Effect of the matrix-edge-forest interior gradient on the phyllostomid bats assemblage in sub-Andean forest fragments

Efecto del gradiente matriz-borde-interior de bosque sobre la comunidad de murciélagos filostómidos en fragmentos de bosque subandino

Aída Otálora-Ardila [iD] [1]*, Hugo F. López-Arévalo [iD] [1,2]

ABSTRACT

The edge effect is one of the consequences of forest fragmentation and is one of the main drivers of alteration of ecological and ecosystem processes. Trophic guilds and species of bats have shown differential responses to this phenomenon. Our goal was to describe the change in bat species richness, abundance, evenness, and species composition of trophic guilds associated with a matrix-edge-forest interior gradient. Therefore, we conducted a bat sampling with 16 mist nets covering such gradient in four sub-andean forest fragments (10-50 ha). In total, we captured 566 individuals of 21 species of phyllostomid bats. Bat species richness and abundance were higher in the matrix and edge and were similar between fragments. Evenness showed the lowest values in the matrix and forest edge and was different between forest patches. Some shrub frugivorous bats were more abundant in the edge, and others were more abundant in two fragments. Species composition of canopy frugivorous bats was similar along the gradient but was significantly different between fragments. In contrast, the species composition of nectarivores was similar throughout the matrix-interior forest gradient and between patches. Our data suggest that bat responses at assemblage-level are affected by the disturbance gradient from the matrix to forest interior, even at short distances form fragment borders, and are dependent on the trophic guild.

Keywords. Edge effects, fragmentation, phyllostomid bats, richness, Andean forests.

[1] Grupo en Conservación y Manejo de Vida Silvestre, Universidad Nacional de Colombia, Bogotá D.C. aotalora@gmail.com
[2] Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia. hflopeza@unal.edu.co
*   Corresponding author

RESUMEN

El efecto de borde es una de las consecuencias de la fragmentación del bosque y es uno de los principales motores de alteración de procesos ecológicos y ecosistémicos. Las especies y gremios tróficos de murciélagos han mostrado diferentes respuestas a este fenómeno. El objetivo de este trabajo fue describir las relaciones entre el efecto de borde y la riqueza de especies, abundancia, equitatividad y composición de gremios de murciélagos asociados a un gradiente matriz-borde-interior de bosque. Para esto, se realizó un muestreo con 16 redes de niebla cubriendo dicho gradiente en cuatro fragmentos de bosque subandino (10-50 ha). En total, capturamos 566 individuos de 21 especies de filostómidos. La riqueza de especies y su abundancia fueron mayores en el borde y en la matriz, pero fueron similares entre los fragmentos. La equitatividad de las especies fue menor en la matriz y el borde, y fue diferente entre los fragmentos. Algunas especies de frugívoros de sotobosque fueron más abundantes en el borde y otras lo fueron en dos de los fragmentos. La composición de los frugívoros de dosel fue similar a lo largo del gradiente, pero difirió entre fragmentos. Por su parte, la composición de los nectarívoros fue similar a lo largo del gradiente y entre los fragmentos. Nuestros resultados sugieren que las respuestas de los murciélagos a nivel comunitario son afectadas por el gradiente de disturbio desde la matriz hacia el interior del bosque, aún a cortas distancias del borde, y son dependientes del gremio trófico.

Palabras clave. Efecto de Borde, fragmentación, murciélagos filostómidos, riqueza, bosques andinos.

INTRODUCTION

Forest edges appear due to discontinuity between two contrasting environments. Although boundaries and edge habitats are constitutive elements in natural landscape heterogeneity, the proportion of edge habitats has increased in tropical environments because of the increment of forest fragmentation (Laurance 2000, Fletcher Jr. *et al.* 2007, Chazdon 2014). The edge effects is understood as abiotic and biotic changes that take place at the boundaries of both forest patches and between adjacent ecosystems (Fletcher Jr. *et al.* 2007). Some deleterious consequences produced by forest fragmentation are determined by edge effects (Laurance *et al.* 2007, Haddad *et al.* 2015), therefore, the edge effect may modify physical gradients, species distribution, species composition, and species abundance (Laurance *et al.* 2007, Broadbent *et al.* 2008, Ries *et al.* 2017).

The relationship between bats assemblages and edge habitats has shown diverse responses, some of them contrasting (Meyer *et al.* 2016). Research made in fragmented landscapes suggest that the edge habitat seems to favor the establishment of opportunist species and affect trophic guilds in different ways (Reis and Muller 1995, Cosson *et al.* 1999, Schulze *et al.* 2000, Estrada and Coates-Estrada 2002, Klingbeil and Willig 2009). In contrast to these results, other investigations did not find significant differences between bat species richness and abundance between interior and edge habitats (Faria 2006, Meyer and Kalko 2008). However, Meyer and Kalko (2008) suggested that edge effects could have deleterious effects for some bat species considered as edge-sensitive, while other bat species could be benefited by edges and classified as edge-preferring. Other surveys indicated that the number of individuals and species richness of bats was higher in the edge than in primary forest but, species diversity was low in edges (Delaval and Charles-Dominique 2006). Sensitivity of bats species to the edge effects is also affected by the type of matrix and its contrast with the contiguous edge (Meyer *et al.* 2016). Significant changes in bat richness or composition were observed in landscapes with matrix highly contrasting to forest patches (e.g. water, Meyer and Kalko 2008), while in landscapes with low contrast between matrix and fragments there were no alterations at the bat community level (Gorresen and Willig 2004).

Modifications of vegetation structure are significant in forest edges where regenerating secondary forest and habitat disturbance is frequent (Faria *et al.* 2009). Studies

on bat responses to second-growth vegetation in tropical environments show contrasting patterns (García-Morales *et al.* 2013, Meyer *et al.* 2016). For example, bat richness and abundance increase across succession gradients (Avila-Cabadilla *et al.* 2009), but this tendency is not evident in others (Castro-Luna *et al.* 2007). Regarding the trophic guilds, some studies indicate that frugivore and nectarivore bats are more abundant in secondary forests (Brosset *et al.* 1996, Castro-Luna *et al.* 2007, Willig *et al.* 2007), while foliage insectivores and gleaning animalivores tend to show low abundances in second-growth forests or disturbed habitats (Fenton *et al.* 1992, Brosset *et al.* 1996, Rocha *et al.* 2017).

The edge effects has been explored through comparisons of bat assemblages found in the forest interior against those found in the boundaries of forest fragments or continuous forest (Faria 2006, Meyer and Kalko 2008). However, there is scarce information about the relationship between bat assemblages throughout spatial gradients spanning the forest interior to the surrounding matrix (Delaval and Charles-Dominique 2006, Meyer *et al.* 2016). In addition, most of these studies were developed in tropical forests at low elevations and there is scarce information about edge effects or habitat disturbance on the bat assemblage structure in Andean forests (Pérez-Torres and Ahumada 2004, Montaño-Centellas *et al.* 2015). In contrast to lowland forests, Andean bat communities have fewer insectivorous species and are dominated by frugivorous and nectarivorous species where some genera are more diversified in the Andes than in lowlands (e.g. *Sturnira* and *Anoura* Soriano 2000). Therefore, understanding how Andean bat species could be affected by habitat transformation is crucial, especially because current Andean forest represents only 38 % of its original extent in Colombia (Rodríguez Eraso *et al.* 2013).

Our goal was to describe changes in species richness, abundance, evenness, and species composition of trophic guilds of phyllostomid bats related to a matrix-edge-interior forest gradient in four sub-Andean forest fragments. Considering abiotic and biotic modifications that take place in edges such as reduced humidity, greater temperature variability, changes in forest structure and floristic composition (Murcia 1995, Didham and Lawton 1999, Laurance *et al.* 2002), we hypothesize that species richness, abundance, evenness, and species composition of trophic guilds of phyllostomid bats should be modified along the

matrix-edge-forest interior gradient of the patches. We expect that species richness and abundance would be higher and evenness would be lower in the edges than in the interior of the patches, due to the increase of food resources associated with second-growth habitats typically found at the edges (Rocha *et al.* 2020). In contrast, we predict that richness and abundance would be lower in the matrix because of the low food availability in a hostile matrix such as pastures, except for sanguinivorous bats, which would be more abundant in this habitat in association to livestock commonly found there. Due to edges being biased toward pioneer shrubs and secondary species of plants (Laurance *et al.* 2002), we expect that shrub frugivorous bats would be more abundant in the edge, while canopy frugivores, foliage insectivores, and nectarivores would be more abundant in the interior of the fragments.

MATERIALS AND METHODS

Study area
Fieldwork was carried out in four sub-Andean forest fragments in the Encino municipality (Santander, Colombia), located on the western flank of the Eastern mountain range at elevations from 1600 to 2200 (06º10' N, 73º08' W). This region has a mean annual temperature of 21 ºC and a total mean annual rainfall of 3111 mm with a bimodal regime. There are two rainy seasons (March-May and October-November) and two dry periods (June-August and December-February) (Solano *et al.* 2005). Andean and sub-Andean forests in this region are dominated by oaks (*Quercus humboldtii* Kotschy ex A. DC.) and are highly fragmented by agricultural and livestock activities. In Encino, sub-Andean forest is currently distributed in only 53 fragments with less than 100 ha that represents only 5.1 % of its original distribution (Otálora-Ardila and López-Arévalo 2006).

Bat sampling
We selected four sub-Andean forest fragments, each of them less than 50 ha: Cachalú, Tapias, San Benito, and Pericos. Tapias and Cachalú fragments were considered as non-isolated fragments because the mean distance to the closest neighbor was less than 200 m, considering other fragments and riparian vegetation (Tapias: 94 m, Cachalú: 172 m). In the case of Cachalú fragment, this patch was close to the continuous forest of the Cachalú Biological Reserve (CBR), which is a private area that protects sub-Andean and Andean forests (Solano 2006). In contrast, San

Benito and Pericos patches were considered isolated because the mean distance to the closest neighbor was higher than 200 m (San Benito: 874 m, Pericos: 378 m). All patches had a similar shape, edge density, and surrounding type of matrix (Otálora-Ardila and López-Arévalo 2006). Inside of the patches, selective logging at a small scale was frequently observed. Matrix was considered hostile for bats because it was constituted of open livestock pastures area.

Total sampling was made during 35 nights from March 2004 to July 2004 (nine nights for Pericos, Tapias and San Benito, and eight nights for Cachalú), using 16 mist nets set at ground level in each fragment. We established three sampling lines that covered a gradient from the forest interior to the matrix in each patch. Considering that edge effects on vegetation and bat responses at community-level and activity have been detected between 50 and 100 m (Laurance *et al.* 2002, Delaval and Charles-Dominique 2006, Jantzen and Fenton 2013), in each line we established four sampling stations at 75 meters between them: matrix, edge, 75m, and 150m. Matrix station was located 75 m from the edge to the pasture, edge station was placed in the patch border, 75m and 150m stations were placed 75 and 150 meters inside the patch, respectively. In each station, four mist nets were opened from 18:00 to 24:00, except on rainy or full moon nights. Sampling effort was calculated as m² x mist net x hours (mnh) reaching a total effort of 83791 mnh. Sampling effort was similar between stations (matrix: 20884, edge: 20982, 75m: 20961, 150m: 20964). Captured bats were measured and marked in the wing membrane using tattoos and were released in the same place of capture. Some individuals were collected and deposited in the Mammals Collection of the Instituto de Ciencias Naturales at Universidad Nacional de Colombia (ICN).

Data analyses

Species richness was defined as the number of species found in each sampling station (matrix, edge, 75m, and 150m). We used randomized (100x) sample-based species accumulation curves to verify inventory accuracy. Additionally, we used the non-parametric estimator Jack1 to assess the expected species number in each gradient sampling station because this estimator considers the movement heterogeneity of mobile animals such as bats (Brose and Martínez 2004). Accumulation curves and species richness estimators were obtained using EstimateS 9.1.0

software (Colwell c2013). Sampling effort was statistically similar between sampling stations (F= 0.0007, df= 3, *P*= 1) and between fragments (F= 0.0008, df= 3, *P*= 1). Bat abundance was defined as the number of individuals captured in each sampling station and each fragment. Recaptured individuals were not included in the calculations of relative abundance. Evenness was estimated with the inverse of the Simpson index (Magurran 1988) using iNEXT package (Hsieh *et al.* 2016). Each bat species was assigned to a trophic guild as follows: shrub frugivorous and canopy frugivorous according to Soriano (2000), and foliage insectivorous, nectarivorous and sanguinivorous following Kalko *et al.* (1996).

We analyzed the variation of species richness and abundance of bats using Generalized Linear Mixed-effects Models (GLMM) with a Poisson distribution. Response variables in these GLMMs were richness and abundance of bats, the gradient sampling stations (matrix, edge, 75 m, and 150 m) were understood as fixed factors and fragment was included as a random factor. When GLMMs indicated significant differences, we performed post-hoc Tukey HSD tests using the multcomp package (Hothorn *et al.* 2008). We compared the inverse of the Simpson index across the gradient sampling stations performing a Kruskal-Wallis test, and we made post-hoc comparisons using the Wilcoxon rank-sum test. To determine differences in the species composition of the trophic guilds across the gradient, we did a multivariate generalized linear model analysis with sampling stations and fragments as predictor variables using the mvabund package (Wang *et al.* c2019) for R software. These analyses were not performed for sanguinivores and foliage insectivores because these trophic guilds were represented by only one species. All analyses were conducted in the program R v.3.4.4 (R Core Team c2018). Values were expressed as mean ± s.d, and results were considered significant at *P*<0.05.

RESULTS

We captured a total of 566 individuals of 21 species belonging to the family Phyllostomidae in the four sampled fragments. We recaptured 27 bats of eight species along the gradient, but we did not recapture any bat across fragments. *Carollia brevicauda* (Schinz, 1821), *Artibeus lituratus* (Olfers, 1818), *Dermanura glauca* (Thomas, 1893), *Platyrrhinus dorsalis* (Thomas, 1900), and *Desmodus rotundus* (É. Geoffroyi Saint Hilaire, 1810) were the most

abundant species (Table 1). The Jack1 estimator indicated high-level inventory completeness for the total sampling (> 78 % for total sampling, Supplementary Material Fig 1). In each sampling station, the phyllostomids species that were captured reached between 75 % and 91 % of total species (matrix= 75 %, edge= 89 %, 75m= 91 %, 150m= 83 %).

Species richness was significantly different across sampling stations (Dev= 193, df= 43, Supplementary Material Table 1). Richness was similar between matrix and edge and between 75m and 150m sampling stations (Fig 1a, Supplementary Material Table 2). Matrix and edge species richness was significantly higher than at 75m and 150m (Supplementary Material Table 2).

Bat abundance was significantly different between sampling gradient stations (Dev= 501.2, df= 43, Supplementary material Table 1). Abundance was significantly higher in the matrix than in 75m and in 150m (Fig. 1b, Supplementary Material Table 2). The most abundant species found in the matrix were *D. glauca*, *A. lituratus*, and *P. dorsalis*, and at the edge were *C. brevicauda* and *D. rotundus*. At 75m, the most abundant species were *C. brevicauda* and *Vampyressa thyone* Thomas, 1909, and at 150m *C. brevicauda* and *A. lituratus* (Table 1, Figs. 2a-d).

Species evenness was significantly different between sampling gradient stations (KW= 13.64, df=3, *P* = 0.003) and between fragments (KW= 9.81, df=3, *P* =0.02). Simpson diversity index was significantly higher at 75m and 150m than in matrix and edge (Fig. 1c). Evenness in San Benito was similar to Cachalú but was significantly higher than the evenness registered in Tapias and Pericos fragments (Fig. 1d). Evenness registered in Cachalú was like Pericos and Tapias (Fig. 1d, Supplementary Material Table 3).

Trophic guilds were diverse: six shrub frugivores, nine canopy frugivores, four nectarivores, one foliage insectivore and one sanguinivore. Species composition of the shrub frugivorous guild was different along the sampling gradient (*P* = 0.04, Figs. 2a-d, Supplementary Material Table 4) and between fragments (*P* = 0.01, Figs. 3a-d, Supplementary Material Table 4). Only *S. lilium* (É. Geoffroyi Saint Hilaire, 1810) was significantly affected by the gradient, and there was a significant effect of fragment for *C. brevicauda* and *S. ludovici* Anthony, 1924 (Supplementary Material Table 4). In the case of canopy frugivores, the species composition was similar along the gradient (*P* = 0.14, Figs. Figs. 2a-d, Supplementary Material Table 4)
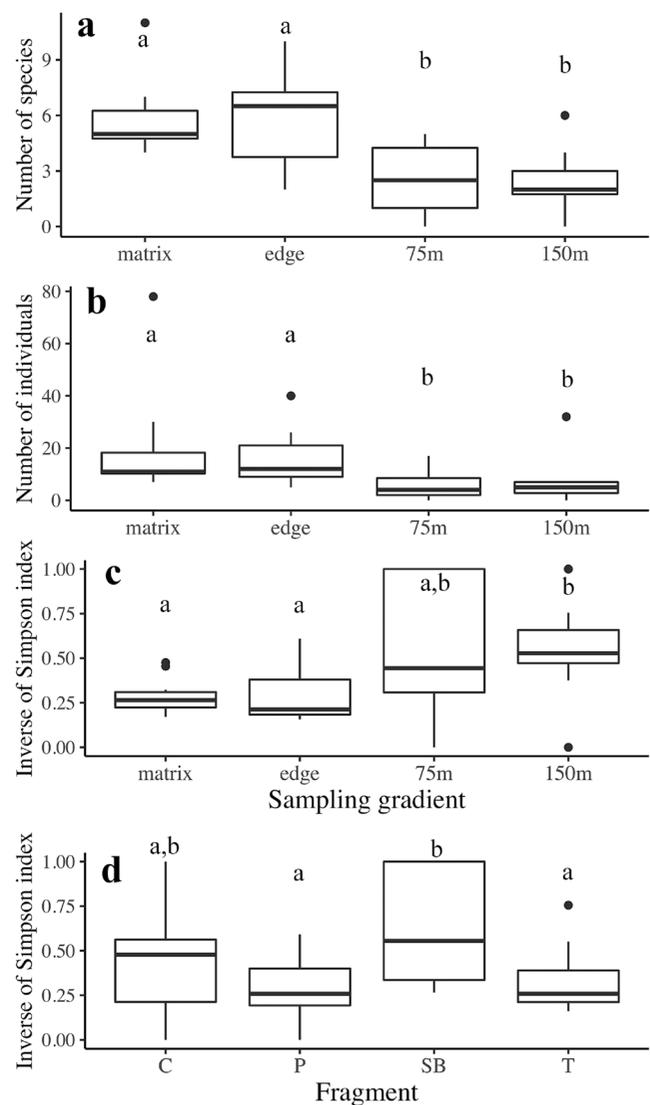
Figure 1. Ecological indexes of the bat diversity in the area. **a.** Number of species, **b.** number of individuals, **c.** inverse of Simpson index along the gradient matrix-edge-forest interior in four Sub-Andean forest fragments, and **d.** inverse of Simpson index in the four Sub-Andean forest fragments sampled in Encino (Santander, Colombia). Boxes represent the 25th and 75th percentiles, whiskers represent the 95 % confidence limits, and black lines within boxes represent medians. Black points represent outliers. Letters indicate significant differences (*P* < 0.05) according to the post hoc Tukey's all-pairwise comparisons for the number of species and number of individuals, and Wilcoxon pairwise comparisons for the inverse of Simpson index along the gradient and among fragments. C= Cachalú, P= Pericos, SB= San Benito, T= Tapias

but was different across fragments (*P* = 0.001, Figs. 3a-d, Supplementary Material Table 4). There was a significant effect of fragment only for *A. lituratus* (Supplementary Material Table 4). In contrast, the nectarivorous guild´ species composition did not vary in the sampling gradient or between fragments (Supplementary Material Table 4). *D. rotundus* was the only sanguinivorous species captured,

Table 1. Bat species and number of individuals captured in the matrix-edge-forest interior gradient in four Sub-Andean forest fragments in Encino (Santander, Colombia). Trophic guild is mentioned for each species.

SPECIES	Matrix C	Matrix T	Matrix SB	Matrix P	Matrix total	Edge C	Edge T	Edge SB	Edge P	Edge total	75m C	75m T	75m SB	75m P	75m total	150m C	150m T	150m SB	150m P	150m total	TOTAL	Trophic Guild
Micronycteris megalotis (Gray, 1842)							1			1											1	Fol-Ins
Anoura cultrata Handley, 1960				1	1																1	Nec-Pol
Anoura geoffroyi Gray, 1838		1			1		1	1	1	3							1			1	5	Nec-Pol
Anoura luismanueli Molinari, 1994		3			3	2	1		2	5		1		1	2		2	1		3	13	Nec-Pol
Lonchophylla robusta Miller, 1912		1			1																1	Nec-Pol
Carollia brevicauda (Schinz, 1821)	1	7	4	4	16	5	11	17	9	42	3	6	6	7	22		9	13	1	23	103	Shr-Fru
Carollia perspicillata (Linnaeus, 1758)	2			1	3	2	1	1	11	15		2		3	5				2	2	25	Shr-Fru
Sturnira aratathomasi Petterson & Tamsitt, 1968	1				1																1	Shr-Fru
Sturnira erythromos (Tschudi, 1844)	2	1			3	1	1			2							1			1	6	Shr-Fru
Sturnira lilium (É. Geoffroy Saint Hilaire, 1810)	21	1	2		24	16			3	19											43	Shr-Fru
Sturnira ludovici Anthony, 1924	10	16	5		31	1	6	1	1	9	2	5			7		2		1	3	50	Shr-Fru
Artibeus jamaicensis Leach, 1821				1	1												1			1	2	Can-Fru
Artibeus lituratus (Olfers, 1818)	2	4	4	22	32	1	6		14	21		1		2	3				24	24	80	Can-Fru
Dermanura glauca (Thomas, 1893)	25	5		6	36	6	4	1	10	21	1			6	7				5	5	69	Can-Fru
Enchisthenes hartii (Thomas, 1892)		1			1																1	Can-Fru
Platyrrhinus dorsalis (Thomas, 1900)	26	5	3	2	36	11		3	4	18		1	1		2				5	5	61	Can-Fru
Platyrrhinus vittatus (Peters, 1859)	1	1		2	4	1			1	2				1	1				5	5	12	Can-Fru
Vampyressa sp						1				1											1	Can-Fru
Vampyressa thyone (Thomas, 1909)	2	1			3	1	1		1	3	14			6	20	3				3	29	Can-Fru
Mesophylla macconnelli Thomas, 1901																	2			2	2	Can-Fru
Desmodus rotundus (É. Geoffroy Saint Hilaire, 1810)	4	8	11	5	**28**	6	8	5	8	**27**		1	1		**2**	1	2			**3**	60	Sang
TOTAL SPECIES	12	14	6	9	**18**	13	11	7	12	**15**	4	7	3	7	**10**	4	6	2	9	**14**	21	
TOTAL INDIVIDUALS	97	55	29	44	225	54	41	29	65	189	20	17	8	26	71	4	20	14	43	81	566	

C= Cachalú, T= Tapias, SB= San Benito, P= Pericos. Fol-Ins= Foliage insectivorous, Nec-Pol= Nectarivorous-Polinivorous, Shr-Fru= Shrub frugivorous, Can-Fru= Canopy frugivorous, Sang= Sanguinivorous. **Bold**= Total individuals captured in each sampling station.
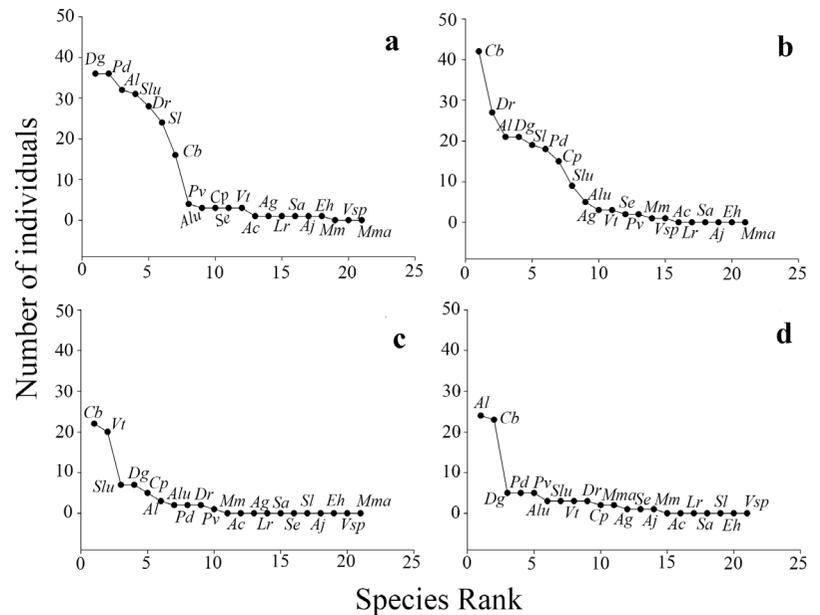
Figure 2. Rank abundance curves for captured individuals in **a**. matrix, **b.** edge, **c.** 75m, **d.** 150m in four Sub-Andean forest fragments in Encino (Santander, Colombia). *Dg= D. glauca, Pd= P. dorsalis, Al= A. lituratus, Slu= S. ludovici, Cb= C. brevicauda, Pv= P. vittatus, Alu=A. luismanueli, Cp= C. perspicillata, Se= S. erythromos, Vt= V. thyone, Ac= A. cultrata, Ag= A. geoffroyi, Lr= L. robusta, Sa= S. aratathomasi, Aj= A. jamaicensis, Eh= E.hartii, Mm= M. megalotis, Vsp= Vampyressa sp., Mma= M. macconnelli.*

and it was registered in all sampling stations of the gradient across all fragments. *Micronycteris megalotis* (Gray, 1842) was the only foliage insectivorous species registered and was captured only on the edge of the Tapias fragment.

DISCUSSION

Our data show evidence that edge effects have a significant influence in Andean bat communities even at short distances from the fragment borders (~75 m), where bat species richness, abundance, evenness, and species composition of trophic guilds showed significant variation along the matrix-edge-forest interior gradient of the patches. The highest richness and abundance in the matrix can be related to the landscape configuration. In Encino´s landscape, the matrix showed high contrast with forest fragments because it was an open area of habitat non-suitable for bats because it was mainly constituted by pastures that no offer food or refuge resources. In this landscape, the matrix can be used by bat species as a movement area and, therefore, the richness and abundance in the matrix increased. This agrees with the idea that not only the species within a specific habitat determine the local diversity, but that it may also be influenced by transitory or tourist species that come from surrounding areas (Moreno and Halffter 2001). High species richness and low evenness of bats found in the edges may be related to the indirect edge effects suggested by Murcia (1995). Indirect edge effects refer to changes in species interactions such as herbivory, parasitism, pollination, seed dispersal or invasions of generalist animals and

plants (Valladares *et al.* 2006). In this study, shrub frugivores such as *C. brevicauda* and *S. lilium* and canopy frugivores such as *A. lituratus*, *D. glauca* and *P. dorsalis* were more abundant in the edges. High richness and abundance of these frugivorous species may be associated with the growth of plant species typical of initial succession stages and commonly found in the same locality studied (Camargo and Vargas 2006) and in other Andean forest edges (Berg *et al.* 2005, Cortés-Delgado and Pérez-Torres 2011, Lippok *et al.* 2014). Although we did not measure vegetation composition, qualitative observations indicated a high abundance of pioneer plants in the edges, such as those of the families Piperaceae, Cecropiaceae, Solanaceae, and Moraceae. These pioneer plants constitute the main food resource for generalist frugivores such as *S. lilium, C. brevicauda, D. glauca,* and *P. dorsalis* and they are mainly dispersed by these bat species in other tropical localities (Brosset *et al.* 1996, Kalko 1998, Giannini and Kalko 2004, Estrada-Villegas *et al.* 2010).

Our data indicated that shrub frugivorous bats were more abundant in the edge supporting our prediction. However, the only shrub frugivorous species significantly affected by the gradient matrix-forest interior was *S. lilium* because this species was only captured in the matrix and the edge. These responses of shrub frugivorous bats to the matrix-edge-interior gradient were congruent with other studies focused on bat assemblages in lowland tropical fragmented forests in Guatemala, the Atlantic forest, and the Amazonia in Brazil (Schulze *et al.* 2000, Delaval
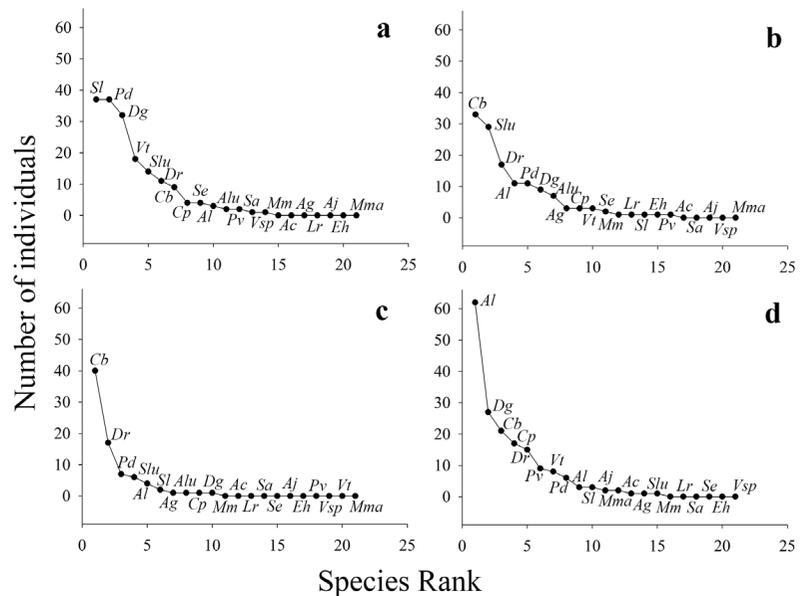
Figure 3. Rank abundance curves for captured individuals in four Sub-Andean forest fragments: **a.** Cachalú, **b.** Tapias, **c.** San Benito and **d.** Pericos, in Encino (Santander, Colombia). *Dg= D. glauca, Pd= P. dorsalis, Al= A. lituratus, Slu= S. ludovici, Cb= C. brevicauda, Pv= P. vittatus, Alu=A. luismanueli, Cp= C. perspicillata, Se= S. erythromos, Vt= V. thyone, Ac= A. cultrata, Ag= A. geoffroyi, Lr= L. robusta, Sa= S. aratathomasi, Aj= A. jamaicensis, Eh= E.hartii, Mm= M. megalotis, Vsp= Vampyressa sp., Mma= M. macconnelli*

and Charles-Dominique 2006, Faria *et al.* 2006, Klingbeil and Willig 2009), and it is also consistent with research developed in an Andean forest fragment in Colombia (Cortés-Delgado and Pérez-Torres 2011). Abundance of *C. brevicauda* and *S. ludovici* was significantly different between fragments, and this could be related to the type of perturbation occurring in the edge. These two bat species were more frequently captured in the edge of Tapias and San Benito fragments, where we observed some portions of the boundaries covered with shrubs of pioneer plants generating a less contrasting edge before the matrix. In contrast, the edges of Cachalú and Pericos fragments were abrupt and frequently cut down, therefore, the transition between forest and matrix was highly evident. A similar pattern was observed for frugivorous bat species in the edge of an Andean fragment, considered as a permeable edge because the presence of pioneer plants allows the bat presence in this portion of the fragment (Cortés-Delgado and Pérez-Torres 2011).

In contrast to our expectations, canopy frugivorous bats were more abundant in the matrix and the edge. This pattern agrees with other studies in lowland tropical forests affected by fragmentation such as the Atlantic forest and the Amazonian forests (Cosson *et al.* 1999, Gorresen and Willig 2004, Meyer and Kalko 2008, Klingbeil and Willig 2009). It is possible that canopy frugivores were less affected by the matrix-forest interior gradient because they are more mobile and can fly longer distances than the shrub frugivores (Meyer and Kalko 2008). The abundance of *A. lituratus,* a canopy frugivore, was significantly different

among fragments and this could be related to spatiotemporal variation in the abundance of food resources. Most individuals of *A. lituratus* (77.2 %) were captured in Pericos fragment (Fig. 3d), where we observed several fig trees (*Ficus* sp.). These fig trees were bearing fruit during the sampling season and we captured several individuals of *A. lituratus* carrying figs, similarly to reports in other localities in Panamá and Venezuela (August 1981, Handley *et al.* 1991). Although our data indicated a higher abundance of canopy frugivorous at the matrix and edges, it is possible that this pattern could be biased by the fact that we used mist nets only at ground-level along the sampling gradient. Some studies using canopy mist netting in tropical lowland forests have detected more Stenodermatinae species at the canopy level (Kalko and Handley 2001, Pereira *et al.* 2010). Therefore, it is possible that abundance data for some species may be underestimated, particularly for the genus *Plathyrrhinus* and *Vampyressa* of which we captured few individuals.

The sanguinivorous trophic guild was represented by only one species, *D. rotundus*, and in agreement with our prediction, this species was more abundant in the matrix and edge, than at 75m and 150m. High abundance in the matrix and the edge could be related to the presence of livestock in these two types of habitats. In line with our results, this species is more abundant in intermediate successional-stage habitats (Avila-Cabadilla *et al.* 2009) and in fragments surrounded by pastures (Estrada and Coates-Estrada 2002). Among foliage insectivores, we captured only one individual of *M. megalotis*. The low abundance of foliage insectivores and

the absence of animalivorous species could be associated with their reluctance to inhabit altered habitats, being considered edge-sensitive species (Gorresen and Willig 2004, Meyer and Kalko 2008). In contrast to our prediction, nectarivorous species were more abundant in matrix and edge. The edge effects seem to not negatively affect the abundance of nectarivorous bats, where probably the current size of sampled fragments still allows the persistence of these species and maintenance of the pollination process. Similar patterns were suggested for bird assemblages, where alteration of the pollination processes was more drastic in fragments smaller than 10 ha (Murcia 1995).

Overall, we found that richness, abundance, evenness, and composition of trophic guilds were affected along the gradient sampled, suggesting that edge effects have significant influence even at short distances from the border (~75 m). Although bats are highly mobile organisms, other studies have shown that edge effects modified bat richness, abundance, and diversity at distances less than 100m. For example, research carried out in lowland forests indicates that bat species richness and abundance were significantly different between the forest edge and the contiguous 50 m inside the forest (Delaval and Charles-Dominique 2006). Similarly, the activity of insectivorous bats was significantly higher within 20 m of the edge and stabilized up to 40 m (Jantzen and Fenton 2013). Additionally, we did not have any recapture between fragments, but we recaptured 16 individuals along the gradient, and eleven were recaptured at the same site of their original capture, suggesting that few bats moved regularly among the sampled stations. The total recapture rate (4.8 %) was similar to those reported in other mountain agroecosystems (Williams-Guillén and Perfecto 2010), and lower than in other Andean (Montaño-Centellas et al. 2015) and lowland landscapes (Bianconi et al. 2006, Zortéa and Alho 2008).

In spite of the highly fragmented nature of the locality studied, we captured bat species considered rare and, based on our best knowledge, this is currently one of the localities with the highest number of phyllostomids bats species (21) reported among Colombian Andean localities (e.g., 6 to 20 species, Cadena et al. 1998, Pérez-Torres and Ahumada 2004, Numa et al. 2005, Estrada-Villegas et al. 2010, Rodríguez-Posada 2010, Cortés-Delgado and Pérez-Torres 2011, Mora-Beltrán and López-Arévalo 2018). In agreement with other studies in fragmented localities, bat species richness was similar to that registered

in small forest patches immersed in an agriculture mosaic (Numa et al. 2005). Our data suggest that sub-Andean forest patches sampled in Encino still preserve some structural elements of vegetation that may support high bat species richness even when these patches are immersed in a non-suitable matrix. Similarly, Sáenz Jiménez (2010) suggests that the diversity and structure of Andean forests in Encino and nearby areas, which are dominated by oaks, offer food resources, roosts and, microhabitat conditions suitable especially for small mammals. In this sense, these fragments might constitute an important habitat for bat assemblages especially because these sub-Andean forests have experienced a drastic fragmentation and currently represent only 5 % of their original coverage (Otálora-Ardila and López-Arévalo 2006). Although we show here that bat richness is still high despite the edge modifications, we did not consider other variables such as activity patterns or bat behavior that might be affected by disturbance gradients. Although phyllostomid bat species may persist in transformed landscapes (Law et al. 1999, Estrada and Coates-Estrada 2002, Bernard and Fenton 2007), we must consider that if habitat loss and isolation between forest remnants increase, some bat species probably will be threatened. However, in highly fragmented localities, small patches might function as a network of forest islands that promote the maintenance of vertebrate diversity. Thus, the gradient studied has allowed maintaining an important portion of the biodiversity of bats in the Andean region and probably of other components of its biodiversity. However, effective conservation strategies should be promoted focused on maintaining adequate amounts of mature forests, and at the same time, promoting successional processes that minimize the effect of a hostile matrix.

economic, field equipment and logistic support to carry out this research. Likewise, we are grateful to the Grupo Conservación y Manejo de Vida Silvestre and Mammalogy Collection at the Universidad Nacional de Colombia for loaning equipment and field supplies. Our fieldwork would not have been possible without the help of María A. Tobón, Juan F. Díaz, Rodrigo Sarmiento, and Carlos Vargas. We give special acknowledgments to local people of Encino and AOA is especially grateful to her family.

CONFLICT OF INTEREST

The authors declare that they do not have conflict of interest.

LITERATURE CITED

August PV. 1981. Fig fruit consumption and seed dispersal by *Artibeus jamaicensis* in the Llanos of Venezuela. Biotropica. 13(2):70–76.

Avila-Cabadilla LD, Stoner KE, Henry M, Añorve MYA. 2009. Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. For. Ecol. Manage. 258(6):986–996. doi: https://doi.org/10.1016/j.foreco.2008.12.011

Berg CC, Rosselli PF, work(s): DWDR. 2005. Cecropia. Flora Neotrop. 94:1–230.

Bernard E, Fenton MB. 2007. Bats in a fragmented landscape: Species composition, diversity and habitat interactions in savannas of Santarém, Central Amazonia, Brazil. Biol Conserv. 134(3):332–343. doi: https://doi.org/10.1016/j.biocon.2006.07.021

Bianconi GV, Mikich SB, Pedro WA. 2006. Movements of bats (Mammalia, Chiroptera) in Atlantic Forest remnants in southern Brazil. Rev. Bras. Zool. 23(4):1199–1206. doi: https://doi.org/10.1590/S0101-81752006000400030

Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biol. Conserv. 141(7):1745–1757. doi: https://doi.org/10.1016/j.biocon.2008.04.024

Brose U, Martínez ND. 2004. Estimating the richness of species with variable mobility. Oikos. 105:292–300.

Brosset A, Charles-Dominique P, Cockle A, Cosson J-F, Masson D. 1996. Bat communities and deforestation in French Guiana. Can. J. Zool. 74(11):1974–1982. doi: https://doi.org/10.1139/z96-224

Cadena A, Anderson RP, Rivas-Pava P. 1998. Colombian mammals from the chocoan slopes of Nariño. Occasional Papers Museum of Texas Tech University. 108:1–15.

Camargo C, Vargas S. 2006. La relación dispersor-planta de aves frugívoras en zonas sucesionales tempranas como parte de la restauración natural del bosque subandino (Reserva Biológica Cachalú, Santander, Colombia). In: Solano C, Vargas N, editors. Memorias del I Simposio Internacional de Robles y ecosistemas asociados. Bogotá, D.C, Colombia: Fundación Natura Colombia-Pontificia Univesidad Javeriana. p. 157–172.

Castro-Luna AA, Sosa VJ, Castillo-Campos G. 2007. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. Anim. Conserv. 10(2):219–228. doi: https://doi.org/10.1111/j.1469-1795.2007.00097.x

Chazdon RL. 2014. Second growth: The promise of tropical forest regeneration in an age of deforestation. Chicago: University of Chicago Press.

Colwell RK. c2013. EstimateS 9.1.0. User's Guide and Application. University of Connecticut. [Last accessed: 15 Dec 2019]. http://viceroy.eeb.uconn.edu/estimates/EstimateSPages/EstSUsersGuide/EstimateSUsersGuide.htm

Cortés-Delgado N, Pérez-Torres J. 2011. Habitat edge context and the distribution of phyllostomid bats in the Andean forest and anthropogenic matrix in the Central Andes of Colombia. Biodivers. Conserv. 20(5):987–999. doi: https://doi.org/10.1007/s10531-011-0008-1

Cosson J-F, Pons J-M, Masson D. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. J. Trop. Ecol. 15(4):515–534.

Delaval M, Charles-Dominique P. 2006. Edge effects on frugivorous and nectarivorous bat communities in a Neotropical primary forest in French Guiana. Rev. Ecol. 61:343–352.

Didham RK, Lawton JH. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica. 31(1):17. doi: https://doi.org/10.2307/2663956

Estrada A, Coates-Estrada R. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biol. Conserv. 103(2):237–245. doi: https://doi.org/10.1016/S0006-3207(01)00135-5

Estrada-Villegas S, Pérez-Torres J, Stevenson PR. 2010. Ensamblaje de murciélagos en un bosque subandino colombiano y análisis sobre la dieta de algunas especies. Mastozool. Neotrop. 17:31–41.

Faria D. 2006. Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. J. Trop. Ecol. 22(5):531–542. doi: https://doi.org/10.1017/S0266467406003385

Faria D, Laps RR, Baumgarten J, Cetra M. 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic forest of Southern Bahia, Brazil. Biodivers. Conserv. 15(2):587–612. doi: https://doi.org/10.1007/s10531-005-2089-1

Faria D, Mariano-Neto E, Martini AMZ, Ortiz JV, Montingelli R, Rosso S, Paciencia MLB, Baumgarten J. 2009. Forest structure in a mosaic of rainforest sites: The effect of fragmentation and

recovery after clear cut. For. Ecol. Manage. 257(11):2226–2234. doi: https://doi.org/10.1016/j.foreco.2009.02.032

Fenton MB, Acharya L, Audet D, Hickey MBC, Merriman C, Obrist MK, Syme DM, Adkins B. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica. 24(3):440. doi: https://doi.org/10.2307/2388615

Fletcher Jr RJ, Ries L, Battin J, Chalfoun AD. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Can. J. Zool. 85(10):1017–1030. doi: https://doi.org/10.1139/Z07-100

García-Morales R, Badano EI, Moreno CE. 2013. Response of Neotropical Bat Assemblages to Human Land Use: Bat Responses to Habitat Modification. Conserv. Biol. 27(5):1096–1106. doi: https://doi.org/10.1111/cobi.12099

Giannini NP, Kalko EKV. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos. 105(2):209–220. doi: https://doi.org/10.1111/j.0030-1299.2004.12690.x

Gorresen PM, Willig MR. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. J. Mammal. 85(4):688–697. doi: https://doi.org/10.1644/BWG-125

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1(2):e1500052. doi: https://doi.org/10.1126/sciadv.1500052

Handley CO, Wilson DE, Gardner AL. 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. Washington, DC: Smithsonian Institution Press (Smithsonian Contributions to Zoology).

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biomet. J. 50(3):346–363.

Hsieh TC, Ma KH, Chao A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). McInerny G, editor. Methods. Ecol. Evol. 7(12):1451–1456. doi: https://doi.org/10.1111/2041-210X.12613

Jantzen MK, Fenton MB. 2013. The depth of edge influence among insectivorous bats at forest–field interfaces. Can. J. Zool. 91(5):287–292. doi: https://doi.org/10.1139/cjz-2012-0282

Kalko EKV. 1998. Organization and diversity of tropical bat communities through space and time. Zoology. 101:281–297.

Kalko EKV, Handley CO. 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. Plant Ecol. 153:319–333. doi: https://doi.org/10.1007/978-94-017-3606-0_26

Kalko EKV, Handley CO, Handley D. 1996. Organization, diversity and long-term dynamics of a neotropical bat community. In: Cody ML, Smallwood JA, editors. Long-term studies of vertebrate communities. San Diego: Academic Press. p. 503–553.

Klingbeil BT, Willig MR. 2009. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. J. Appl. Ecol. 46(1):203–213. doi: https://doi.org/10.1111/j.1365-2664.2008.01594.x

Laurance W. 2000. Do edge effects occur over large spatial scales? Trends Ecol. Evol. 15(4):134–135.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E. 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conserv. Biol. 16(3):605–618. doi: https://doi.org/10.1046/j.1523-1739.2002.01025.x

Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers RM, Harms KE, Luizão RCC, Ribeiro JE. 2007. Habitat Fragmentation, variable edge effects, and the landscape-divergence hypothesis. Bennett P, editor. Plos One. 2(10):e1017. doi: https://doi.org/10.1371/journal.pone.0001017

Law BS, Yerson J, Chidel M. 1999. Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. Biol. Conserv. 88:333–345.

Lippok D, Beck SG, Renison D, Hensen I, Apaza AE, Schleuning M. 2014. Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. Nakashizuka T, editor. J. Veg. Sci. 25(3):724–733. doi: https://doi.org/10.1111/jvs.12132

Magurran AE. 1988. Ecological diversity and its measurement. London, UK: Chapman & Hall.

Meyer CFJ, Kalko EKV. 2008. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. J. Biogeogr. 35(9):1711–1726. doi: https://doi.org/10.1111/j.1365-2699.2008.01916.x

Meyer CFJ, Struebig MJ, Willig MR. 2016. Responses of tropical bats to habitat fragmentation, logging and deforestation. In: Voigt C, Kingston T, editors. Bats in the anthropocene: Conservation of bats in a changing world. Springer Open. p. 63–105.

Montaño-Centellas F, Moya MI, Aguirre LF, Galeón R, Palabral O, Hurtado R, Galarza I, Tordoya J. 2015. Community and species-level responses of phyllostomid bats to a disturbance gradient in the tropical Andes. Acta Oecol. 62:10–17. doi: https://doi.org/10.1016/j.actao.2014.11.002

Mora-Beltrán C, López-Arévalo HF. 2018. Interactions between bats and floral resources in a premontane forest, Valle del Cauca, Colombia. Therya. 9(2):129–136. doi: https://doi.org/10.12933/therya-18-560

Moreno C, Halffter G. 2001. Spatial and temporal analysis of α, β and γ diversities of bats in a fragmented landscape. Biodivers. Conserv. 10:367–382.

Murcia C. 1995. Edge effects in fragmented forests: Implications for conservation. Trends Ecol. Evol. 10(2):58–62.

Numa C, Verdu JR, Sánchez-Palomino P. 2005. Phyllostomid bat diversity in a variegated coffee landscape. Biol. Conserv. 122:151–158.

Otálora-Ardila A, López-Arévalo HF. 2006. Incidencia de algunos elementos del paisaje fragmentado de Encino (Santander, Colombia) sobre la riqueza y diversidad de murciélagos. In: Solano C, Vargas Tovar N, editors. Memorias del I seminario internacional de Roble y ecosistemas asociados. Bogotá: Fundación Natura Colombia Pontificia Universidad Javeriana. p. 83–95.

Pereira MJR, Marques JT, Palmeirim JM. 2010. Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. Curr. Zool. 56(4):469–478. doi: https://doi.org/10.1093/czoolo/56.4.469

Pérez-Torres J, Ahumada JA. 2004. Murciélagos en bosques alto-andinos, fragmentados y continuos, en el sector occidental de la Sabana de Bogotá (Colombia). Universitas Scientiarum. 9:33–46.

R Core Team. c2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Last accessed: 13 Aug 2020]. http://www.R-project.org

Reis N, Muller M. 1995. Bat diversity of forests and open areas in a subtropical region of South Brazil. Ecol. Austral. 5:31–36.

Ries L, Murphy SM, Wimp GM, Fletcher RJ. 2017. Closing persistent gaps in knowledge about edge ecology. Curr. Landscape Ecol. Rep. 2(1):30–41. doi: https://doi.org/10.1007/s40823-017-0022-4

Rocha R, López-Baucells A, Farneda FZ, Ferreira DF, Silva I, Acácio M, Palmeirim JM, Meyer CFJ. 2020. Second-growth and small forest clearings have little effect on the temporal activity patterns of Amazonian phyllostomid bats. Curr. Zool. 66(2):145–153. doi: https://doi.org/10.1093/cz/zoz042

Rocha R, López-Baucells A, Farneda FZ, Groenenberg M, Bobrowiec PED, Cabeza M, Palmeirim JM, Meyer CFJ. 2017. Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. Landscape Ecol. 32(1):31–45. doi: https://doi.org/10.1007/s10980-016-0425-3

Rodríguez Eraso N, Armenteras-Pascual D, Alumbreros JR. 2013. Land use and land cover change in the Colombian Andes: dynamics and future scenarios. J. Land Use Sci. 8(2):154–174. doi: https://doi.org/10.1080/1747423X.2011.650228

Rodríguez-Posada ME. 2010. Murciélagos de un bosque en los andes centrales de Colombia con notas sobre su taxonomía y distribución. Caldasia 32(1):205–220.

Sáenz Jiménez FA. 2010. Aproximación a la fauna asociada a los bosques de roble del corredor Guantiva - La Rusia - Iguaque (Boyacá-Santander, Colombia). Colomb. For. 13(2):299–344. doi: https://doi.org/10.14483/udistrital.jour.colomb.for.2010.2.a08

Saunders DA, Arnold GW, Burbidge AA, Hopkins AJM. 1987. The role of remnants of native vegetation in nature conservation: Future directions. In: Saunders DA, Arnold GW, Burbidge AA, Hopkins AJM, editors. Nature conservation: the role of remnants of native vegetation. Surrey Beatty & Sons Pty Limited. p. 387–392.

Schulze MD, Seavy NE, Whitacre DF. 2000. A comparison of the phyllostomid bat assemblages in undisturbed neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Peten, Guatemala. Biotropica. 32(1):174–184.

Solano C. 2006. Reserva Biológica Cachalú: 10 años de investigación en bosques de roble. In: Solano C, Vargas N, editors. Memorias del I Simposio Internacional de Roble y Ecosistemas Asociados. Bogotá, D.C, Colombia: Fundación Natura Colombia Pontificia Universidad Javeriana. p. 11–23.

Solano C, Roa C, Calle Z, editors. 2005. Estrategia de desarrollo sostenible: Corredor de conservación Guantiva-La Rusia-Iguaque, Boyacá-Santander (Colombia). Bogotá, D.C, Colombia: Fundación Natura.

Soriano PJ. 2000. Functional structure of bat communities in tropical rainforests and andean cloud forests. Ecotropicos. 13(1):1–20.

Valladares G, Salvo A, Cagnolo L. 2006. Habitat fragmentation effects on trophic processes of insect-plant food webs. Conserv. Biol. 20:212–217.

Wang Y, Naumann U, Wright S, Warton D. c2019. mvabund: statistical methods for analysing multivariate abundance data. R package version 4.0.1. [Last accessed: 13 Aug 2020]. http://CRAN.R- project.org/package=mvabund

Williams-Guillén K, Perfecto I. 2010. Effects of Agricultural Intensification on the Assemblage of Leaf-Nosed Bats (Phyllostomidae) in a Coffee Landscape in Chiapas, Mexico: Phyllostomid Diversity in Shade Coffee Plantations. Biotropica. 42(5):605–613. doi: https://doi.org/10.1111/j.1744-7429.2010.00626.x

Willig MR, Presley SJ, Bloch CP, Hice CL, Yanoviak SP, Díaz MM, Chauca LA, Pacheco V, Weaver SC. 2007. Phyllostomid bats of lowland Amazonia: Effects of habitat alteration on abundance. Biotropica. 39(6):737–746. doi: https://doi.org/10.1111/j.1744-7429.2007.00322.x

Zortéa M, Alho CJR. 2008. Bat diversity of a Cerrado habitat in central Brazil. Biodivers. Conserv. 17(4):791–805. doi: https://doi.org/10.1007/s10531-008-9318-3