



# Silvopastoral and conventional management of extensive livestock and the diversity of bats in fragments of tropical dry forest in Córdoba, Colombia

Jesús Ballesteros-Correa · Jairo Pérez-Torres

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**Abstract** The establishment of extensive livestock systems in the Colombian Caribbean Region has historically generated a strong loss of the tropical dry forest (TDF) with negative effects on biodiversity. Currently, the implementation of silvopastoral systems (SPS) has been proposed with strategy to curb the loss of biodiversity caused by the conventional management system (CS). The objective was to evaluate the effect of SPS and CS of extensive livestock on the assemblage of bats associated with fragments of TDF. During a continuous year and a sampling effort of 30,240 h-net/night, the structure and composition of bat assemblage between SPS and CS were compared. 2788 bats belonging to six families, 23 genera, and 39 species were captured. The *Phyllostomidae* family presented the highest species richness ( $S = 30$ ), with the greatest abundance

in the *Stenodermatinae* subfamily ( $n = 1543$ ). Bat assemblage in the SPS fragments was more equitable; and the relative abundance per species, per genera, and per foraging guilds was also significantly higher. The capture success showed significant variations between the climatic seasons (dry and rainy). The rate of species turnover was higher in the CS fragments. The species *Artibeus planirostris*, *Artibeus lituratus*, *Carollia perspicillata*, *Carollia castanea*, *Phyllostomus discolor*, *Dermanura phaeotis*, *Uroderma convexum*, *Glossophaga soricina*, *C. brevicauda*, and *Sturnira lilium* accounted for 92% of the captures. In conclusion, frugivorous bats were more abundant in the SPS, type of extensive livestock management that can generate greater temporal stability of bat assemblage. This research provides the first scientific evidence of the positive effect of silvopastoral management on the diversity of bats in tropical dry forest areas of the Colombian Caribbean region.

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J. Ballesteros-Correa (✉)  
Departamento de Biología, Grupo Investigación  
Biodiversidad Unicórdoba, Universidad de Córdoba,  
Montería, Colombia  
e-mail: [jballesteros@correo.unicordoba.edu.co](mailto:jballesteros@correo.unicordoba.edu.co)

J. Ballesteros-Correa · J. Pérez-Torres  
Departamento de Biología, Unidad de Ecología y  
Sistemática (UNESIS), Pontificia Universidad Javeriana,  
Bogotá, Colombia  
e-mail: [jaiperez@javeriana.edu.co](mailto:jaiperez@javeriana.edu.co)

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## Introduction

Bats perform important roles in different ecological processes of tropical forests (Lobova et al. 2009;

Carpenter et al. 2009), considered ecosystems of utmost importance for biodiversity conservation (Barrance et al. 2009) and ecosystem services (Kunz et al. 2011). Bats are seed-dispersing agents of pioneering species (*Solanum*, *Cecropia*, *Piper*, and *Vismia*) and dominant plants in secondary vegetation; and they also participate in the control of pest insect populations in the crops (Boyles et al. 2011; Kunz et al. 2011). It is estimated that more than 800 species of neotropical plants depend on bats for pollination (Fleming et al. 2009; Lobova et al. 2009).

The establishment of extensive livestock systems and crop areas in the Colombian Caribbean has transformed the landscape causing fragmentation and habitat loss of large areas of tropical dry forest (TDF), an ecosystem with a high degree of endemism (Díaz 2006). In Colombia, the remaining TDF is currently represented by small fragments corresponding to less than 1.5% of its original coverage, with extensive livestock being the most problematic factor. Despite representing the only refuge of regional biodiversity in much of the Caribbean region, TDF fragments immersed in extensive livestock conditions are at high risk of extinction.

It has been suggested that in the scenarios of landscape transformation, habitat alteration, and climate change, many faunistic groups change their structure and composition of species (Krauss et al. 2010) because as the availability of resources is altered, some species are favored and some others are affected (Presley et al. 2008). In the particular case of bats, tolerance to landscape modifications and habitat alteration depends on their mobility and ability to cross open areas between fragments (Castro et al. 2007; Meyer et al. 2008). Studies have been conducted evaluating landscape transformation effects and habitat modifications on bat assemblage, and described changes in the structure and composition of species assemblages in fragmented environments (Willig et al. 2007; Pérez-Torres et al. 2009); yet, studies evaluating the effect of extensive livestock management type on bat assemblage in TDF are unknown.

We believe that in the Colombian Caribbean region, extensive livestock system with silvopastoral management (SPS) can be a viable strategy for the conservation of TDF and its associated biodiversity; however, the effect of extensive livestock management type on bat diversity in TDF fragments is unknown. This research provides, for the first time,

data regarding the effects of the implementation of the extensive livestock SPS on the assemblage of bat species in TDF.

## Materials and methods

### Study area

The study was carried out on four livestock farms with fragments of TDF with less than 100 ha, associated with the silvopastoral (SPS) and conventional (CS) systems of extensive livestock in Córdoba, Colombia. This region is characterized by a tropical warm climate with an average temperature of 28 °C, average annual precipitation of 1300 mm with unimodal distribution, a dry season (December–March), and a rainy season (April–November). The main use of the land aims at extensive livestock and agriculture. Among the locations evaluated, two of them are associated with the SPS of extensive livestock (Palmeras Farm-Montería with 560 ha, geographic coordinates 08°30′37.1″ N–076°06′12.9″ W, and San Lorenzo Farm-Los Cordoba with 860 ha, 08°53′20.0″ N–076°18′42.6″ W); the other two fragments are associated with the CS of extensive livestock (Chimborazo Farm-Canalete with 470 ha, 08°44′32.4″ N–076°19′23.4″ W, and Guacamayas Farm-Buenavista with 450 ha, 08°11′05.3″ N–075°31′49.2″ W).

In the recent past, in the evaluated fragments of the SPS, there was selective use of arboreal timber species, but some of the existing species were conserved; and then, for more than 15 years, the conservation of the natural vegetation relics began, the planting of trees in living fences, and paddocks (*Crescentia cujete*, *Gliricidia sepium*, *Guazuma ulmifolia*, *Citrus limon*, *Spondia mombin*, *Tabebuia rosea*, *Samanea saman*, *Enterolobium cyclocarpum*, and other timber species); and the natural regeneration of the vegetation was allowed. Next to the natural forest fragment, there is a 10-year-old teak forest plantation (*Tectona grandis*) for future use.

Currently, the TDF fragments of SPS, are secondary forests in stages of mixed plant succession, surrounded by a matrix of extensive livestock system with poly-specific natural grasslands, stubble areas, pastures with abundant trees and shrubs, living fences and farming practices, agroforestry management for more than 12 years, without the use of agrochemicals.

The vascular plant of the families Malvaceae, Boraginaceae and Fabaceae were dominant. The arboreal, shrubby and herbaceous vegetation of the pastures is used to feed cattle, native and improved breeds, which freely browse the timber, forage and fruit trees. The cattle have free entry to the forest fragments during the dry season of the year, guaranteeing the feeding and sustainability of the cattle system with good carrying capacity; but during the rainy season entry is not allowed, allowing the recovery of vegetation, where many species of plants are dispersed by fruit bats (*Guazuma ulmifolia*, *Spondia mombin*, *Ficus* sp., *Piper* sp., *Cecropia* sp., *Maclura tinctoria*, *Ficus* sp., *Aegiphila* sp., *Solanum* sp., *And Vismia* sp., among others).

While the TDF fragments in CS, are secondary forests in advanced succession stage, with more than 50 years, characterized by presenting herbaceous, shrub, arboreal and liana strata, with a canopy height of 18–24 m; where the Rubiaceae, Rutaceae and Fabaceae families have the highest relative abundance. Although they are fragments of moderately conserved forests, timber trees are selectively removed for timber extraction and use in fences in pastures. Connected with the natural forest fragments, there are forest plantations of teak (*Tectona grandis*) with 6 years of age. In the CS, traditional cattle raising takes place in open paddocks with monospecific pastures and few trees in paddocks, with paddock rotation management. During the dry season there is a significant decrease in the supply of forage, reducing the load capacity of the system. The use of agrochemicals is frequent to control herbaceous and shrub vegetation in pastures (Glyphosate, 24-D, Paraquat), and to control livestock parasites (Pyrethroids, Ivermectin), affecting biodiversity and the sustainability of the productive system.

The diversity in the taxonomic composition presented highly significant differences between SPS and CS (Shannon test,  $p < 0.0001$ ); with significantly higher alpha diversity in the SPS fragments. In the plants structure in fragments of SPS, the species *Bactris major*, *Guazuma ulmifolia*, *Hura crepitans*, and *Cordia collococca* presented the highest importance value index (IVI); while in the fragments of CS fragments, *Cavanillesia platanifolia*, *Ceiba pentandra* (L), *Astrocaryum* sp., and *Lecithys minor* had the highest importance value (Fig. 1). For more details on the plant structure and floristic composition of TDF

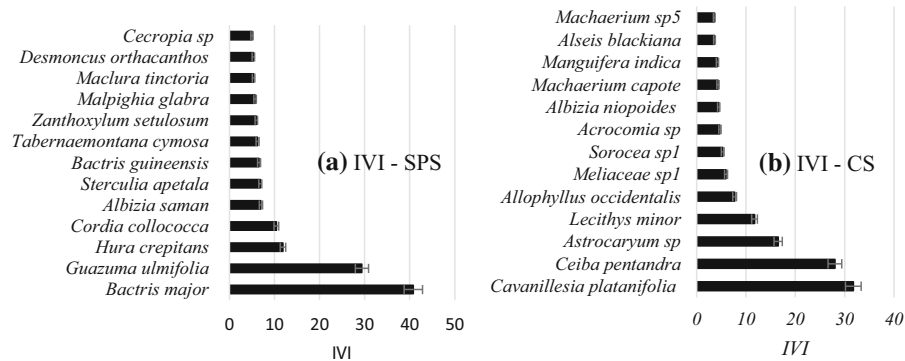
fragments associated with SPS and CS, see supplementary information and publication realized by Ballesteros et al., (2019).

#### Sampling and processing of bats

During an annual cycle, 15 samples of three consecutive nights were performed for each location, for a total sampling effort of 45 nights in each fragment (7560 h-net/night). The bats were captured using mist nets (6 × 3 m), according to the methodology of Brower and Zar (1998) and Kunz and Parson (2009). Fourteen (14) mist nets were installed: five floor-level nets (0–4 m), five elevated nets within each fragment, and four nets outside the fragment. The nets were deployed from 18:00 to 06:00 h the next day and checked every 45 min, for a total sampling effort of 30,240 h-net/night. The captured bats were individually placed into cloth bags and processed in situ; and standard morphology measures (wingspan, body length, tail, ear, tragus, nose leaf, forearm, tibia, and calcaneus), weight and sex were taken. Wilson and Reeder (2005) were followed to determine taxonomy. The species were classified into trophic guilds according to Giannini and Kalko (2005). The *Boucher* collection of reference was deposited in the collection of mammals of the Museo Javeriano de Historia Natural de la Pontificia Universidad Javeriana in Bogotá (MPUJ-MAMM), under the collection numbers MPUJ-MAMM: 1911-2186. Ethical, scientific, and administrative standards for animal research contained in Law 84 (National Congress of Colombia 1989) were considered, with research permission by The Regional Autonomous Corporation of the Sinú and San Jorge Valleys, CVS—Montería, Resolution N° 2-1033 (22-05-2015).

#### Data processing

For the analysis of bat assemblage, the relative abundance ( $AR = Ni/Nt \times 100$ ) and the capture success rate ( $EC = Nm/hn$ , where  $N$  is number of individuals,  $m$  number of nets,  $h$  number of hours of sampling and  $n$  number of nights of sampling) were calculated. To purchase EC according to the type of matrix management (SPS and CS), variance analysis was performed by species, gender, and foraging guild, prior review of assumptions (normality: Shapiro–Wilk and Kolmogorov–Smirnov; variance homogeneity:



**Fig. 1** Importance value index (IVI) of plant species (Diameter at chest height > 1 cm, four plots of 0.1 ha) in TDF fragments associated with extensive livestock systems in: **a** SPS (San

Lorenzo- Las Palmeras); and **b** SC (Chimborazo- Guacamayas), in Córdoba- Colombia (Ballesteros et al. 2019)

Barlett), as well as transformations for normality adjustment, and a posteriori testing (Tukey) when it was the case. The means of capture success ( $EC$ ) were plotted, transformed for grouped species ( $EC^{-0.2}$ )  $Y_{ijkl} = \mu + E_i + M_j + S_k + (MS)_{jk} + \epsilon_{ijkl}$ ; for genera ( $EC^{-0.25}$ )  $Y_{ijkl} = \mu + E_i + M_j + G_k + (MG)_{jk} + \epsilon_{ijkl}$ ; and grouped foraging guilds ( $EC^{-0.1}$ )  $Y_{ijkl} = \mu + E_i + M_j + Gr_k + (MGr)_{jk} + \epsilon_{ijkl}$ ; where:  $Y$  is the transformed capture success variable,  $E$  is the time of year (considered as a blocking factor),  $M$  is the type of management,  $S$  the grouped species,  $G$  the grouped genus,  $Gr$  the grouped guild.

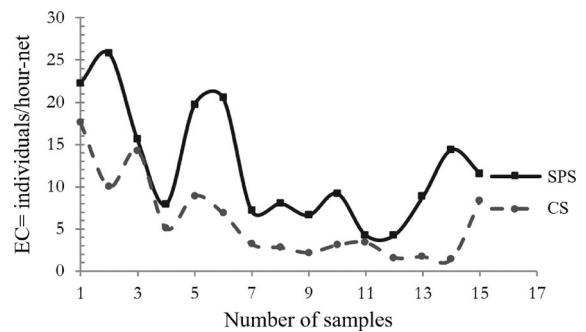
All statistical analyses were carried out on the R Platform, version 3.0.3 (R Development Core Team 2014). For the analysis of the species assemblage structure, the dominance was calculated with the Simpson index  $D = \sum n(n-1)/N(N-1)$  where,  $D$  is Simpson index,  $n$  total number of organisms of a species, and  $N$  total number of organisms of all species; and the Equity Index of Pielou  $J' = H'/\log 2S$ , where  $S$  is the maximum number of species in the sample (Magurran 2004). The representativeness of sampling was evaluated using species accumulation curves for each factor level of design, and it was also adjusted to the *Chao1* and *Bootstrap* non-parametric Models, with a Confidence Index (IC) of 95% (Colwell 2013).

Analysis of the diversity of bat assemblage was performed using the concept of “true diversity”  $q_D = (\sum_{i=1}^s p_i^q)^{1/(1-q)}$ , where,  $q_D$  is “true diversity”,  $p_i$  is relative abundance of the umpteenth species that make up the assembly,  $S$  is number of species and the exponent  $q$  is the order of diversity (Jost 2006; Moreno

et al. 2011) using the iNEXT package (Hsieh et al. 2016) through the external RStudio command editor in the R Language version 3.0.3. The degree of change in the composition of bat species between SPS and CS fragments was evaluated between the dry-rainy times of the year in both management systems (Moreno and Rodríguez 2010; Anderson et al. 2011). The Morisita’s similarity index (Magurran 2004) was determined between locations and types of management, and the species complementarity in bat assemblage between SPS and CS was also evaluated.

## Results

The capture success ( $EC$ ) showed temporal variation between Tropical Dry Forest (TDF) fragments in silvopastoral systems (SPS), as well as between conventional management system (CS) fragments



**Fig. 2** The capture success ( $EC$ ) of bats in TDF fragments in the silvopastoral (SPS) and conventional (CS) system of extensive livestock in Córdoba, Colombia

(Fig. 2). The EC in the SPS fragments (12.42 individuals/hour-net) was significantly higher ( $F = 34.45$ ,  $SC = 15.943$ ,  $gl = 1$ ,  $p < 0.001$ ) than in CS fragments (6.02 individuals/hour-net), with 67.4% of captures. EC had significant differences between SPS and CS fragments, in terms of grouped species ( $F = 3.117$ ,  $SC = 1.137$ ,  $gl = 11$ ,  $p < 0.001$ ); gender ( $F = 2.035$ ,  $SC = 1.857$ ,  $gl = 18$ ,  $p = 0.007$ ); and grouped foraging guilds ( $F = 5.659$ ,  $SC = 0.1747$ ,  $gl = 4$ ,  $p < 0.001$ ). In all three cases, bat EC was higher in SPS, with no significant differences between fragments of the same management system.

There were significant differences in temporal variation (rainy season and dry season) in bat abundances, with significant effects on the mean response ( $EC^{-0.2}$ ) of the bat species ( $F = 3.913$ ,  $SC = 0.028$ ,  $gl = 1$ ,  $p < 0.05$ ), with higher EC during the rainy season; and in SPS the abundance of bats was significantly higher by species ( $F = 28.73$ ,  $SC = 0.953$ ,  $gl = 1$ ,  $p < 0.001$ ), by genders ( $F = 24,597$ ,  $SC = 1.247$ ,  $gl = 1$ ,  $p < 0.001$ ) and by foraging guilds ( $F = 10.289$ ,  $SC = 0.0794$ ,  $gl = 1$ ,  $p < 0.001$ ). The *Phyllostomidae* family presented the greatest abundance and species richness, at both times of the year; and *Carollia perspicillata*, *C. castanea*, *Artibeus lituratus*, *Dermanura phaeotis*, *Uroderma convexum*, and *Sturnira lilium*, presented the greatest abundance (Table 1). There was temporal variation of abundance in foraging guilds in both management systems; and during the rainy season, all foraging guilds consistently had a greater relative abundance than in the dry season (Fig. 3). In SPS fragments, frugivores were 2.42 times more abundant than in CS.

#### Composition and structure of bat assemblage

In this research 2788 bats from six families (*Phyllostomidae*, *Emballonuridae*, *Vespertilionidae*, *Molossidae*, *Mormopidae*, and *Noctilionidae*), 23 genera, and 39 species were captured. The *Phyllostomidae* family had the highest species richness (30 species); and the sub-family *Stenodermatinae* presented the greatest richness (12 species) and abundance ( $n = 1545$ ); while, *Lonchophyllinae* presented the least abundance (Table 1). *Artibeus planirostris* and *A. lituratus* had more than 100 individuals, in both SPS and CS. The frugivorous species *Uroderma convexum*, *Dermanura phaeotis*, *Carollia perspicillata* and *Carollia castanea* had a greater abundance

only in the fragments associated with SPS (Table 1) and accounted for 76.84% and 61.87% in the SPS and CS, respectively. The remaining 29 species constituted only 8% of captures, with abundances between 1–2 individuals. Ten species were recorded exclusive to the SPS-associated fragments, while five species were exclusive to CS-associated fragments. Among the 30 species recorded in the CS fragments, only four (*A. planirostris*, *P. discolor*, *A. lituratus*, and *C. perspicillata*) recorded more than 40 individuals. The species accumulation curve suggests that the  $39 \pm 2.7$  species observed (IC 95% 33.6–44.4) are representative, for both SPS fragments (IC 95%  $27.7 < 33 < 38.3$ ) and CS fragments (IC 95%  $26.4 < 30 < 33.6$ ).

In both management systems with TDF fragments, the relative abundance of bats was significantly higher during the rainy season ( $F = 5.976$ ,  $SC = 0.198$ ,  $gl = 1$ ,  $p < 0.0148$ ), without significant differences in the sex relationship. Mann–Whitney observed significant differences in the average weights of individuals within the species *A. lituratus* ( $p < 0.001$ ), *U. convexum* ( $p < 0.003$ ), and *C. brevicauda* ( $p < 0.05$ ), with higher biomass for bats of SPS fragments.

From a trophic point of view, the EC of frugivorous bats was significantly higher in the SPS fragments (82%) than in the CS ( $F = 8.657$ ,  $SC = 34,003.3$ ,  $gl = 1$ ,  $p < 0.01$ ) throughout the sampling cycle. The EC of the other guilds (nectarivores, insectivores, and omnivores) did not show significant differences between the two types of management. A highly significant association of frugivorous bats was found with SPS fragments, by grouped species ( $F = 19.403$ ,  $SC = 7.076$ ,  $gl = 11$ ,  $p < 0.0001$ ), and by grouped genera ( $F = 14.262$ ,  $SC = 15.184$ ,  $gl = 21$ ,  $p < 0.0001$ ) and by grouped guilds ( $F = 63.974$ ,  $SC = 1.9746$ ,  $gl = 4$ ,  $p < 0.0001$ ). Highly significant effects of the management type on capture success by inter-local foraging guilds ( $F = 67.688$ ,  $SC = 1.9706$ ,  $gl = 4$ ,  $p < 0.0001$ ) were detected, with higher EC of frugivorous bats in fragments associated with SPS.

The species richness ( ${}^0D$ ) was higher in Las Palmeras (SPS) with 29 effective species, while Chimborazo (CS) had the lowest richness with 22 species. As a general trend, SPS fragments had a higher richness of bat species ( ${}^0D$ ), with a completeness level of more than 98% in all cases. The “true” alpha diversity ( ${}^1D$ ) type followed the same trend

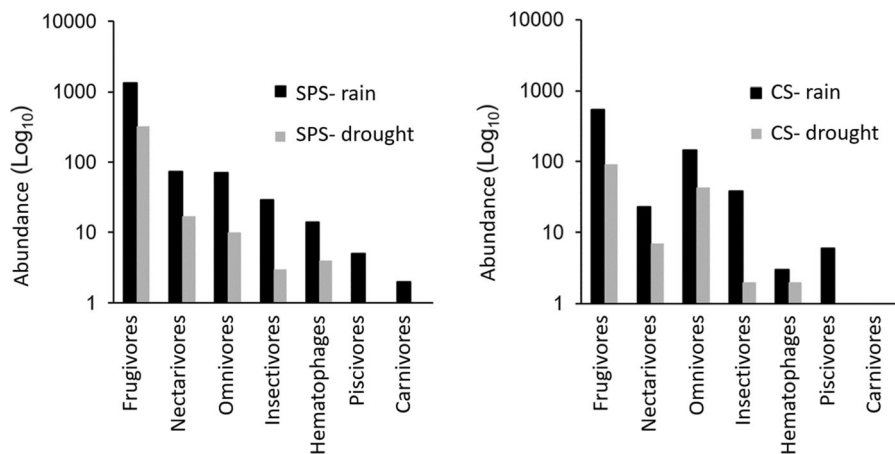
**Table 1** Taxonomic diversity and abundance of bats in TDF fragments associated with SPS and CS of extensive livestock in Córdoba, Colombia. *Palm* Palmeras, *SLor* San Lorenzo, *Chim* Chimborazo, *Guac* Guacamayas

FAMILY/ Sub-family	SPECIES	GUILD*	SPS		CS		TOTAL
			Palm	SLor	Chim	Guac	
<b>PHYLLOSTOMIDAE</b>							
Stenodermatinae	<i>Artibeus planirostris</i>	F	110	166	111	187	574
	<i>Artibeus lituratus</i>	F	52	254	73	30	409
	<i>Artibeus jamaicensis</i>	F	2	1	1	0	4
	<i>Platyrrhinus helleri</i>	F	4	10	2	5	21
	<i>Platyrrhinus angustirostris</i>	F	0	0	2	1	3
	<i>Platyrrhinus umbratus</i>	F	1	0	0	0	1
	<i>Uroderma convexum</i>	F	66	70	1	38	175
	<i>Uroderma magnirostrum</i>	F	4	1	0	1	6
	<i>Vampyriscus nymphaea</i>	F	2	5	3	4	14
	<i>Sturnira lilium</i>	F	56	25	1	16	98
	<i>Dermanura phaeotis</i>	F	4	187	8	23	222
	<i>Dermanura c.f. watsoni</i>	F	0	18	0	0	18
	Carollinae	<i>Carollia perspicillata</i>	F	86	228	39	37
<i>Carollia castanea</i>		F	98	122	11	14	245
<i>Carollia brevicauda</i>		F	28	49	12	19	108
Glossophaginae	<i>Glossophaga soricina</i>	N	26	61	22	7	116
	<i>Glossophaga commissarisi</i>	N	0	2	1	0	3
	<i>Lionycteris spurrelli</i>	N	0	1	0	0	1
Lonchophyllinae	<i>Lonchophylla robusta</i>	N	1	0	0	0	1
	<i>Hsundaycteris thomasi</i>	N	0	0	1	0	1
Phyllostominae	<i>Lophostoma silvicolum</i>	I	2	0	0	15	17
	<i>Lophostoma brasiliense</i>	I	0	0	1	1	2
	<i>Micronycteris megalotis</i>	I	0	0	0	2	2
	<i>Micronycteris hirsuta</i>	I	0	1	0	0	1
	<i>Phyllostomus discolor</i>	O	24	37	125	37	223
	<i>Phyllostomus hastatus</i>	O	6	13	20	6	45
	<i>Phyllostomus elongatus</i>	O	1	0	0	0	1
	<i>Gardnerycteris crenulatum</i>	I	1	0	2	0	3
Desmodontinae	<i>Trachops cirrhosus</i>	C	2	0	0	1	3
	<i>Desmodus rotundus</i>	H	13	5	3	2	23
<b>EMBALLONURIDAE</b>							
Emballonurinae	<i>Saccopteryx leptura</i>	I	3	6	1	3	13
	<i>Saccopteryx bilineata</i>	I	1	0	0	0	1
<b>VESPERTILIONIDAE</b>							
	<i>Myotis nigricans</i>	I	1	2	0	0	3
	<i>Myotis nesopolus</i>	I	0	0	1	0	1
	<i>Rhogeessa io</i>	I	5	2	0	2	9
<b>MOLOSSIDAE</b>							
	<i>Molossus molossus</i>	I	3	4	0	9	16
	<i>Molossops temminckii</i>	I	0	0	0	2	2
<b>MORMOOPIDAE</b>							
	<i>Pteronotus davyi</i>	I	1	0	0	0	1

**Table 1** continued

FAMILY/ Sub-family	SPECIES	GUILD*	SPS		CS		TOTAL
			Palm	SLor	Chim	Guac	
NOCTILIONIDAE							
	<i>Noctilio albiventris</i>	P	1	4	0	7	12
TOTAL			604	1274	441	469	2788

F frugivores, N nectarivores, I insectivores, H hematophages, P piscivores, O omnivores, C carnivores



**Fig. 3** Temporal changes (rain-drought) in the relative abundance (RA) of foraging guilds in TDF fragments in the SPS (left) and CS (right) of extensive livestock in Córdoba, Colombia

presented by species richness (<sup>0</sup>D), with a greater number of effective species in the SPS compared to CS (Table 2). The location with the most <sup>1</sup>D diversity was Las Palmeras (11.51 effective species), while the lowest <sup>1</sup>D diversity was found in Chimborazo (7.54 effective species). On average, TDF fragments of the SPS had 1.16 times more <sup>1</sup>D diversity of bats than in CS fragments; in other words, CS fragments have 86% of the species in the SPS fragments; and on average, SPS fragments had 2.87 more species than in CS fragments.

The “true” beta diversity between TDF fragments associated with SPS and CS of extensive livestock resulted in 1.24 communities (61.9%) with q = 0. Beta diversity of order q = 1 was 1.11 effective communities (55.4%); while beta diversity of order q = 2, which only includes typical species, resulted in a degree of replacement of 1.16 effective communities (58.2%). Species replacement (<sup>0</sup>D) between dry and

rainy seasons was higher in CS fragments with 1.36 effective communities (68.2%), compared to SPS with 1.29 communities (64.7%), with no significant differences. In forest fragments of SPS, there was greater equitability with 0.70 (IC 95% between 0.69 and 0.73) and lower dominance with 0.11 (IC 95% between 0.10 and 0.12) in bat assemblage, compared to CS fragments. The similarity of species between SPS and CS was 65%; the complementarity between SPS and CS fragments resulted in 38.5%, and 61.3% in the overlap of species.

**Discussion**

The SPS of extensive livestock raising with fragments of TDF, often there are mixtures of patches of natural vegetation in different stages of succession., which increases the heterogeneity of habitats (López et al.

**Table 2** True alpha diversity of bat assemblage in four TDF fragments, with extensive livestock SPS and CS management in Córdoba, Colombia. Three diversity measures are presented:

${}^0D$ ,  ${}^1D$ , and  ${}^2D$  with a 95% confidence index, and completeness of the sampling

Locations/ Management/season	N (Abundance)	${}^0D$ (sp. Richness)	${}^1D$ Exp (entropy $H'$ )	${}^2D$ (1/Simpson)	Completeness (%)
Las Palmeras	604	29 ± 4.14	11.51 ± 1.00	8.76 ± 0.72	98.7
San Lorenzo	1274	25 ± 2.90	10.12 ± 0.51	7.82 ± 0.42	99.7
Guacamayas	469	25 ± 2.72	9.76 ± 1.06	5.25 ± 0.80	99.2
Chimborazo	441	22 ± 4.32	7.55 ± 0.86	5.40 ± 0.58	98.2
SPS management	1878	33 ± 4.26	11.44 ± 0.50	8.88 ± 0.37	99.6
CS management	910	30 ± 3.18	9.83 ± 0.87	6.01 ± 0.65	99.3
Rainy season	2285	36 ± 4.20	11.90 ± 0.52	8.68 ± 0.46	99.7
Dry season	503	23 ± 5.35	10.06 ± 0.90	7.89 ± 0.66	98.2
Rainy season-SPS	1522	31 ± 4.09	11.61 ± 0.56	9.00 ± 0.43	99.5
Rainy season-CS	763	29 ± 3.38	9.46 ± 0.94	5.60 ± 0.64	99.2
Dry season-SPS	356	20 ± 4.14	8.79 ± 0.89	6.70 ± 0.61	98.3
Dry season-CS	147	15 ± 2.85	9.35 ± 1.23	7.61 ± 1.12	97.3

2014) and the structural complexity in the paddocks (Zuluaga et al. 2011); an aspect that can improve functional connectivity and increase species diversity (Gardner et al. 2009; García and Santos 2014; De Oliveira et al. 2017). The richness of bat species found is comparable to the richness reported for other similar habitats in South America (Aguirre and Barquez 2013; Medina et al. 2007; Pérez-Torres et al. 2009; Vela-Vargas and Pérez-Torres 2012), representing the highest record of bat species associated with TDF fragments, and representing 57.5% of the species reported for Córdoba (Ballesteros and Linares 2015), and 34.3% for Colombia (Solari et al. 2013). The results indicate greater richness and abundance of bats in SPS-associated fragments, compared to fragments immersed in CS matrices. The assemblage structure dominated by *Phyllostomidae* bats (Table 1) was similar to that recorded for other neotropical environments (Bernard and Fenton 2007; Zortéa and Alho 2008; Avila et al. 2012).

The greater abundance of frugivorous bats in the fragments associated with SPS (Fig. 3), especially of the genera *Artibeus*, *Carollia* and *Uroderma* (Table 1), could be result of the structural complexity of the vegetation, the heterogeneity of the habitat, supply of permanent shelters, and presence of shrubs and trees in the pastures. The presence of many pioneering plants (*Guazuma*, *Piper*, *Cecropia*, *Vismia*, *Maclura*,

*Aegiphila* and *Solanum*) increase the supply of resources at the edges that favor species such as *C. perspicillata*, typical of intervened environments (Faria 2006; Griscom et al. 2007; Bobrowiec and Gribel 2009). Comparable results obtained in other geographical areas (Avila et al. 2012) indicate that SPS arrays of extensive livestock, having better conditions of food niche and shelters, favor bats positively. The dominance of *C. perspicillata*, *A. lituratus*, *A. planirostris*, *C. castanea*, and *D. phaeotis* in the fragments of the SPS, is consistent with other studies that have shown their generalist diet and wide range of home setting (Montiel et al. 2006; Meyer et al. 2008; Avila et al. 2012).

Among nectarivorous bats, *G. soricina* had greater abundance in SPS, which may be related to the ability to forage, and as a generalist, they can exploit more resources (Avila et al. 2012). The low abundance found for this group is consistent with that found for other tropical regions with secondary vegetation (Willig et al. 2007) and in agricultural production systems, where they are usually not that abundant (Estrada et al. 1993). The pronounced seasonality in flowering and fruiting of plants in areas of TDF, subject frugivorous and nectarivorous bats to important variations in food availability (Saldaña et al. 2010), especially during the dry season. These habitat quality conditions can improve comparatively in the



extensive livestock farming SPS (Medina et al. 2007), taking into account that in the wooded pastures there are additional foraging areas to those offered by the forest fragment; a case that does not occur in the CS, where the supply of resources is very low.

#### Temporal variation (rain-drought) of bat assemblage

The greatest abundance of species and foraging guilds during the rainy season, mainly in the SPS, is related to the highest fruit production (Avila et al. 2012, Ávila-Cabadilla et al. 2014), which increases the abundance of frugivorous bats (Stoner 2001; Avila et al. 2009); similar results were found in fragmented TDF ecosystems in Central America and other geographic areas (Stoner 2005; Montiel et al. 2006; Mello and Marco 2009; Ceballos 2010). Changes in the abundance of insectivorous bats are related to food availability, which depends on precipitation and primary productivity; positively related aspects to tropical forests displaying differences in abundance between the rainy season and the dry season (Stoner 2005; Ávila-Cabadilla et al. 2014), where the generalist species are less susceptible to habitat alteration (Henle et al. 2004). It was observed that species unique to SPS fragments (Table 1) usually fly within the forest and can live in low, medium, or high vegetation; while, the unique species found in CS fragments are usually associated with open areas and sparse vegetation.

The *Phyllostomidae* family, with greater species richness and functional diversity, integrate most neotropical bat guilds (Dela Peña et al. 2012), similar to other tropical regions (Stoner 2005; Montiel et al. 2006; Sánchez et al. 2007; Avila et al. 2009). Since most of the Colombian Caribbean has been transformed into extensive livestock systems and farming areas, TDF fragments immersed in livestock landscapes are of utmost importance for the conservation of bats, and the ecosystem services that depend on them, in addition to the contribution to regional biodiversity conservation. Differential responses found in the abundance of species suggest that the implementation of extensive livestock SPS improves the supply and availability of resources, playing an important role in the structure of bat species assemblage (Da Silva et al. 2008; Klingbeil and Willig 2010; De Oliveira et al. 2017).

True diversity ( ${}^1D$ ) follows the same trend of species richness reported for other neotropical locations (Avila et al. 2009). The increased richness of bat species in the TDF fragments associated with SPS, compared to the fragments immersed in CS matrices, may result from the highly structural complexity of vegetation in SPSs, which implies a greater supply of habitats and resources available year-round (Medina et al. 2007; Avila et al. 2009; García and Santos 2014). In areas of TDF, the presence of arboreal vegetation in extensive livestock pastures under silvopastoral management, could be determining the presence and abundance of bats, in response to the availability of roosting sites, shelters, protection and food supply (Medina et al. 2007). These results indicate the potential that SPS has to host greater bat species richness in the TDF of the Caribbean region. Given the ecological role they play in the dynamics of forest ecosystems and the ecosystem services provided by bats (seed dispersal, plant pollination, control of insect populations), it is necessary to deepen on this aspect, to design management strategies sustainable that promote the conservation of biodiversity.

#### The rate of species replacement between communities

Spatial variation in bat assemblage (true beta diversity) between SPS and CS of extensive livestock, is fundamentally associated with the increased environmental heterogeneity present in SPS; since, despite the mobility capacity of bats, tree cover determines their distribution and abundance (López et al. 2012). Wherefore, seasonality (rainy season – dry season) in the CS there was a higher rate of species replacement (68.2%), compared to the SPS (64.7%); indicating that, in fragments of the CS there is less stability of the species assemblage. According to these results, in extensive livestock SPS matrices, in addition to presenting greater richness and abundance of species, there is a lower rate of species replacement (dry season- rainy season), which leads to greater stability of bat assemblage and the ecosystem processes in which they participate.

Similarity of species (65%), complementarity (38.5%), and bat species overlap (61.5%) between SPS and CS, evidence the contribution of each TDF fragment to regional biodiversity. Since the composition and vegetation structure of each forest fragment

has an idiosyncratic character, the elimination of any of them would have negative effects on some species of bats and other taxonomic groups. The increased equity presented in bat assemblage in SPSs reflects the best habitat conditions and supply of resources for bats, especially for frugivores. Oppositely, the low equity in the assemblage of species in the CS was reflected in the high abundance of *A. planirostris* and *P. discolor*, which is probably a consequence of the decrease in habitat quality, especially in the matrix surrounding those fragments. The results are consistent with studies carried out for low and high areas of Colombia (Estrada-Villegas et al. 2010; Cortés-Delgado and Pérez-Torres 2013), where bat assemblage usually presents a dominant species.

SPS management promotes the persistence of frugivorous bats and their role as seed-dispersing agents in extensive livestock landscapes, where bats are facilitators of natural regeneration processes in degraded areas at local and even regional zones. Since CS of extensive livestock is common in the Colombian Caribbean region, conservation programs should consider increasing connectivity between TDF fragments through the establishment of SPSs; which by increasing tree plant coverage, resource diversity, and habitat availability, can maintain common and rare bat species (Melo et al. 2012), benefiting not only bats but other types of wildlife. This counteracts the obvious impoverishment of bat diversity in TDF fragments of CS extensive livestock that dominate the landscape.

On the other hand, SPS can benefit from the dispersal of seeds of species of the genera *Aegiphila*, *Vismia*, *Cordia*, *Albizia* and *Zanthoxylum* (Ballesteros 2015). In Colombia, in silvopastoral systems many of these plants are widely used as shade, living fences and windbreak barriers; In addition, its wood is used for posts and other uses (Castañeda-Álvarez et al. 2016). Under the canopies of the plants of the genus *Aegiphila*, the growth of other plant species is favored (Alcázar-Caicedo 2011) that are useful for shade and livestock forage. Bats disperse seeds of plants of the genus *Brosimum* (Galindo-González 1998) whose leaves are used as forage for cattle (Rojas-Schroeder et al. 2017). The role of bats in the control of pest insects in crops is widely known (Russo et al. 2018). For this reason, we think that by favoring this mutual benefit between bats and extensive livestock systems,

SPS become the main support of other ecosystem services that bats offer to local and regional snow.

## Conclusions

The results found support the hypothesis that extensive cattle ranching silvopastoral systems, compared to conventional management, may favor the diversity and temporal stability of the bat assembly; and the TDF fragments immersed in these productive systems may be of relevant importance for the conservation of bats. In areas of TDF, the conversion of conventional extensive livestock to a silvopastoral management system, can be a viable strategy for favoring the conservation of regional biodiversity, as well as ecosystem services derived from the functional role of the species present.

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