropogenic changes on the structure of bat assemblages is crucial. Indeed, if similarly to what happens in forest ecosystems, land-use intensity in the Cerrado result in changes in the structure of bat assemblages, essential ecosystem services provided by these animals in this highly threatened biome might be disrupted. However, this assessment will only be comprehensive if taken into consideration that the processes behind the patterns of community assembly act on ecological redundancies and complementarities of organisms and not just on the taxonomic diversity present (Cadotte et al., 2013). So, the focus should also lay on the functional and phylogenetic diversities of bat assemblages.

Here we hypothesize that bat diversity differs among Cerrado phytophysiognomies and levels of land-use intensity. Because vertical stratification has been considered an important characteristic of bat communities in Neotropical regions (Bernard, 2001; Kalko and Handley, 2001; Ramos Pereira et al., 2010), we expect to find differences in the composition and functionality of bat species between phytophysiognomies, with more closed-space foraging species in forest-like areas, which are more cluttered across the vertical space, and a higher incidence of open-space species in more open habitats. We also predict that taxonomic, functional and phylogenetic diversity should be higher in pristine sites when comparing to sites showing some level of anthropogenic modification, and that diversity loss should be stronger in highly modified habitats, due to the loss of suitable foraging and roosting sites for bats.

To test this hypothesis, we studied patterns of bat assemblage structure in Central Brazil, core region of the Cerrado biome. The Cerrado phytophysiognomies were chosen according to their representativeness in the region and included forest-like and savanna-like habitats. Within these phytophysiognomies, pristine areas, areas showing low levels of anthropogenic modification, and highly modified habitats by cultivation and/or pasture were chosen and sampled for bats during two consecutive years using a comprehensive sampling scheme of mist-netting and acoustic sampling.

Figure 1 – Map of the study area within the Cerrado biome, in Tocantins State, central Brazil, including the limits of the Serra do Lajeado Environmental Protection Area (larger polygon delimited by the lines) and Lajeado State Park (smaller polygon), as well as the approximate location of the 27 sampling points (dots). The remaining Brazilian biomes are represented for referencing.

Materials and methods

Study area

The study took place at the Serra do Lajeado Environmental Protection Area and vicinities, in Tocantins State, Central Brazil (Fig. 1). This partially protected area is located near the geodesic centre of Brazil and comprises the Lajeado State Park, a strict nature reserve, operated by the State of Tocantins, only opened to controlled visitation and where no human economic activities are allowed. The vast majority of the Tocantins state is situated within the Cerrado biome, though comprising some Cerrado-Amazonia and Cerrado-Caatinga ecotone areas at the northwest and northeast of the state, respectively. The main natural phytophysiognomies of the Serra do Lajeado Environmental Protection Area include cerrado *sensu stricto*, cerradão and semideciduous and evergreen alluvial forests occurring in richer soils or located in the proximity of watercourses, for this reason usually called gallery forests. A few other formations typical of the Cerrado biome, such as campo rupestre, campo limpo and vereda occupy a smaller fraction of the area.

Cerrado *sensu stricto* is here defined as a habitat that includes a large fraction of grassland, but where trees and scrubs often with up to 7 m tall, and more than 20% crown cover occur. The dividing line between cerrado *sensu stricto* and campo cerrado is often complicated and arbitrary, so in this work both were included in the same category (cerrado *sensu stricto*), also because these types of phytophysiognomies frequently occur in a spatial continuum. Cerradão is considered by some authors the climax stage of cerrado *sensu lato*, described as almost closed woodland with crown cover of 50% to 90% made up of trees (Oliveira-Filho and Ratter, 2002) and where the herbaceous and shrub layers are scattered and low. Indeed, physiognomicaly it is a forest of sclerophyllous and xeromorphic features, but floristically very close to more open cerrado physiognomies. In the Serra do Lajeado Environmental Protection Area the canopy height of cerradão is between 7 m and 15 m but reaching 18 m to 20 m in some very well preserved areas of the Lajeado State Park and only for some species of trees. The most represented plant families are Leguminosae, Malpighiaceae, Melastomataceae, Erythroxylaceae, Vochysiaceae, Apocynaceae, Chrysobalanaceae and Rubiaceae and representative species include *Qualea grandiflora*, *Curatella americana*, *Plathymenia reticulata*, *Vellozia squamata*, and *Byrsonima subterranea*. Gallery forests occur as narrow and well-defined strips (no more than 100 m wide) along streams, presenting high tree cover reaching up to 20 m to 30 m at the canopy level. In this region they are mostly evergreen, though water might not be available all year long because some streams get completely waterless during the dry season. In these areas plant species include *Vochysia pyramidalis*, *Guazuma ulmifolia*, and *Calophyllum brasiliense*, among others.

As a result of anthropogenic actions almost 30% of the area has lost partially or completely the natural vegetation, but the severity of these changes is more evident in the bordering region of the protected area and in areas originally occupied by cerradão, in which trees were cut for the use of wood and replaced by monocultures. The area occupied by cerrado *sensu stricto* occupies approximately 65% of the area, with only about 10% area still occupied by pristine cerradão and 25% occupied by gallery forest. Most of the modified areas are dedicated to pasture land planted with *Panicum maximum*, *Andropogon gayanus* and *Brachiara* spp. and grazed by bovine cattle.

Bat sampling

Bats were sampled between 2012 and 2013 using a standardized sampling design protocol of mist-netting and acoustic monitoring in 27 sampling points representing three levels of anthropogenic change: i) pristine (no significant change), ii) scarcely modified (extensive grazing), and iii) highly modified (intensive pasture and grazing) of the three main phytophysiognomies found in the Serra do Lajeado Environmental Protection Area – cerrado *sensu stricto*, cerradão and gallery forest. Sites were chosen at a minimum distance of 3.5 km to minimize spatial autocorrelation.

Bats were captured under permits from the Brazilian Ministry of Science and Technology (343, 2012), SISBIO (33542, 2012) and NATURATINS (1633, 2012), covering all methods used in the study, including netting, measuring and tagging. Because no bats were sacrificed, and all those captured were released shortly after, there was no need to subject the research to the approval of the ethics committee on animal use (law 11.794/2008).

Whereas changes in cerrado *sensu stricto* and cerradão took place within the physiognomy, changes in gallery forest often occurred in the surroundings of the strip of riverine vegetation. For this reason, gallery forest sites were classified according to the level of modification in these bordering areas. However, the actual pasture and grazing activities in the surrounding area frequently reflect some level of anthropogenic modification at the riverine vegetation by the removal of the autochthonous trees and by the plantation of trees with economic interest such as *Copaifera langsdorffii* and *Tabebuia impetiginosa*. The intensity and timing of change, as well as the original phytophysiognomy, were investigated using the land records available at NATURATINS (Nature Institute of Tocantins) and SEMADES (State Secretariat for the Environment and Sustainable Development of Tocantins). This was crucial because in the forest-structured phytophysiognomies, severe changes included widespread tree removal, leaving especially the original cerradão areas almost unrecognizable.

Each site was sampled for a total of six nights using ten mist-nets (Ecotone, 2.5×15 m; mesh 1616 mm, 5 shelves), which remained open for six hours after sunset and checked every 20 min. Sampling was done during the dry season (April and May) and repeated during the rainy season (November and December) for two consecutive years, 2012 (one night/site/season) and 2013 (two nights/site/season). Because mist-nets set at the understory are biased towards the capture of cluttered-space foraging bats, most belonging to the Phyllostomidae, in 2013 each site was also sampled for aerial insectivores using simultaneously an automated real-time ultrasound-recording unit (D500x Pettersson Elektronik AB) set to automatically start recording as a sound was detected (no pre-trigger nor post-trigger functions set).

Each bat captured in the mist nets was identified, and weighted using a 20, 50 or 100 g Pesola®balance. The forearm was measured using a paquimeter. Age was determined by the degree of ossification of the carpal joints and development of nipples and testis (Baagøe, 1977). To identify recaptures, all bats were marked with aluminium rings placed in the forearm or using an aluminium ball-chain collar with a numbered aluminium ring. Recaptures within the same sampling season were inexistent.

Bat calls were analysed using Avisoft Saslab 5.2.09 (Raimund Specht, Avisoft, Berlin, Germany). Call duration, inter-pulse interval, start and end frequencies and peak frequency (frequency containing most energy) were registered. Species identification was done using a reference collection of bat calls and specific literature (e.g. O'Farrell and Miller, 1999; Jung et al., 2007; Barataud et al., 2013; Jung et al., 2014), though often species could not be distinguished and were grouped into genus or family complexes.

Data analysis

Data gathered with acoustic monitoring does not allow the estimation of densities or abundances because two bat-passes from the same species could result from two distinct individuals or from the same individual passing twice by the detector. On the other hand, because all bats captured with mist-nets were marked, this estimation was possible for the mist-netting data. For this reason some analyses were separated by sampling scheme: abundance-based estimators for captures (species of the Phyllostomidae) and incidence-based (presence/absence) estimators for sound detections (aerial insectivores of the Emballonuridae, Molossidae, Mormoopidae, Natalidae, and Vespertilionidae). Though some aerial insectivores were detected using both mist-nets and acoustic monitoring (e.g. *Pteronotus* cf. *parnellii*, *M. albescens*, *M. nigricans*, *M. riparius* and *Rhogeessa* sp., *Saccopteryx bilineata*), we opted for considering them only within the aerial insectivore group when separating the analyses by sampling scheme.

Taxonomic diversity was defined as estimated species richness using Chao1 (abundance-based) and Chao2 (incidence-based) estimators in R package vegan (Oksanen et al., 2016). To calculate functional diversity each species was initially classified according to seven functional traits: foraging guild, main feeding habits, main trophic level, forearm length, aspect ratio, wing load and body mass. Aspect ratio (ratio of the square of the wingspan to the projected wing area) and wing loading (ration of the body to the area of the wing) are metrics derived from wing morphology and frequently used to estimate bat mobility (Norberg and Rayner, 1987). Table S1 presents a detailed description of these traits, including the literature support for the definition of the chosen categories. For those species captured in the mist-nets, our own information on forearm length, body mass and in some cases aspect ratio and wing loading was used; for those only recorded we used published data.

Functional diversity was then estimated as the multidimensional functional dispersion index in R package FD (Laliberté et al., 2014), which is unaffected by species richness (Laliberté et al., 2014), and is consistently less sensitive to undersampling (van der Plas et al., 2017), using the relative abundance for mist-net data and species incidence for acoustic monitoring data.

To calculate phylogenetic diversity in each site, DNA sequences from all the species captured and detected and two outgroups (*Megaderma lyra* and *Rhinolophus ferrumequinum*) were downloaded from GenBank. Sampled genes were two mitochondrial genes: cytochrome b (cytb) with 1140 bp and cytochrome c oxidase subunit I (COI) with 657 bp. Sequence alignments were performed using Clustal Omega (Sievers et al., 2011) that uses seeded guide trees and hidden Markov models (HMM) profile-profile techniques to generate alignments between three or more sequences (Goujon et al., 2010; Sievers et al., 2011; McWilliam et al., 2013). The alignments of the two genes were combined using T-Coffee (Notredame et al., 2000) and the distance matrix phylogenetic tree was done in ClustalW Phylogeny (Larkin et al. 2007). Phylogenetic diversity in each site was then calculated as the total branch length of the tree linking all species represented in that assemblage using the R package BAT (Cardoso et al., 2015).

The effects of phytophysiognomy and level of land-use change on estimated species richness, and indices of functional dispersion and phylogenetic diversity were assessed using linear (LMM) and generalized (GLMM) mixed-effect models in R package nlme (Pinheiro et al., 2017); R^2 values for the models were obtained in MuMIn package (Bartoń, 2013); sampling site and sampling scheme were treated as random-effects. Statistical significance was checked with the Satter-

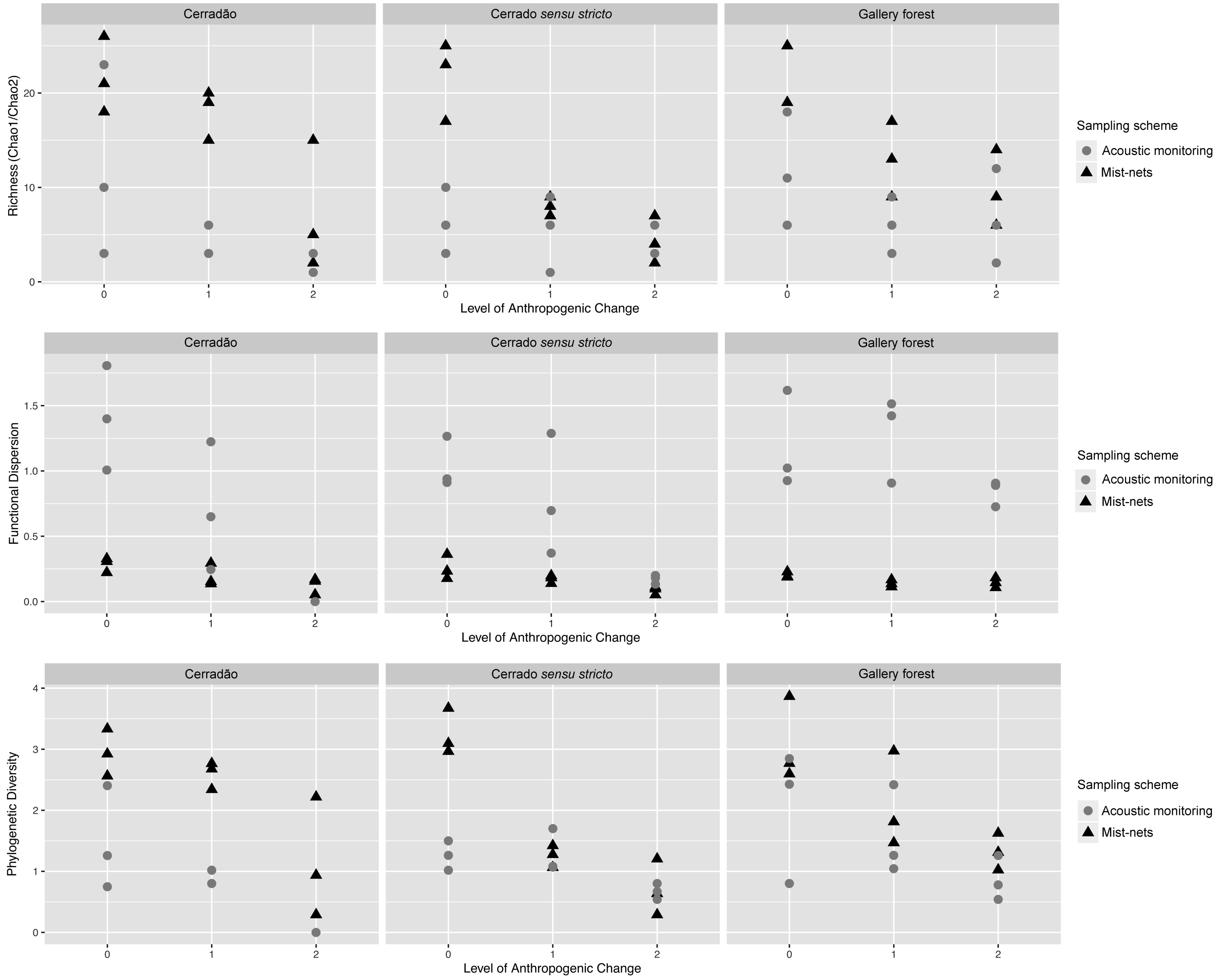

Figure 2 – Estimates of species richness, functional dispersion and phylogenetic diversity in each of the three sampled points in cerradão, cerrado *sensu stricto*, and gallery forest phytophysiognomies, along a gradient of land-use intensity (0=pristine; 1=scarcely modified; 2=highly modified), obtained using abundance-based estimators for mist-net capture data and incidence-based estimators for acoustic data.

thwaite approximations of degrees of freedom for Restricted Maximum Likelihood (REML) (Zuur et al., 2009).

To understand the variation in composition between phytophysiognomies and levels of land-use intensity a regression analysis on dissimilarity matrices incorporating bat incidence data (including all species, those captured in the mist-nets and those acoustically detected) was done in R package vegan using the adonis function (Dixon, 2003).

Results

We captured a total of 3068 bats in the mist-nets and recorded 2062 bat-passes in 327 hours of recording. A total of 64 species was found in the study area (Tab. 1). Species richness ranged from 24 to 41 species in sampling points located in pristine phytophysiognomies, with a maximum of 26 species captured by mist-nets and a maximum of 23 species detected through acoustic monitoring in two pristine cerradão sampling points, respectively.

There were no significant differences between phytophysiognomies for species richness, functional dispersion and phylogenetic diversity (Tab. 2), and this was similar for both the acoustic monitoring incidence data and the mist-net abundance-based data (Fig. 2).

When merging data across all levels of land-use intensity, average species richness varied between 11.333 in cerrado *sensu stricto* and 15.667 in cerradão for mist-net data, and from 5.778 in cerrado and 8.778 in gallery forest for acoustic data. Similarly, average functional diversity varied between 0.081 in gallery forest and 0.101 in cerradão for mist-net data, and from 1.284 in cerrado *sensu stricto* and 1.808 in gallery forest for acoustic monitoring data. Likewise, average phylogenetic diversity did not show any strong trend across phytophysiognomies, varying between 1.736 in cerrado *sensu stricto* to 2.227 in cerradão for mist-net abundance-based data, and between 0.781 in cerradão to 1.459 in gallery forest for the acoustic monitoring incidence data.

On the other hand, there was a significant decrease in all metrics of diversity from pristine sites to those highly or even just scarcely modified. Indeed, highly modified areas showed significant lower species richness (z=-7.612, p<0.001), functional diversity (t=-4.664, p<0.001) and phylogenetic diversity (t=-7.409, p<0.001) than the corresponding pristine environments (Tab. 3). A similar trend was detected in scarcely modified environments, where significant lower species richness (t=-4.559, p<0.001) and phylogenetic diversity (t=-3.461, p=0.001) were found when compared to pristine environments; the estimate for functional dispersion for scarcely modified environments while negative was marginally not significant (t=-1.703, p=0.095).

When analysing separately the acoustic monitoring incidence data and the mist-net abundance-based data, a much stronger decrease trend was found in the distinct metrics of species diversity across intensification levels – from unaltered to highly modified environments – in data resulting from mist-net sampling (which represents mostly Phyllostomidae assemblages) (Fig. 2). Indeed, average species richness varied between 7.111 in highly modified environments and 21.444 in pristine environments for mist-net data, but only between 6.6667 and 8.111 for

Table 1 – Species captured with mist-nets or recorded using acoustic monitoring in each physiognomy and land-use intensity level (PR: pristine; SM: scarcely modified; HM: highly modified). 1=presence; 0=absence.

	Cerrado *s.s.*			**Cerradão**			**Gallery forest**		
	PR	**SM**	**HM**	**PR**	**SM**	**HM**	**PR**	**SM**	**HM**
Emballonuridae									
Cormura brevirostris	0	0	0	0	0	0	1	0	1
Diclidurus ingens	1	0	0	1	1	0	1	1	0
Peropteryx kappleri	0	0	0	0	0	0	1	0	0
Peropteryx macrotis	1	0	0	1	0	0	1	0	0
Peropteryx trinitatis	1	0	0	1	0	0	1	0	1
Saccopteryx bilineata	0	0	1	1	0	0	1	0	0
Saccopteryx canescens	0	1	0	1	0	0	1	0	1
Saccopteryx leptura	1	1	1	1	1	0	1	1	1
Molossidae									
Cynomops abrasus	1	0	0	0	0	0	0	0	0
Eumops sp.	1	1	0	1	1	0	1	1	1
Molossus molossus	1	1	0	1	0	1	0	0	1
Nyctinomops laticaudatus	1	0	0	1	0	0	0	0	0
Promops centralis	1	0	0	0	0	0	0	0	1
Tadarida brasiliensis	1	0	0	0	0	0	0	0	0
Mormoopidae									
Pteronotus gymnonotus	0	0	0	0	0	0	1	0	0
Pteronotus personatus	0	1	1	1	0	0	1	0	0
Pteronotus cf. *parnellii*	1	0	0	1	1	0	1	1	1
Natalidae									
Natalus macrouros	0	0	0	1	0	0	0	0	0
Phyllostomidae									
Anoura caudifer	1	1	0	1	1	0	0	0	0
Anoura geoffroyi	1	0	0	1	1	0	1	0	0
Artibeues cinereus	0	1	0	1	1	0	1	1	1
Artibeus concolor	1	0	1	1	1	1	1	1	1
Artibeus planirostris	1	1	1	1	1	1	1	1	1
Artibeus glaucus	1	1	0	1	1	0	1	1	0
Artibeus gnomus	1	0	0	1	0	0	1	0	0
Artibeus lituratus	1	1	0	1	1	0	1	1	1
Artibeus obscurus	1	1	0	1	1	0	1	1	1
Carollia brevicauda	1	1	1	1	1	1	1	1	1
Carollia perspicillata	1	1	1	1	1	1	1	1	1
Carollia benkeithi	0	0	0	1	1	0	0	0	1
Chiroderma villosum	1	0	0	1	0	0	0	0	1
Desmodus rotundus	1	0	1	0	1	0	1	1	1
Glossophaga soricina	1	0	1	1	1	1	1	1	1
Glyphonycteris daviesi	1	0	1	1	1	1	1	0	0
Lonchophylla dekeyseri	1	1	1	1	1	0	1	1	0
Lonchophylla mordax	1	0	1	0	0	0	1	0	0
Lonchophylla thomasi	1	0	0	1	0	0	1	0	0
Lonchorrhina aurita	1	0	0	1	1	1	1	0	0
Lophostoma brasiliense	1	1	0	1	1	1	0	0	0
Lophostoma carrikeri	1	1	0	1	1	0	1	0	0
Lophostoma silvicolum	0	0	0	1	1	0	1	0	0
Mesophylla macconnelli	0	0	0	0	1	0	0	0	0
Micronycteris megalotis	1	0	0	1	0	0	0	0	0
Micronycteris schmidtorum	1	0	0	1	0	0	1	0	0
Mimon crenulatum	1	0	0	0	1	1	1	0	0
Phylloderma stenops	1	0	0	0	1	0	0	0	0
Phyllostomus discolor	1	0	0	1	1	1	0	1	0
Phylllostomus hastatus	1	0	0	1	1	1	1	1	0
Platyrrhinus lineatus	1	1	0	1	1	0	1	1	0
Rhinophylla pumilio	0	0	0	1	0	0	1	1	0
Sturnira lilium	1	0	0	1	1	1	1	1	1
Sturnira tildae	1	0	0	1	1	1	1	1	1
Tonatia saurophilla	1	0	0	0	0	0	1	0	0
Trachops cirrhosus	0	0	0	0	0	1	1	1	0
Uroderma bilobatum	1	1	0	1	1	1	1	1	1
Vampyrodes caracciolli	1	1	0	1	0	0	1	1	1
Vespertilionidae									
Eptesicus brasiliensis	1	0	1	1	0	0	1	0	1
Eptesicus furinalis	0	1	0	1	0	0	1	1	1
Lasiurus ega	0	1	0	0	0	0	0	0	0
Myotis albescens	1	0	0	1	0	0	1	0	1
Myotis nigricans	1	0	0	1	0	0	1	0	1
Myotis riparius	1	1	0	1	1	0	1	1	1
Rhoghessa sp.	0	0	0	0	0	0	1	0	0

Table 2 – Estimated parameters and confidence intervals for fixed and random effects for the models explaining estimated species richness, functional dispersion and phylogenetic diversity according to phytophysiognomy. SE, standard error for fixed effects; SD, standard deviation for random effects.

	β	**SE/SD**	**z**	p
Species richness				
Fixed effects: R^2m=0.040				
Cerrado *s.s.*	0.231	0.325	0.897	0.671
Cerradão	0.241	0.244	0.989	0.323
Gallery forest	0.117	0.239	0.486	0.627
Random effects: $R^2c - R^2m$=0.413				
Sampling site		0.455		
Sampling scheme		0.389		
Functional dispersion				
Fixed effects: R^2m=0.025				
Cerrado *s.s.*	0.453	0.331	1.369	0.177
Cerradão	0.340	0.125	0.272	0.787
Gallery forest	0.180	0.125	1.439	0.156
Random effects: $R^2c - R^2m$=0.915				
Sampling site		0.450		
Sampling scheme		0.346		
Phylogenetic diversity				
Fixed effects: R^2m=0.026				
Cerrado *s.s.*	0.504	0.495	1.090	0.130
Cerradão	0.107	0.297	0.339	0.736
Gallery forest	0.319	0.296	1.074	0.288
Random effects: $R^2c - R^2m$=0.884				
Sampling site		0.634		
Sampling scheme		0.827		

acoustic monitoring data. Also, average functional diversity increased evidently from highly modified (0.0673) to pristine (0.113) environments for mist-net data, but showed almost no change for acoustic data (1.109 and 1.274 in highly modified and pristine environments, respectively). Average phylogenetic diversity also showed a clear increase trend from highly modified (1.059) to pristine (3.086) environments for mist-net data, but very similar values for acoustic data (1.012 and 1.324 in highly modified and pristine environments, respectively). There was significant variation in species composition between levels of land-use intensity (F=6.31, p<0.001) but not between phytophysiognomies (F=1.6088, p=0.06). More opportunistic frugivores (e.g. *Carollia perspicillata* and *Artibeus planirostris*) tend to persist even in highly modified sites, but members of other ensembles, in particular gleaning animalivores (e.g. *Micronycteris megalotis*), nectarivores (e.g. *Anoura geoffroyi*) and strict open-space insectivores (e.g. *Diclidurus ingens*, *Peropteryx trinitatis*) tend to disappear with increasing levels of anthropogenic disturbance (Tab. 1).

Discussion

We found no significant differences in all metrics of diversity among the studied Cerrado phytophysiognomies, demonstrating that the savanna-like environment, cerrado *sensu stricto*, holds similar levels of taxonomic, functional and phylogenetic diversity to those of the forest-structured environments, cerradão and gallery forest. However, we found a significant decrease trend in all metrics of bat diversity associated with increasing levels of land-use modification, showing that even slight modifications due to extensive grazing cause significant diversity losses, and that in environments highly modified by intensive pasture and grazing taxonomic, functional and phylogenetic diversity are seriously reduced.

Cerrado's mosaicism contributes to high levels of bat diversity

We found similar levels of all metrics of diversity between cerrado *sensu stricto*, cerradão and gallery forest. Whilst at the scale of the biome, Cerrado was already recognized as a bat species hotspot, har-

Table 3 – Estimated parameters and confidence intervals for fixed and random effects for the models explaining estimated species richness, functional dispersion and phylogenetic diversity according to land-use intensity. SE, standard error for fixed effects; SD, standard deviation for random effects.

	β	SE/SD	z	p
Species richness				
Fixed effects: R^2m=0.319				
Pristine	2.675	0.282	9.501	<0.001
Scarcely modified	−0.552	0.1211	−4.559	<0.001
Highly modified	0.117	0.239	0.486	0.627
Random effects: $R^2c - R^2m$=0.413				
Sampling site		0.150		
Sampling scheme		0.382		
Functional dispersion				
Fixed effects: R^2m=0.124				
Pristine	0.729	0.328	2.221	0.030
Scarcely modified	−0.183	0.108	−1.703	0.095
Highly modified	−0.501	0.107	−4.664	<0.001
Random effects: $R^2c - R^2m$=0.829				
Sampling site		0.296		
Sampling scheme		0.452		
Phylogenetic diversity				
Fixed effects: R^2m=0.335				
Pristine	2.336	0.479	4.869	<0.001
Scarcely modified	−0.725	0.209	−3.461	0.001
Highly modified	−1.551	0.209	−7.409	<0.001
Random effects: $R^2c - R^2m$=0.617				
Sampling site		0.643		
Sampling scheme		0.581		

bouring more than 100 species (Paglia et al., 2012; Aguiar et al., 2016), subsisted the idea that, locally, the bat assemblages of Neotropical savannas were much poorer than those of forests (Marinho-Filho and Guimarães, 2001; Aguirre et al., 2002). This was mostly due to the idea that local bat richness is positively correlated to structural complexity along the vertical axis (Ramos Pereira et al., 2009; Fahr and Kalko, 2011), but it seems to neglect not only that some phytophysiognomies in the Cerrado also present high structural vertical complexity, but also, and perhaps more interestingly, others show noteworthy horizontal heterogeneity. As we solely used incidence based-data to test for differences in species composition across physiognomies (due to the constraints of our acoustic monitoring data), we are unable at this point to state if some species, while present in all or most physiognomies, tend to prefer a certain one.

The phyllostomid assemblages of our work (those well sampled through mist-nets, as done almost exclusively by the studies in the literature) together with those of the recent study of Gregorin et al. (2011), far exceed previous figures of species richness in other Cerrado areas (Bordignon, 2006; Zortéa and Alho, 2008) suggesting that those previous numbers of local richness were mainly due to sampling biases resulting from either insufficient mist-net sampling or from inadequate choice of sampling areas. It is possible that bat densities in Cerrado are lower than those in Amazonian or Atlantic Forest; so, to attain similar levels of richness, a larger sampling effort may be required. To our knowledge, our mist-net sampling effort, in terms of the number of mist-nets used, was the largest ever made in studies of bat assemblages in the Cerrado, and this was probably one of the reasons why we attained such figures for phyllostomid richness. Also, it is likely that setting canopy nets in the forest-structured phytophysiognomies would have resulted in even higher numbers. We decided not to do so because we wanted to keep a similar sampling effort between sites, and canopy netting in the open phytophysignomy would be inadequate.

In our study we registered a total of 64 bat species, and when we compare our observed richness values per phytophysiognomy with those obtained in local inventories in the Atlantic Forest this idea of higher richness values in this last biome is refuted. Indeed, in a review made by Bergallo (2003), and only considering localities with a minimum of 1000 captures, average bat richness for the Atlantic Forest biome was 22.4 (varying between 18 and 27). More recently, Muylaert et al. (2017), in a compilation dataset of Atlantic Forest bat assemblages reveal that bat species richness per Atlantic Forest site averages 12.1 species (ranging from 1 to 53 species). In our study, observed Phyllostomidae richness varied between 17 and 26 species in the pristine phytophysiognomies, which are values equivalent (and even higher) than those found in local Atlantic Forest assemblages. Still, Amazonian forests are still clearly richer: for instance Ramos Pereira et al. (2009) observed 44 phyllostomid species in terra firme forests of the lowlands of the Brazilian Amazon, 31 in várzea and 30 in igapó forests, while Rex et al. (2008) indicates 44 phyllostomid species at the Tiputini Biodiversity Station in Ecuador; nonetheless, it should be noted that canopy mist-netting was used in addition to ground netting in both these studies.

Intense land-use modifications threat the diverse bat assemblages of the Cerrado

We found significant trends for decrease in all metrics of bat diversity concomitant with anthropogenic land-use intensity. This was quite evident in terms of species richness, with significantly higher estimates for pristine environments. Easy to interpret, species richness is the most iconic measure of diversity, and for that reason the most used in conservation planning (Gotelli and Colwell, 2001). Comparing richness estimates, however, is insufficient to attain an idea on the functional characteristics that may be loss with the disappearance of some species from a certain assemblage.

Assuming that in ecological terms a species is an assortment of individuals with phenotypic and behavioural traits determining when and where they can exist and interact with other species (McGill et al., 2006; Cadotte et al., 2011), measuring distances between species' traits gives us insights on how certain environmental filters will act on the functional diversity of assemblage species' persistence via functional traits (Lees and Peres, 2008; Quesnelle et al., 2014). We expect harsher environmental conditions, such as low availability of roosting, feeding and drinking resources resulting from anthropogenic changes in the landscape, to strongly select for bat species that possess traits imbuing them with the ability to tolerate abiotic stresses, basically preventing other, more sensitive or specialized, from inhabiting such areas, resulting in an under-dispersed functional space. We found a significant decrease in the functional diversity metric between highly modified environments and pristine environments showing that, up to a certain level of anthropogenic change, the functional space occupied by the bat assemblage is similar, but over a certain limit of land-use modification more specialized species tend to disappear, thus resulting in a decrease in functional diversity.

Phylogenetic diversity metrics are based on the assumption that species ecological differences are proportional to the amount of time since they diverged from a common ancestor (Cadotte et al., 2013), under a model of evolution assuming homogeneous rates of trait evolution across the tree, which may not always apply (Harvey and Pagel, 1991; Webb et al., 2002). Here, we added a measure of phylogenetic diversity to that of functional diversity because probably more often than not we may overlook potentially important biological traits in our empirical data. Our results were consistent using these complementary approaches, as we also found phylogenetic diversity to be negatively correlated with land-use intensity in the Cerrado. In other words, there is a gradual loss of evolutionarily distinct lineages associated with increasing levels of land-use change. Our results are in line with those of studies done in Neotropical forests (Meyer and Kalko, 2008b; Estrada-Villegas et al., 2010) and show that bat assemblages rapidly react to habitat loss, even when anthropogenic changes are moderate. As expected, the decline in all metrics of diversity was steeper between pristine and highly modified sites.

Within the Phyllostomidae, we found that more opportunistic frugivores seem to be able to persist in somewhat altered Cerrado areas, whereas members of other ensembles, in particular gleaning animalivores and nectarivores tend to disappear with increasing levels of land-use modification (Tab. 1). A similar result was obtained by Farneda et al. (2015) in Central Amazonia forest fragments, who found that gleaning animalivorous bats were clearly associated with large continuous areas of preserved habitats. The sanguinivore *D. rotundus* occurred frequently in severely modified areas, but not always in pristine habitats, indicating that the density of this species tends to be low in unaltered habitats. In fact, Gomes et al. (2007) demonstrate that patterns of sanguinivore attacks on cattle are better explained by 'distance to forest', 'proportion of sugarcane', and 'cattle density'. Therefore, since livestock is a major economic activity all over Brazil and pastures replace natural Cerrado areas at a fast pace, the densities of *D. rotundus* will certainly increase as will the probability of rabies outbreaks. Because roost destruction is, regrettably, one of the methods used in Brazil to control populations of sanguinivores, other species that cohabit with *D. rotundus*, such as the Cerrado endemic and globally endangered *L. dekeyseri* (Aguiar and Bernard, 2016) may be also seriously threatened (Aguiar et al., 2010). Even some open-space aerial insectivores, such as *Diclidurus ingens*, *Peropteryx kappleri*, *P. macrotis*, *P. trinitatis*, *Nyctinomops laticaudatus*, and even high-flying species as *Cynomops abrasus* and large *Eumops* almost disappear from modified environments showing that, even for species that are able to cross open environments, the loss of natural vegetation cover in Cerrado phytophysiognomies, rapidly leads to a decrease in the availability of foraging and roosting resources.

Our data support the theory that anthropogenic environmental changes act as a non-random filter, selecting those species best able to thrive within modified ecosystems (Smart et al., 2006), while more sensitive species, often those with narrower niches (Laidre et al., 2008; Devictor et al., 2008; Boulangeat et al., 2012), are likely to suffer local extinctions. Habitat loss, rather than changes in landscape configuration, seems to underlie bat responses (Meyer and Kalko, 2008b; Farneda et al., 2015). Also, if bats, that are highly vagile, are affected by land-use intensification even at a low level, it is likely that other animal groups, especially those with lower dispersal abilities are equally or more strongly affected by that factor. Consequently, the fast rate of loss of natural vegetation in the Cerrado will undoubtedly result in a decrease in γ-diversity, i.e., in a species-poorer biome, as more similar assemblages will be the outcome of a non-random species turnover (McKinney and Lockwood, 1999). Besides the evident loss in biodiversity, the other immediate consequence of our results is that, if the species supporting the most distinct combinations of traits are not effectively protected, some functions may disappear, imperilling bat-mediated ecosystem processes. Indeed, in highly impoverished assemblages, ecosystem processes mediated by bats may be strongly disrupted affecting biodiversity as a whole and seriously threatening the maintenance of traditional livelihoods and the economical sustainability of people that depend on natural Cerrado products to subsist.

Further investigation is necessary to understand bat responses to land-use changes in other areas of Cerrado, but our study clearly emphasizes the need to focus conservation efforts on the maintenance of distinct pristine phytophysiognomies characteristic of the Cerrado biome, in order to guarantee the persistence of bat diversity in all its dimensions, fundamental for the sustainability of key ecological services in the Cerrado biodiversity hotspot. Besides this, maintaining corridors between well-preserved areas within the Cerrado may be equally pivotal for bat conservation, as already been recognized for non-volant mammals (Magioli et al., 2016).

References

Aguiar L.M.S., Bernard E., 2016. *Lonchophylla dekeyseri*. IUCN Red List Threat. Species 2016: e.T12264A22038149. doi:10.2305/IUCN

Aguiar L.M.S., Bernard E., Ribeiro V., Machado R.B., Jones G., 2016. Should I stay or should I go? Climate change effects on the future of Neotropical savannah bats. Global Ecol. Conserv. 5: 22–33.

Aguiar L.M.S., Brito D., Machado R.B., 2010. Do current vampire bat (*Desmodus rotundus*) population control practices pose a threat to Dekeyser's nectar bat (*Lonchophylla dekeyseri*) long-term persistence in the Cerrado? Acta Chiropterol. 12: 275–282.

Aguirre LF. 2002. Structure of a Neotropical savanna bat community. J. Mammal. 83: 775–784.

Aguirre L.F., Herrel A., Van Damme R., Matthysen E., 2002. Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. Proc. R. Soc. London. Ser. B Biol. Sci. 269: 1271–1278.

Azevedo J.A.R., Valdujo P.H., de C. Nogueira C., 2016. Biogeography of anurans and squamates in the Cerrado hotspot: coincident endemism patterns in the richest and most impacted savanna on the globe. J. Biogeogr. 43: 2454–2464.

Baagøe H.J., 1977. Age determination in bats (Chiroptera). Vidensk. Meddelelser Dansk Naturhistorisk Foren. 140: 53–92.

Barataud M., Giosa S., Leblanc F., Rufray V., Disca T., Tillon L., Delaval M., Haquart A., Dewynter M., 2013. Identification et écologie acoustique des chiroptères de Guyane Française. Le Rhinolophe 19: 103–145. [in French]

Bartoń K., 2013. MuMIn: multi-model inference, R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn

Bergallo H.G., 2003. Bat species richness in atlantic forest: what is the minimum sampling effort? Biotropica 35: 278–288.

Bernard E., 2001. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. J. Trop. Ecol. 17: 115–126.

Bernard E., Aguiar L.M.S., Machado R.B., 2011. Discovering the Brazilian bat fauna: A task for two centuries? Mamm. Rev. 41: 23–39.

Bernard E., Fenton M.B., 2002. Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. Can. J. Zool. 80: 1124–1140.

Bernard E., Fenton M.B., 2007. Bats in a fragmented landscape: Species composition, diversity and habitat interactions in savannas of Santarem, Central Amazonia, Brazil. Biol. Conserv. 134: 332–343.

Bordignon M.O., 2006. Diversidade de morcegos (Mammalia, Chiroptera) do Complexo Aporé-Sucuriú, Mato Grosso do Sul, Brasil. Rev. Bras. Zool. 23: 1002–1009. [in Portuguese]

Boulangeat I., Lavergne S., Van Es J., Garraud L., Thuiller W., 2012. Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. J. Biogeogr. 39: 204–214.

Brosset A., Charles-Dominique P., 1990. The bats from French Guiana: a taxonomic, faunistic and ecological approach. Mammalia 54: 509–560.

Bustamante E., Casas A., Búrquez A., 2010. Geographic variation in reproductive success of *Stenocereus thurberi* (Cactaceae): effects of pollination timing and pollinator guild. Am. J. Bot. 97: 2020–2030.

Cadotte M., Albert C.H., Walker S.C., 2013. The ecology of differences: Assessing community assembly with trait and evolutionary distances. Ecol. Lett. 16: 1234–1244.

Cadotte M.W., Carscadden K., Mirotchnick N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48: 1079–1087.

Cardoso P., Rigal F., Carvalho J.C., 2015. BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods Ecol. Evol. 6: 232–236.

Devictor V., Julliard R., Jiguet F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. 117: 507–514.

Dixon P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14: 927–930.

Espírito-Santo M.M., Leite M.E., Silva J.O., Barbosa R.S., Rocha A.M., Anaya F.C., Dupin M.G.V., 2016. Understanding patterns of land-cover change in the Brazilian Cerrado from 2000 to 2015. Phil. Trans. R. Soc. 371: 20150435.

Estrada-Villegas S., McGill B.J., Kalko E.K.V., 2012. Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. Ecology 93: 1183–1193.

Estrada-Villegas S., Meyer C.F.J., Kalko E.K.V., 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. Biol. Conserv. 143: 597–608.

Fahr J., Kalko E.K.V., 2011. Biome transitions as centres of diversity: habitat heterogeneity and diversity patterns of West African bat assemblages across spatial scales. Ecography 34: 177–195.

Farneda F.Z., Rocha R., López-Baucells A., Groenenberg M., Silva I., Palmeirim J.M., Bobrowiec P.E.D., Meyer C.F.J., 2015. Trait-related responses to habitat fragmentation in Amazonian bats. J. Appl. Ecol. 52: 1381–1391.

Fearnside P.M., 2001. Soybean cultivation as a threat to the environment in Brazil. Environ. Conserv. 28: 23–38.

Findley J.S., 1993. Bats: a community perspective. Cambridge University Press, Cambridge.

Fleming T.H., 1982. Foraging strategies of plant-visiting bats. In: Kunz T.H. (Ed.) Ecology of bats. Plenum Press, New York. 287–325

Fleming T.H., Sahley C.T., Holland J.N., Nason J.D., Hamrick J.L., 2001. Sonoran Desert columnar cacti and the evolution of generalized pollination systems. Ecol. Monogr. 71: 511–530.

Garcia L.C., Ribeiro D.B., de Oliveira Roque F., Ochoa-Quintero J.M., Laurance W.F., 2017. Brazil's worst mining disaster: Corporations must be compelled to pay the actual environmental costs. Ecol. Appl. 27: 5–9.

Gomes M.N., Monteiro A.M.V., Nogueira V.S., Goncalves C.A., 2007. Areas prone for vampire bat (*Desmodus rotundus*) attack on cattle in the Sao joao da Boa Vista region, State of Sao Paulo. Pesqui. Vet. Bras. 27: 307–313.

Gorresen P.M., Willig M.R., 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. J. Mammal. 85: 688–697.

Gotelli N.J., Colwell R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

Goujon M., McWilliam H., Li W., Valentin F., Squizzato S., Paern J., Lopez R., 2010. A new bioinformatics analysis tools framework at EMBL-EBI. Nucleic Acids Res. 38: W695–W699.

Gregorin R., Gonçalves E., Aires C.C., Carmignotto A.P., 2011. Morcegos (Mammalia: Chiroptera) da Estação Ecológica Serra Geral do Tocantins: composição específica e considerações taxonômicas. Biota Neotrop. 11: 299–311. [in Portuguese]

Harvey P.H., Pagel M.D., 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hutchinson G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93: 145–159.

Jung K., Kalko E.K.V., Von Helversen O., 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. J. Zool. 272: 125–137.

Jung K., Molinari J., Kalko E.K.V., 2014. Driving factors for the evolution of species-specific echolocation call design in new world free-tailed bats (Molossidae). PLoS ONE 9: e85279.

Kalka M.B., Smith A.R., Kalko E.K.V., 2008. Bats limit arthropds and herbivory in a tropical forest. Science 320: 71.

Kalko E.K.V., 1997. Diversity in tropical bats. In: Ulrich H. (Ed.) Tropical biodiversity and systematics. Zool Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. 13–43.

Kalko E.K.V., 1998. Organisation and diversity of tropical bat communities through space and time. Zool. Complex Syst. 101: 281–297.

Kalko E.K.V., Handley C.O., 2001. Neotropical bats in the canopy: Diversity, community structure, and implications for conservation. Plant Ecol. 153: 319–333.

Kalko E.K., Handley C., Handley D., 1996. Organization, diversity, and long-term dynamics of a Neotropical bat community. In: Cody M., Smallwood J. (Eds.) Academic Press, Los Angeles. 503–553.

Klink C.A., Machado R.B., 2005. Conservation of the Brazilian Cerrado. Conserv. Biol. 19: 707–713.

Kunz T.H., de Torrez E.B., Bauer D., Lobova T., Fleming T.H., 2011. Ecosystem services provided by bats. Ann. N. Y. Acad. Sci. 1223: 1–38.

Laidre K.L., Stirling I., Lowry L.F., Wiig Ø., Heide-Jørgensen M.P., Ferguson S.H., 2008. Quanifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol. Appl. 18: S97–S125.

Laliberté E., Legendre P., Shipley B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package version 1.0–12.

Laranjeiras T.O., Gomes De Moura N., Cardoso L., Vieira G., Angelini R., Carvalho A.R., 2012. Bird communities in different phytophysiognomies of the cerrado biome. Stud. Neotrop. Fauna Environ. 47: 41–51.

Larkin M.A., Blackshields G., Brown N.P., Chenna R., McGettigan P.A., McWilliam H., Valentin F., Wallace I.M., Wilm A., Lopez R., Thompson J.D., Gibson T.J., Higgins D.G., 2007. Clustal W and Clustal X version 2.0. Bioinformatics 23: 2947–2948.

Lees A.C., Peres C.A., 2008. Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape. Anim. Conserv. 11: 128–137.

MacArthur R.H., Macarthur J.W., 1961. On bird species diversity. Ecology 42: 594–598.

Machado R.B., Neto M.B.R., Pereira P.G.P., Caldas E.F., Gonçalves D.A., Santos N.S., Tabor K., Steininger M., 2004. Estimativas de perda da área do Cerrado brasileiro. Conservation International, Brasília, D.F. [in Portuguese]

Magioli M., Ferraz K.M.P.M.B., Setz E.Z.F., Percequillo A.R., Rondon M.V.S.S., Kuhnen V.V., Canhoto M.C.S.C., Almeida dos Santos K.E., Kanda C.Z., Fregonezi G.L., Prado H.A., Ferreira M.K., Rebeiro M.C., Villela P.M.S., Coutinho L.L., Rodrigues M.G., 2016. Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. Eur. J. Wildl. Res. 62: 431–446.

Marinho-Filho J., Guimarães M.M., 2001. Mamíferos das matas de galeria e das matas ciliares do Distrito Federal. Cerrado: caracterização e recuperação de matas de galeria. Embrapa Cerrados, Planatina. 529–557. [in Portuguese]

McGill B.J., Enquist B.J., Weiher E., Westoby M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21: 178–185.

McKinney M., Lockwood J., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14: 450–453.

McWilliam H., Li W., Uludag M., Squizzato S., Park Y.M., Buso N., Cowley A.P., Lopez R., 2013. Analysis Tool Web Services from the EMBL-EBI. Nucleic Acids Res. 41: W597–W600.

Medellín R.A., Equihua M., Amin M.A., 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. Conserv. Biol. 14: 1666–1675.

Meyer C.F.J., Kalko E.K.V., 2008a. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. Divers. Distrib. 14: 644–654.

Meyer C.F.J., Kalko E.K.V., 2008b. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. J. Biogeogr. 35: 1711–1726.

Muylaert R.L., Stevens R.D., Esbérard C.E., Mello M.A., Garbino G.S., Varzinczak L.H., Faria D., Weber M.M., Rogeri P.K., Regolin A.L., Oliveira H.F.M., Costa L.M., Barros M.A.S., Sabino-Santos G.Jr., Morais M.A.C., Kavagutti V.S., Passos F.C., Marjakangas E.L., Maia F.G.M., Rebeiro M.C., Galetti M., 2017. Atlantic Bats: a dataset of bat communities from the Atlantic Forests of South America. Ecology 98(12): 3227.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A., Kent J., 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nogueira C., Colli G.R., Martins M., 2009. Local richness and distribution of the lizard fauna in natural habitat mosaics of the Brazilian Cerrado. Austral Ecol. 34: 83–96.

Nogueira M.R., de Lima I.P., Moratelli R., Tavares V.C., Gregorin R., Peracchi A.L., 2014. Checklist of Brazilian bats, with comments on original records. Check List 10: 808–821.

Nogueira C., Ribeiro S., Costa G.C., Colli G.R., 2011. Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. J. Biogeogr. 38: 1907–1922.

Norberg U.M., Rayner J.M.V., 1987. Ecological morphology and flight in bats (Mammalia, Chiroptera) - Wing adaptations, flight performance, foraging strategy and echolocation. Philos. Trans. R. Soc. London Ser. B-Biological Sci. 316: 337–419.

Notredame C., Higgins D.G., Heringa J., 2000. T-Coffee: A novel method for fast and accurate multiple sequence alignment. J. Mol. Biol. 302: 205–217.

O'Farrell M.J., Miller B.W., 1999. Use of vocal signatures for the inventory of free-flying neotropical bats. Biotropica 31: 507–516.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H., 2016. Vegan: Community ecology package. R package. Version 2.3-5. https://cran.r-project.org/web/packages/vegan/index.html

Oliveira-Filho A.T., Ratter J.A., 2002. Vegetation Physiognomies and woody flora of the Cerrado biome. In: Oliveira P.S., Marquis R.J. (Eds.) The Cerrados of Brazil – Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. 91–120.

Paglia A.P., Fonseca G.A.B., Rylands A.B., Herrmann G., Aguiar L.M.S., Chiarello A.G., Leite Y.L.R., Costa, L.P., Siciliano S., Kierulff M.C.M., Mendes S.L., Tavares V.C., Mittermeier R.A., Patton J.L., 2012. Lista Anotada dos Mamíferos do Brasil / Annotated Checklist of Brazilian Mammals. 2ª Edição / 2nd Edition. Occasional Papers in Conservation Biology 6. Conservation International, Arlington, VA.

Patterson B.D., Willig M.R., Stevens R.D., 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. In: Kunz T.H., Fenton M.B. (Eds.) Bat ecology. University of Chicago Press, Chicago. 536–579.

Peña-Cuéllar E., Stoner K.E., Avila-Cabadilla L.D., Martínez-Ramos M., Estrada A., 2012. Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. Biodivers. Conserv. 21: 1381–1397.

Pielke R.A., Pitman A., Niyogi D., Mahmood R., McAlpine C., Hossain F., Goldewijk K.K., Nair U., Betts R., Fall S., Reichstein M., Kabat P., de Noblet N., 2011. Land use/land cover changes and climate: modeling analysis and observational evidence. Wiley Interdiscip. Rev. Clim. Chang. 2: 828–850.

Pinheiro J., Bates D., DebRoy S., Sarkar D., R Core Team, 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131.1. https://CRAN.R-project.org/package=nlme

Qian H., Kissling W.D., 2010. Spatial scale and cross-taxon congruence of terrestrial vertebrate and vascular plant species richness in China. Ecology 91: 1172–83.

Quesnelle P.E., Lindsay K.E., Fahrig L., 2014. Low reproductive rate predicts species sensitivity to habitat loss: a meta-analysis of wetland vertebrates. PLoS One 9: e90926.

Ramos Pereira M.J., Marques J.T., Palmeirim J.M., 2010. Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. Current Zoology 56: 469–478.

Ramos Pereira M.J., Marques J.T., Santana J., Santos C.D., Valsecchi J., De Queiroz H.L., Beja P., Palmeirim J.M., 2009. Structuring of Amazonian bat assemblages: The roles of flooding patterns and floodwater nutrient load. J. Anim. Ecol. 78: 1163–1171.

Ratter J., 1997. The Brazilian Cerrado Vegetation and Threats to its Biodiversity. Ann. Bot. 80: 223–230.

Redford K.H., Fonseca G.A.B., 1986. Cerrado Zoogeography. Biotropica 18: 126–135.

Rex K., Kelm D.H., Wiesner K., Kunz T.H., Voigt C.C., 2008. Species richness and structure of three Neotropical bat assemblages. Biol. J. Linn. Soc. 94: 617–629.

Rocha R., López-Baucells A., Farneda F.Z., Groenenberg M., Bobrowiec P.E.D., Cabeza M., Palmeirim J.M., Meyer C.F.J., 2017. Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. Landsc. Ecol. 32: 31–45.

Rojas D., Vale Á., Ferrero V., Navarro L., 2012. The role of frugivory in the diversification of bats in the Neotropics. J. Biogeogr. 39: 1948–1960.

Sievers F., Wilm A., Dineen D., Gibson T.J., Karplus K., Li W., Lopez R., McWilliam H., Remmert M., Söding J., Thompson J.D., Higgins D.G., 2011. Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. Mol. Syst. Biol. 7: 539.

Simmons N.B., Voss R.S., 1998. The mammals of Paracou, French Guiana: A neotropical lowland rainforest fauna part - 1. Bats. Bull. Am. Museum Nat. Hist. 237: 1–219.

Smart S.M., Thompson K., Marrs R.H., Le Duc M.G., Maskell L.C., Firbank L.G., 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. Proc. R. Soc. B-Biological Sci. 273: 2659–65.

Stevens R.D., López-González C., Presley S.J., 2007. Geographical ecology of Paraguayan bats: spatial integration and metacommunity structure of interacting assemblages. J. Anim. Ecol. 76: 1086–1093.

Stickler C.M., Nepstad D.C., Coe M.T., McGRATH D.G., Rodrigues H.O., Walker W.S., Soares-Filho B.S., Davidson E., 2009. The potential ecological costs and cobenefits of REDD: a critical review and case study from the Amazon region. Glob. Chang. Biol. 15: 2803–2824.

Tews J., Brose U., Grimm V., Tielbörger K., Wichmann M.C., Schwager M., Jeltsch F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31: 79–92.

Valdujo P.H., Silvano D.L., Colli G., Martins M., 2012. Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. South Am. J. Herpetol. 7: 63–78.

van der Plas F., van Klink R., Manning P., Olff H., Fischer M., 2017. Sensitivity of functional diversity metrics to sampling intensity. Methods Ecol. Evol. 8: 1072–1080.

Vitt L.J., Caldwell J.P., 1993. Ecological observations on cerrado lizards in Rondonia, Brazil. J. Herpetol. 27: 46–52.

Webb C.O., Ackerly D.D., McPeek M., Donoghue M.J., 2002. Phylogenies and Community Ecology. Annu. Rev. Ecol. Syst. 33: 475–505.

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

Willig M.R., 1983. Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from Northeast Brazil. Bull. Carnegie Museum Nat. Hist. 23: 1–131.

Zortéa M., Alho C.J.R., 2008. Bat diversity of a Cerrado habitat in central Brazil. Biodivers. Conserv. 17: 791–805.

Zuur A.F., Ieno E.N., Walker N., Saveliev A., Smith G.M., 2009. Mixed effects models and extensions in ecology with R. Statistics (Ber).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental Table S1 List, description and literature support for the functional traits attributed to each species.