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Highlights

- The structure of Neotropical bat assemblages varies regardless of the disturbance level of the study sites.
- No differences in assemblage diversity and composition between well-preserved and disturbed sites of the Yungas Forests.
- The responses of bats to habitat alteration tend to be highly species-specific.

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Assemblage-level responses of Neotropical bats to forest loss and fragmentation

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Abstract

Habitat loss and fragmentation are the most important causes of biological diversity loss, changing the properties of the remaining environment. The Neotropical Region is one of the most affected areas due to the conversion of natural habitats into agricultural activities and deforestation. In this region, bats represent almost 50% of all mammal species, reaching the highest taxonomic and functional diversity. Bats are valuable indicators of biodiversity and ecosystem health, but their response to habitat loss and fragmentation was poorly studied in Argentina. The aim of this study was to analyze the response of bat assemblages to habitat alteration in Northwestern Argentina. The specimens were collected in eight different localities, four well-preserved and four disturbed sites of the Yungas Forests. To describe the structure of bat assemblages, rank-abundance curves, species richness and Shannon (H') and Simpson (D') diversity indexes were calculated. To test the assemblage variations among sites, PCA and NPMANOVA analysis were performed. After 96 sampling nights, a total of 565 bats from 23 species were captured. A great variation in the assemblage structure was registered, regardless the disturbance level of the sites. These variations were not significantly different according to statistical analysis. The results support the hypothesis that areas with moderate fragmentation can sustain a high diversity of bat species. Moreover, these results showed that consistent responses to landscape composition at the assemblage level are harder to identify in fragmented Neotropical Forests. The responses of bats to habitat alteration tend to be highly species-specific.

Keywords: Assemblage diversity, Chiroptera, Community ecology, Habitat loss, Habitat fragmentation.

Introduction

Alteration in land use is one of the principal aspects of global environmental change and a key driver of biodiversity loss in terrestrial ecosystems (Meyer, Struebig & Willig 2016). Indeed, biodiversity impacts of land-use change are generally considered to be more immediate than those from climate change (Sala et al. 2000; Jetz, Wilcove & Dobson 2007; Pereira et al. 2010). However, human pressures on the natural environments are not uniformly distributed on the planet (Myers et al. 2000). In this sense, the Neotropics is one of the regions under stronger pressure for the conversion of its natural landscapes due to logging, creation of pastures and agricultural activities, mining or growing urbanization (Asner et al. 2009; Lewis et al. 2009; FAO 2011). This situation is alarming, considering that the Neotropics contain some of the highest levels of biodiversity, several centers of endemism, with rare and endangered species (Young et al. 2004; Schipper et al. 2008).

In the Neotropical Region, bats can represent more than 50% of the species in a mammalian fauna (Aguirre 2002; Sampaio et al. 2003). They exhibit the general mammalian pattern of greatest diversity in the tropics, from both a taxonomic and a functional perspective (Willig, Patterson & Stevens 2003). Bats also provide ecosystem services that are critically important in tropical ecosystems—as pollinators and seed dispersers for hundreds of plant species and as agents of suppression of arthropod herbivores and pest species (Muscarella & Fleming 2007; Kalka, Smith & Kalko 2008; Williams-Guillén, Perfecto & Vandermeer 2008; Kunz et al. 2011; Maas, Clough & Tschardtke 2013). Moreover, bats are valuable indicators of biodiversity and ecosystem health, and respond to a range of stressors related to environmental change (Jones et al. 2009).

Regarding the current understanding of tropical bat responses to anthropogenic disturbance, there was a general increase in the number of studies over the last 30 years (Fenton et al. 1992; Wilson, Ascorra & Solari 1996; Kalko 1998; Medellín, Equihua & Amin 2000; Soriano & Ochoa 2001; Gorresen & Willig 2004; Peters, Malcolm & Zimmerman 2006; Coutinho Cunto & Bernard 2012). However, despite these numerous attempts to detect consistent responses of tropical bats to habitat fragmentation, studies to date suggest relatively few generalizations (Meyer, Struebig & Willig 2016). At the assemblage level, studies that have compared fragmented and continuous forest in terms of species richness, diversity, and composition demonstrate inconsistent responses (Cosson, Pons & Masson 1999; Schulze, Seavy & Whitacre 2000; Estrada & Coates-Estrada 2002; Faria 2006).

With a few exceptions (Estrada et al. 2004; Estrada-Villegas, Meyer & Kalko 2010; Rodríguez-Durán & Otero 2011; Williams-Guillén & Perfecto 2011; Rodríguez-Durán & Feliciano-Robles 2016), Neotropical bat studies focused on the Phyllostomidae family, in turn largely reflecting the use of mist nets to capture bats (Meyer, Struebig & Willig 2016). Thus, little is still known about the effects of environmental disturbances in the Neotropics on bats of other poorly studied families, such as Molossidae and Vespertilionidae (Coutinho Cunto & Bernard 2012). A similar pattern is observed regarding the studied trophic guilds. Most of the studies were conducted on frugivorous species, whereas the effects of environmental disturbances on bats of other trophic groups, such as arthropodophagous or carnivorous species, remain uncertain (Coutinho Cunto & Bernard 2012). In America, the conducted studies included 11 countries (Coutinho Cunto & Bernard 2012), with no previous information about bat response to fragmentation in Argentina. The Yungas Forests of Northwestern Argentina are the third most diverse area

for bats in the country, containing 65% of the 67 species in the country (Díaz et al. 2016, 2019; Barquez & Díaz 2020). Moreover, these forests represent a biodiversity hotspot for being one of the richest and most diverse areas on Earth (Mittermeier et al. 1999; Ceballos & Ehrlich 2006). However, over the last decades, large areas of the Yungas Forests have been affected and altered by human activities through deforestation and cattle-raising in the piedmont areas (Brown et al. 2001); as well as energy and mining projects and exploitation of forest resources in the montane areas (Pacheco & Cristóbal 2009).

In the present study, we analyzed the response of bat assemblages to habitat alteration in Northwestern Argentina. According to this, we described the structure of bat assemblages in terms of composition, species richness and diversity, and evaluated their differences between well-preserved and disturbed sites from the Yungas Forests. Because a greater degree of disturbance is associated with drastic changes in the floristic composition and structure of vegetation (Castro-Luna, Sosa & Castillo-Campos 2007), we hypothesized that well-preserved sites would support greater bat species richness, composition, and abundance in comparison to disturbed sites. In accordance to similar studies (Medellín, Equihua & Amin 2000), we expected to observe in well-preserved sites assemblages characterized by higher number of total and rare species and low relative abundance of the most common species, while the reverse combination of values is expected to be found in disturbed sites of Yungas Forests.

Materials and methods

Study area

The study area belongs to the Yungas Forests ecoregion (Burkart et al. 1999), which is distributed from the borderline with Bolivia to the north of the province of Catamarca,

including three neighboring provinces, namely, Jujuy, Salta and Tucuman (Brown et al. 2001). The area is represented by typical vegetation dominated by tall trees such as *Cedrela lilloi* (cedar), *Enterobium contortisiliquum* (earpod tree) and *Cinnamomun porphyrium* (laurel). There are also smaller trees that do not exceed 20 m such as *Allophyllus edulis* (chalchal), *Celtis boliviensis* (tala), among others. Bushes such as *Urera baccifera*, *Piper tucumanum*, and *Solanum* sp. are present, as well as herbs which range from smaller forms to taller than two meters (Cabrera 1976); epiphytes are abundant, and lichens, ferns, bromeliads, and mosses are dominant (Brown et al. 2001). The climate in the area is warm and humid; the annual precipitation varies between 900 and 1000 mm, and the rainfalls are concentrated mainly in summer, 750 mm approximately from October to March (Burkart et al. 1999).

Sampling

The specimens were collected in eight different localities (Fig. 1), four well-preserved and four disturbed sites of the Yungas Forests (see Appendix), during ten field surveys of three nights each, between September 2012 and October 2015. The sites were selected from pairs at different latitudes, and the separation distance between each pair ranged from three to 18 km. In well-preserved sites, the vegetation is typical of the montane forest district, where all vegetation strata were recorded; whereas in disturbed sites, the structure of the vegetation is modified and some strata are missing, usually bushes and small trees. In the study sites, deforestation for cattle raising and croplands, as well as selective cutting, are the main causes of habitat alteration. Over the last decades, these actions generated a strong retraction of the Yungas Forests, transforming natural forests in isolated patches (Gamboa Alurralde et al. 2016). The conversion of natural habitat to pastoral land is

registered mainly in the southern portion of the Yungas Forests (Cabrera 1976), where the typical vegetation form patches separated by open grassland areas (Fig. 1, localities 5–8). In the middle portion of the Yungas Forests (Fig. 1, localities 3 and 4), the patches of old-growth forests are separated by huge extensions of cropland, mainly soybean crops (Gamboa Alurralde 2017). At the northern study sites (Fig. 1, localities 1 and 2), the commercial logging is also a major force of forest degradation (Brown et al. 2001), where the native tree species were completely replaced by exotic timber species, such as eucalyptus and pines. We used ArcGIS 10.1 (ESRI 2011) to calculate the proportion of native forest in the landscape as a measure of forest loss, and the density of edge habitat as a measure of fragmentation (Rodríguez-San Pedro & Simonetti 2015). Forest amount ranged from 98 to 100% in well-preserved sites and from 79 to 88% in disturbed sites. The bats were captured using six 12-m mist nets, set after sunset inside the forest and over streams or rivers, and kept open for periods of six hours. External measurements, age, sex, and reproductive condition were recorded from all collected specimens following Díaz, Flores and Barquez (1998). Bats were grouped by trophic guilds following Aguirre (2002).

Statistical analysis

To determine whether the surveys were representative of the bat assemblages, we calculated and plotted the species accumulation curves using the surveyed years as a sampling unit. The curves were calculated using the non-parametric estimators Chao 1 to estimate the number of species present in the area. Chao 1 is based on the number of rare species in a sample as a way to calculate the percentage of completeness of an inventory (Colwell 2005). To describe the structure of bat assemblages, in terms of composition and diversity, we calculated rank-abundance curves, species richness and Shannon (H') and Simpson (D') diversity indexes (Medellín, Equihua & Amin 2000). These analyses were

conducted using the free software EstimateS (Colwell 2005). We used Principal Components Analysis (PCA; Legendre & Legendre 1998) to analyze the assemblage variation among sites. Additionally, to test for significant differences in assemblage structure, we performed a Nonparametric Multivariate Analysis of Variance (NPMANOVA; Anderson 2001). We determined species richness and diversity indexes as the response variables, and the disturbance level of capture site (well-preserved/disturbed), the proportion of native forest and the density of edge habitat as explanatory variables. For each run, we used the Bray-Curtis similarity index for 10,000 permutations. These analyses were conducted using the free software PAST 3.11 (Hammer, Harper & Ryan 2001).

Results

After 96 survey nights and a total sampling effort of 41,472 m × h, we captured 565 specimens of bats belonging to 13 genera and 23 species, representing three families (Table 1). The most abundant species was *Sturnira lilium* (40% of the total captures), followed by *Artibeus planirostris* (12%), and *Myotis dinellii* (9%). Regarding the trophic guilds, we registered assemblages dominated by slow-flying arthropodophagous species, in terms of their species richness. We recorded 10 species of slow-flying arthropodophagous bats, eight fast-flying arthropodophagous, and three species of frugivorous bats. The remaining guilds, carnivorous and sanguivorous, were represented by only one species each (Table 1). In terms of abundance, we observed assemblages to be dominated by frugivorous species, such as *S. lilium* and *A. planirostris*. The species accumulation curves reached values close to the asymptote, and Chao 1 estimated a total number of species close to the species numbers recorded from the different sites. Based on this estimator, the assemblages

represented between 69 and 100% (Table 1), indicating that the number of recorded species was optimal for most of the study sites.

The structure of bat assemblages, in terms of their composition, was described calculating the range-abundance curve for each study site; a great variation in the assemblage structure among sites (Fig. 2) was observed, regardless the disturbance level of the site (well-preserved vs. disturbed). Some of the studied sites, both well-preserved and disturbed ones, showed assemblages of bats with high species richness, high number of rare species, and no dominant species in terms of abundance. On the contrary, in some of the other sites the opposite situation was recorded, showing assemblages with lower species richness, low number of rare species and few dominant species (Fig. 2). These results were also observed with the diversity indexes, with high values in both well-preserved and disturbed sites (Table 1).

The variation among assemblages of the different sites was studied using a Principal Components Analysis. The first two principal components (PC1 and PC2) summarized 97.32% of the variation in the sample (Fig. 3, Table 2). PC1 (88.83% of explained variation) represented mainly the proportion of native forest (NF) in the study sites. Positive scores on PC1 are associated with higher amount of forests found in well-preserved sites. On the other hand, PC2 (8.42% of explained variation) was highly correlated with species richness (SR) and moderately associated with the Simpson diversity index (D'). Positive scores on PC2 were correlated to assemblages with higher number of species and higher diversity. Finally, to test for significant differences in the assemblage structure among sites we performed a NPMANOVA. According to this analysis, the registered variations were not significantly different, neither based on the species richness ($P = 0.797$) nor the diversity indexes ($P = 0.714$).

Discussion

In this study, we analyzed the response of bat assemblages to habitat alteration in Northwestern Argentina. We described the structure of bat assemblages in terms of composition, species richness and diversity, and evaluated their differences between well-preserved and disturbed sites in the Yungas Forests. Our results showed no significant differences between bat assemblages from well-preserved and disturbed sites. In general terms, we registered bat assemblages characterized by few abundant common species, along with a high number of rare and less abundant species. This structure is similar to those obtained in other studies conducted in the Yungas Forests in Argentina (Bracamonte 2010; Jayat & Ortiz 2010; Gamboa Alurralde et al. 2016; Sánchez 2016).

Although most species of bats are arthropodophagous (Shiel et al. 1997), in tropical environments they are usually not the dominant guild, whereas at higher latitudes the importance of arthropodophagous species increases in the bat communities (Gamboa Alurralde, Barquez & Díaz 2017), as was recorded in this study. These results were also consistent with other studies carried out in the Neotropical Region (Aguirre 2002; Flores-Saldaña 2008). In terms of abundance, the high abundance of frugivorous species such as *Sturnira lilium* is in line with bat studies conducted in tropical (Kalko & Handley 2001) and subtropical environments (Moya et al. 2008; Gamboa Alurralde et al. 2016).

In contrast with our expectations, the structure of bat assemblage composition was not directly related to the disturbance level of the study sites. We expected to observe in well-preserved sites a greater bat species richness, diversity and abundance than in disturbed sites. However, based on the rank-abundance curves, we observed both well-preserved and disturbed sites with high and low species richness of bats and high and low

values of diversity indexes. Except for one of the well-preserved sites which showed the highest diversity of all, the disturbed sites were equal or more diverse than well-preserved sites. These results support the hypothesis that areas with moderate amounts of fragmentation, associated with conversion of forest habitat, can sustain a high diversity of bat species (Gorresen & Willig 2004; Clarke, Pio & Racey 2005; Clarke, Rostant & Racey 2005; Bernard & Fenton 2007; Willig et al. 2007; Klingbeil & Willig 2009; Rodríguez-Durán & Otero 2011; Rodríguez-Durán & Feliciano-Robles 2016). The tolerance of bats to habitat loss and fragmentation would be related to their capacity to traverse open areas between forest fragments or between fragments and continuous forest (Meyer, Struebig & Willig 2016), and to exploit all the resources of the landscape matrix, including roosts and food (Law, Anderson & Chidel 1999; Schulze, Seavy & Whitacre 2000; Presley et al. 2009; Trevelin et al. 2013).

A clear example of this was the pattern observed in *Chrotopterus auritus*. This species is usually collected in undisturbed forests (Fenton et al. 1992; Medellín, Equihua & Amin 2000; Gorresen & Willig 2004), but is also present in disturbed forests, as was recorded in our study (Wilson, Ascorra & Solari 1996; dos Reis et al. 2007). Although *C. auritus* depends on primary forests to find roost (Medellín 1989), human pressure on natural environments makes this species use disturbed areas as foraging habitats within its large home range (Brooke 1988), taking advantage of the high abundance of food that this type of area offers (Moras 2011). Another example of bat tolerance to habitat fragmentation, observed in this study, was showed by *Artibeus planirostris*. This frugivorous bat species was very abundant in disturbed sites, in line with several previous studies (Cosson, Pons & Masson 1999; Pinto & Keitt 2008; Chambers et al. 2016). The species of *Artibeus* have large home ranges (Morrison 1978), allowing them to be

generalists in terms of the areas used (Bonaccorso 1979) and to occur in both well-preserved and disturbed forests (Pinto & Keit 2008; Mena 2010; García-García & Santos-Moreno 2014).

The analysis of the assemblage variation among sites included environmental variables and assemblage variables. In this study, temporal variables to analyse the dynamics of the bat assemblages over time were not included. But it is known that, while the total number of species belonging to a community is often relatively constant in time, species composition is likely to change as some populations become extinct and are replaced by others (Russel et al. 1995). Moreover, it has been shown for bats that species relying on food resources that change over time (e.g. fruits) were more likely to be absent in particular years, due to temporal availability of the preferred food resource (Bonaccorso 1979). In contrast, species relying on more permanent food supplies (such as aerial insects) were present all year round. Because most of the species reported in this study belong to aerial insectivorous guild, we strongly believe that the assemblages evaluated would be characterized by low rates of species turnover, in line with previous studies (Aguirre et al. 2003).

Regarding the spatial variables analysed here, and in accordance with other studies, forest amount, a measure of habitat loss, was the best feature to separate the different assemblages of bats (Klingbeil & Willig 2009; Ethier & Fahrig 2011). This supported the use of habitat loss measures as a reliable factor to evaluate the bat response to habitat alteration (Meyer & Kalko 2008; Henry, Cosson & Pons 2010; Rodríguez-San Pedro & Simonetti 2015). Based on all variables, we conducted a NPMANOVA and no significant results were obtained. Similar results were observed in previous studies, showing that consistent responses to landscape composition at the assemblage level are harder to identify

in studies conducted in fragmented Neotropical Forests (Gorresen & Willig 2004; Klingbeil & Willig 2009, Montaña-Centellas et al. 2015; Meyer, Struebig & Willig 2016). A difficulty facing bat fragmentation studies is that responses tend to be highly species-specific, which is often overlooked by diversity metrics applied at the assemblage level (Klingbeil & Willig 2009). In addition to this, recent studies provide evidence for widespread scale dependence in associations between landscape metrics and bat responses at the assemblage, population, and species level (Gorresen & Willig 2004; Meyer & Kalko 2008; Pinto & Keitt 2008; Cisneros, Fagan & Willig 2015). Thus, future research should focus on the mechanisms behind responses of the individual bat species to fragmentation in multiple-scale assessments.

This study provides baseline research in Argentina and adds important information about the assemblage ecology of bats in the Yungas Forests. These are the first data about the response of bat to northwestern forests fragmentation, one of the most diverse areas for bats in the country. Considering that large areas of the Yungas Forests have been altered by human activities in the last decades, more studies are needed to understand the effect of these changes on bats.

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Appendix

Collection localities. The localities from the Yungas Forests are listed from north to south and according to its numbers in Fig. 1. For each locality is provided the acronym, specific site, department and province in brackets, coordinates and altitude in meters above sea level, and type of site.

- 1 – LCP. Las Capillas, 15 km al N de Las Capillas (Dr. Manuel Belgrano, Jujuy).
24°02'37'' S, 65°07'55'' W, 1061 m. Well-preserved site.
- 2 – FLC. Finca Las Capillas, 3 km al E del cruce entre río Las Capillas y ruta provincial n°
20 (Dr. Manuel Belgrano, Jujuy). 24°05'35.77'' S, 65°09'07.86'' W, 1141 m. Disturbed site.
- 3 – RLCH. Metán, 6 km al O, sobre río Las Conchas (Metán, Salta). 25°28'09'' S,
65°02'11.58'' W, 986 m. Well-preserved site.
- 4 – MET. Metán, 3.5 km al W (Metán, Salta). 25°29'34.76'' S, 65°00'29.95'' W, 1019 m.
Disturbed site.
- 5 – AGCH. Reserva Provincial Aguas Chiquitas, sobre río Aguas Chiquitas (Burruyacú,
Tucumán). 26°36'32.40'' S, 65°10'36.60'' W, 605 m. Well-preserved site.
- 6 – ELC. El Cadillal, camping La Curva (Burruyacú, Tucumán). 26°37'52.08'' S,
65°11'10.87'' W, 555 m. Disturbed site.
- 7 – ESC. Villa de Batiruaná (La Cocha, Tucumán). 27°38'11.61'' S, 65°44'40.29'' W, 515
m. Disturbed site.
- 8 – PAC. Villa de Escaba, 22 km al SE, sobre ruta provincial n° 9 (Paclín, Catamarca).
27°47'48.48'' S, 65°46'56.70'' W, 538 m. Well-preserved site.

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Figure captions

Fig. 1. Studied localities in the Yungas Forests (shaded area), Northwestern Argentina.

These included four well-preserved sites (white dots) and four disturbed sites (white squares). Localities: 1. Las Capillas (Jujuy); 2. Finca Las Capillas (Jujuy); 3. Río Las Conchas (Salta); 4. Metán (Salta); 5. Reserva Aguas Chiquitas (Tucumán); 6. El Cadillal (Tucumán); 7. Villa de Batiruaana (Tucumán); 8. Villa de Escaba (Catamarca). For details see Appendix.

Fig. 2. Rank-abundance curves calculated as $\text{Log}_{10}(\text{Pi})$ from the samples. The localities are listed from north to south and, for each of them, the type of site (well-preserved or disturbed) is indicated with superscript letters. Localities: LCP, Las Capillas; FLC, Finca Las Capillas; RLCH, Río Las Conchas; MET, Metán; AGCH, Aguas Chiquitas; ELC, El Cadillal; PAC, Villa de Escaba; ESC, Villa de Batiruaana. Bat species: E.g, *Eumops glaucinus*; T.b, *Tadarida brasiliensis*; D.r, *Desmodus rotundus*; S.e, *Sturnira erythromos*; A.p, *Artibeus planirostris*; M.a, *Myotis albescens*; M.d, *Myotis dinellii*; D.e, *Dasypterus ega*; E.c, *Eptesicus chiriquinus*; E.f, *Eptesicus furinalis*; H.v, *Histiotus velatus*; L.b, *Lasiurus blossevillii*; L.c, *Lasiurus cinereus*; M.m, *Molossus molossus*; S.l, *Sturnira lilium*; M.r, *Myotis riparius*; C.a, *Chrotopterus auritus*; E.b, *Eumops bonariensis*; E.d, *Eptesicus diminutus*; P.n, *Promops nasutus*; M.k, *Myotis keaysi*; H.m, *Histiotus macrotus*; H.l, *Histiotus laephotis*.

Fig. 3. Principal component analysis of bat assemblages between well-preserved (black symbols) and disturbed sites (white symbols) in the Yungas Forests, Argentina. Localities: LCP, Las Capillas; FLC, Finca Las Capillas; RLCH, Río Las Conchas; MET, Metán; AGCH, Aguas Chiquitas; ELC, El Cadillal; PAC, Villa de Escaba; ESC, Villa de Batirua. For details see Appendix.

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Figures

Fig. 1

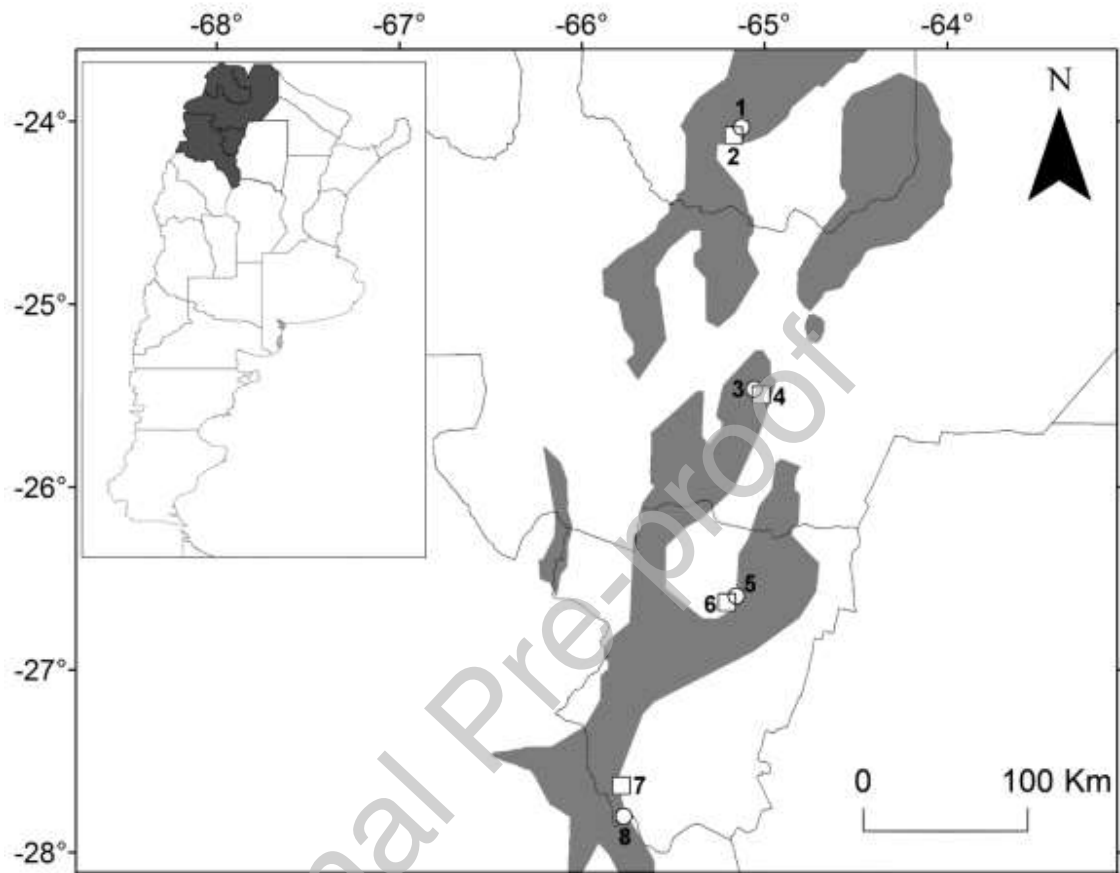


Fig. 2

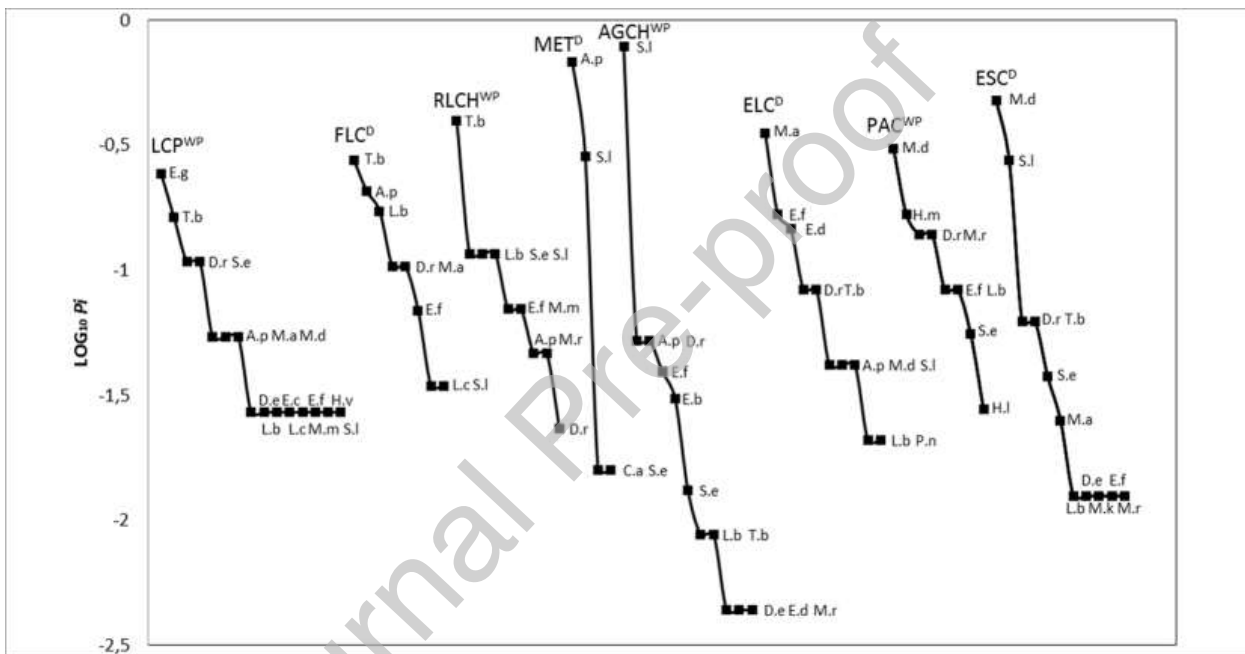
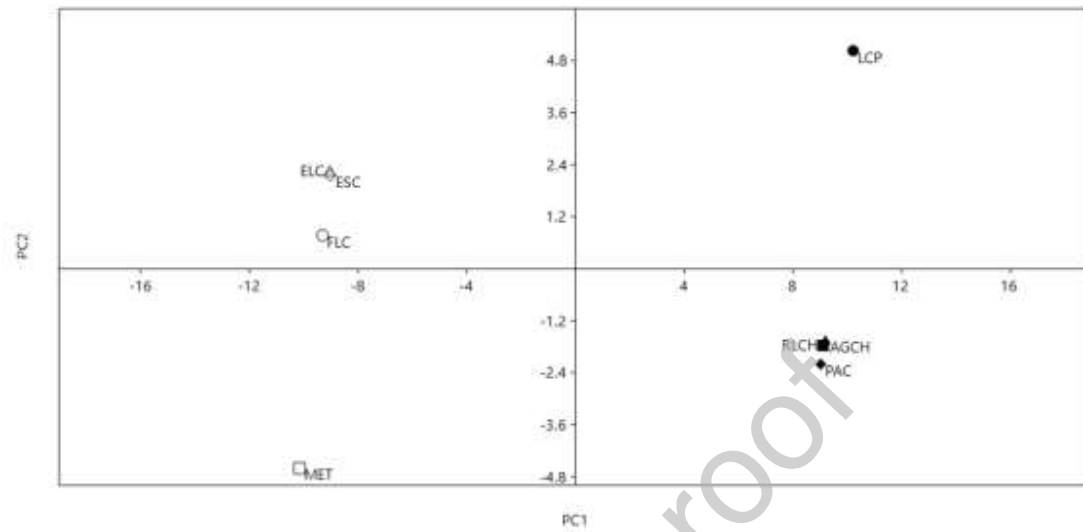


Fig. 3



Tables

Table 1. Species of bats captured from eight sites of Yungas Forests, Argentina. The family, number of individuals in total and from each site, and the trophic guild are indicated for each species. The values of Chao 1, Shannon (H') and Simpson (D') diversity indexes are indicated for each site. The well-preserved sites are indicated in bold. Families: Phy, Phyllostomidae; Mol, Molossidae; Ves, Vespertilionidae. See the acronyms for the localities in Appendix. Trophic guilds are indicated as follows: Car, carnivorous; Fru, frugivorous; San, sanguivorous; F-F art, fast-flying arthropodophagous; S-F art, slow-flying arthropodophagous.

Species	Fam.	N	Localities								TG
			LCP	FLC	RLCH	MET	AGCH	ELC	ESC	PAC	
<i>Chrotopterus auritus</i>	Phy	1	-	-	-	1	-	-	-	-	Car
<i>Artibeus planirostris</i>	Phy	67	2	6	2	43	12	2	-	-	Fru
<i>Sturnira erythromos</i>	Phy	18	4	-	5	1	3	-	3	2	Fru
<i>Sturnira lilium</i>	Phy	228	1	1	5	18	179	2	22	-	Fru
<i>Desmodus rotundus</i>	Phy	34	4	3	1	-	12	4	5	5	San
<i>Eumops bonariensis</i>	Mol	7	-	-	-	-	7	-	-	-	F-F art
<i>Eumops glaucinus</i>	Mol	9	9	-	-	-	-	-	-	-	F-F art
<i>Molossus molossus</i>	Mol	4	1	-	3	-	-	-	-	-	F-F art
<i>Promops nasutus</i>	Mol	1	-	-	-	-	-	1	-	-	F-F art
<i>Tadarida brasiliensis</i>	Mol	42	6	8	17	-	2	4	5	-	F-F art
<i>Dasypterus ega</i>	Ves	3	1	-	-	-	1	-	1	-	F-F art
<i>Eptesicus chiriquinus</i>	Ves	1	1	-	-	-	-	-	-	-	S-F art
<i>Eptesicus diminutus</i>	Ves	8	-	-	-	-	1	7	-	-	S-F art
<i>Eptesicus furinalis</i>	Ves	27	1	2	3	-	9	8	1	3	S-F art
<i>Histiotus laephotis</i>	Ves	1	-	-	-	-	-	-	-	1	S-F art
<i>Histiotus macrotus</i>	Ves	6	-	-	-	-	-	-	-	6	S-F art
<i>Histiotus velatus</i>	Ves	1	1	-	-	-	-	-	-	-	S-F art
<i>Lasiurus blossevillii</i>	Ves	18	1	5	5	-	2	1	1	3	F-F art
<i>Lasiurus cinereus</i>	Ves	2	1	1	-	-	-	-	-	-	F-F art
<i>Myotis albescens</i>	Ves	24	2	3	-	-	-	17	2	-	S-F art
<i>Myotis dinellii</i>	Ves	53	2	-	-	-	-	-	38	11	S-F art

<i>Myotis keaysi</i>	Ves	1	-	-	-	-	-	-	1	-	S-F art
<i>Myotis riparius</i>	Ves	9	-	-	2	-	1	-	1	5	S-F art
Total individuals		565	37	29	43	63	229	48	80	36	
Total species		23	15	8	9	4	11	10	11	8	
Chao 1			21.8	8.5	9	4.98	12	10.2	15.9	8	
Shannon (H')			2.37	1.87	1.86	0.75	0.95	1.92	1.54	1.88	
Simpson (D')			8.1	5.64	4.73	1.82	1.61	5.14	3.21	5.63	

Table 2. Factor loadings of variables for the first two PCs. Variables: SR, species richness; H', Shannon diversity index; D', Simpson diversity index; NF, proportion of native forest; DE, density of edge habitat.

Variables	PC 1	PC 2
SR	0.147	0.858
H'	0.015	0.127
D'	0.064	0.472
NF	0.987	-0.160
DE	-0.002	0.0003
Total variance	88.83%	8.49%