



OPEN Response of phyllostomid bat diversity to tree cover types in North-western Ecuador

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Agricultural activities affect tropical forest biodiversity; however, some bat species can survive under these anthropogenic changes. We described the characteristics of phyllostomid bat assemblages in tree covers located in 48 plots among four agricultural landscapes of North-western Ecuador. Bats were captured with mist nets installed at a ground level reaching three meters' height. For each of the plots, we installed a mist net in four types of tree cover (polyspecific live fences, monospecific live fences, cacao plantations, and isolated trees in pastures). We captured 250 phyllostomid bats belonging to 16 species with a trapping effort of 19,200 m² of net coverage. Polyspecific live fences showed significant differences in relative abundance, richness, and diversity of phyllostomid bats compared to the other three. Frugivorous and nectarivorous guilds were the most abundant, and also exhibited the highest richness among other guilds present in agricultural landscapes. In addition, frugivorous, and nectarivorous guilds increase their abundance and richness in agricultural landscapes, while the animalivorous guild is negatively affected. We recommend installing polyspecific live fences in tropical production systems to support the conservation of phyllostomid bats. We conclude that living fences composed of various plant species favour the abundance, richness, and diversity of phyllostomid bats.

Natural habitat reduction and landscape fragmentation lead to biodiversity loss¹. In North-western Ecuador, habitat loss results from fuelwood extraction, deforestation, and the implementation of agricultural production systems, and accounts for more than 80% of the loss of original forest cover². The Ecuadorian Northwest Region harbours at least 61 different species of bat (Order Chiroptera), representing almost 35% of the Ecuadorian bat fauna³. The composition and diversity of phyllostomid bats (Phyllostomidae) vary with the environment; and the responses of bats to anthropogenic changes in nature vary with the characteristics of the landscape⁴.

Knowledge of diversity in areas of natural habitat loss is crucial for biodiversity conservation decision-making in highly disturbed environments. Several species of bats can adapt to live in anthropogenic environments⁴. For example, patches of natural forest remnants and corridors (e.g. live fences, riparian forests, or isolated trees in pastures) are common elements in Neotropical agricultural landscapes that support wildlife⁵. In one hand, live fences are linear vegetation structures formed by rows of living trees (multiple trees, or dense shrubs) connected with wire or interwoven branches. These fences may consist of natural remnants or be intentionally planted for purposes such as property demarcation, wind protection, and firebreaks^{6,7}, while isolated trees in pastures are considered to provide shade for cattle⁸. On the other hand, riparian's forests are forested lands located alongside streams or water bodies⁹. These common elements are suitable habitats for a diversity of birds, mammals, and insects, among others^{10–14} and are considered a type of tree cover in agricultural landscapes¹⁵. Tree cover is defined as a unit of land covered by a set of tree canopies which have no productive interest for timber^{11,16}. Meyer et al.¹⁷ stated that it is a priority to assess bat diversity in agroforestry systems, and in plantations such as cacao (*Theobroma cacao*) to study the importance of residual tree canopies of agricultural matrices in bat conservation.

In this study, our objectives were: first, to identify the type of tree cover that best promotes the increase in abundance, richness, and diversity of phyllostomid bats present in tropical agricultural landscapes of northwestern Ecuador; and second, to evaluate which trophic guilds are best adapted to agricultural landscapes without natural habitat fragments.

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Results

We captured 250 phyllostomid bats belonging to 16 species among the four types of tree cover types, designated as: polyspecific live fences (PLF): linear live fences composed of several tree species; monospecific live fences (MLF): live fences of a single tree species: *Erythrina smithiana*; cacao plantation (C): land portion of the agricultural system dedicated to the management of *Theobroma cacao*; and, isolated trees in pasture (ITP): *Brachiaria brizantha* crop where trees are distant from each other). The PLF presented the highest values of abundance, richness, and diversity among all types of tree cover sampled (Table 1). The most abundant species was *Glossophaga soricina* representing 21% of the total in PLF, 46% in MLF, 37% in C, and 41% in ITP (Table 1). The second most abundant species changed between tree cover types, i.e.: *Sturnira bakeri* was the second most abundant in PLF, MLF, and C (16, 10, and 23%, in respective order); while *Carollia perspicillata* was the second most captured species in ITP with 31%. The greatest capture rates were found in PLFs, which show significant differences compared to the other types of tree cover ($F_{3,12} = 12.69, P = 0.0005$); however, the same variable did not show significant differences between MLF, C, and ITP (Fig. 1A).

Polyspecific live fences exhibited the highest number of phyllostomid species (14 spp.), followed by MLF (9 spp.), C (7 spp.), and ITP (5 spp.). The high value of richness in PLF presented significant differences when compared with the richness found in C and ITP ($F_{3,12} = 5.74, P = 0.0113$), but none with MLF (Fig. 1B). The Chao 2 richness estimate explained that the observed richness of phyllostomid bats represented 100% in PLF and ITP, 82% in MLF, and 88% in C. The diversity of species in PLF presented significant differences in relation to the other tree cover types ($F_{3,12} = 14.89, P = 0.0002$); however, this metric does not show significant differences when comparing MLF, C, and ITP (Fig. 1C). The proportion of observed diversity of phyllostomid bats in relation to the maximum expected diversity (Pielou's evenness index), revealed no differences among tree cover types ($F_{3,12} = 0.65, P = 0.5991$) (Fig. 1D). There is a clear separation of the PLF from the other types of tree covers monitored; the first two dimensions of non-metric multidimensional scaling, explained 99% of the variation contained in the matrix of Euclidean distances, the difference between disparities and distances (Kruskal' Stress) was 0.01 (Fig. 2A). Cluster analysis, performed with Euclidean distances of abundance, richness and diversity of species of phyllostomid bats, allowed us to visualize the presence of three groups: the first composed exclusively by PLF, the second consisting of ITP and C, and a third grouping mostly MLF; the cophenetic correlation coefficient of groupings was 0.98 (Fig. 2B).

We recorded only four trophic guilds (Table 1). Frugivorous and nectarivorous bats were recorded in all tree cover types and represented 98% of the individuals (99% in PLF, 100% in MLF, 97% in C, and 91% in ITP) and 81% of the species captured (93% in PLF, 100% in MLF, 86% in C, and 80% in ITP), while sanguivorous and animalivorous represented 2% of the individuals and 19% of the species captured. The abundance and

Species	Trophic guilds*	Threat status**	Tree cover types			Landscape	
			PLF	MLF	C	ITP	
<i>Glossophaga soricina</i>	N	LC	27 (0.206)	24 (0.462)	13 (0.371)	13 (0.406)	77 (0.308)
<i>Sturnira bakeri</i>	F	LC	21 (0.160)	5 (0.096)	8 (0.229)	5 (0.156)	39 (0.156)
<i>Carollia perspicillata</i>	F	LC	14 (0.107)	5 (0.096)	3 (0.086)	10 (0.313)	32 (0.128)
<i>Carollia brevicauda</i>	F	LC	20 (0.153)	5 (0.096)	3 (0.086)		28 (0.112)
<i>Artibeus aequatorialis</i>	F	LC	16 (0.122)	4 (0.077)	1 (0.029)		21 (0.084)
<i>Uroderma convexum</i>	F	LC	12 (0.092)	3 (0.058)	6 (0.171)		21 (0.084)
<i>Artibeus ravenus</i>	F	LC	5 (0.038)	2 (0.038)		1 (0.031)	8 (0.032)
<i>Vampyriscus nymphaea</i>	F	VU	5 (0.038)	3 (0.058)			8 (0.032)
<i>Chiroderma villosum</i>	F	LC	6 (0.046)	1 (0.019)			7 (0.028)
<i>Desmodus rotundus</i>	S	LC				3 (0.094)	3 (0.012)
<i>Chiroderma</i> sp.	F	?	1 (0.008)				1 (0.004)
<i>Chiroderma salvini</i>	F	LC	1 (0.008)				1 (0.004)
<i>Lonchophylla robusta</i>	N	LC	1 (0.008)				1 (0.004)
<i>Micronycteris hirsuta</i>	A	LC			1 (0.029)		1 (0.004)
<i>Garderycteris crenulatum keenani</i>	A	NT	1 (0.008)				1 (0.004)
<i>Platyrrhinus dorsalis choocoensis</i>	F	VU	1 (0.008)				1 (0.004)
Total abundance			131	52	35	32	250
Observed richness			14	9	7	5	16
Diversity, exp. Shannon index			8.94	5.81	5.10	3.86	8.01
Evenness, Pielou index			0.83	0.80	0.84	0.84	0.75

Table 1. Abundance (proportional abundance of species), richness, diversity, and evenness of phyllostomid bats captured in four types of tree cover, and studied landscape. *: Trophic guilds are based in food habits^{46,49}: N = nectarivorous, F = frugivorous, S = sanguivorous, A = animalivorous. PLF = polyspecific live fence, MLF = monospecific live fence, C = *Theobroma cacao* plantation, ITP = isolated trees in pastures. ** Threat status: LC = least concern, NT = near threatened, VU = vulnerable⁴².

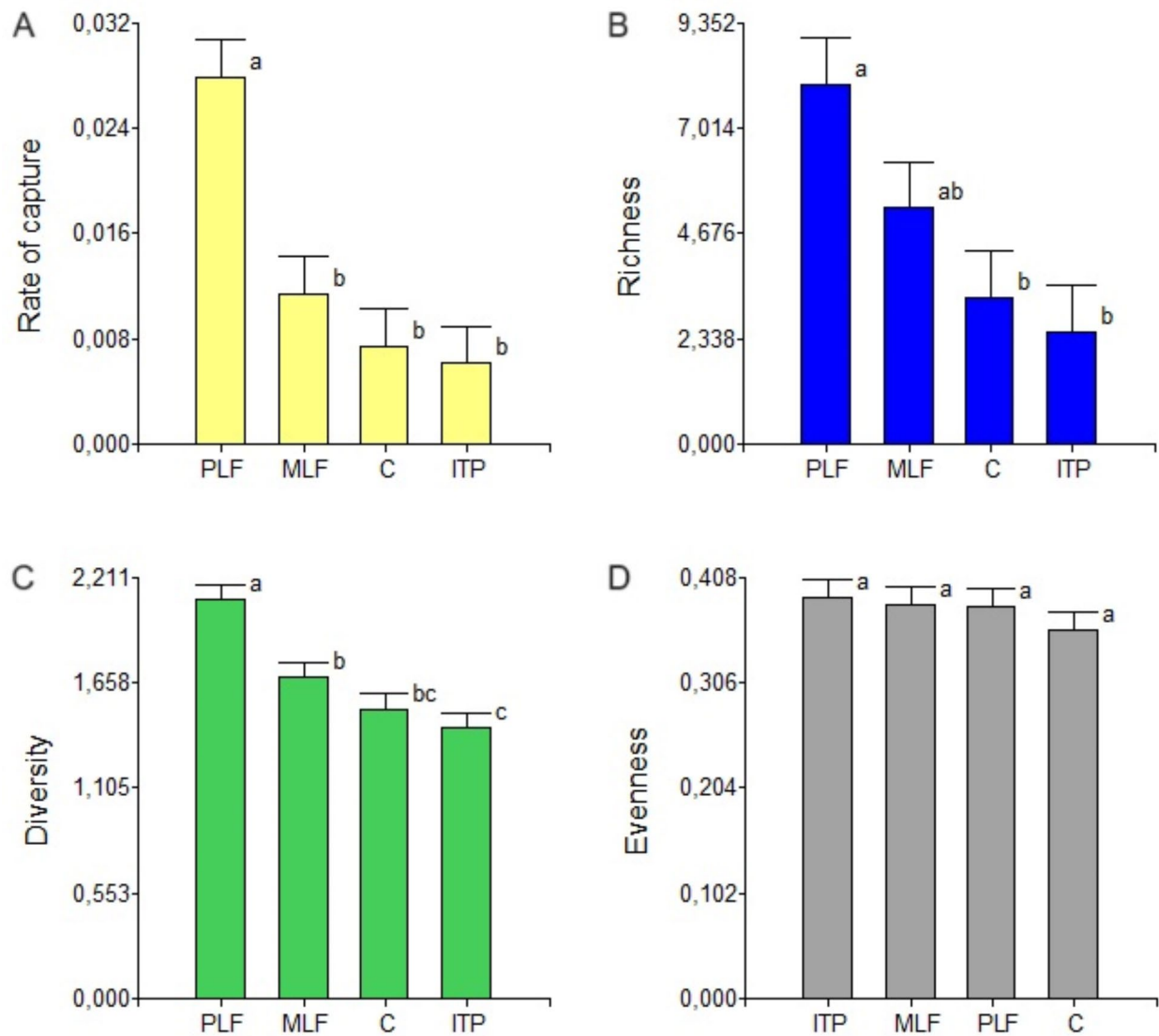


Fig. 1. Rate of capture (A), richness (B), diversity (C), and evenness (D) of phyllostomid bats between types of tree cover. Expressed as the mean \pm standard error obtained in the LSD test at 5% level. PLF=polyspecific live fences, MLF=monospecific live fences, C= *Theobroma cacao* plantations, ITP=isolated trees in pastures.

richness of frugivorous and nectarivorous species were considerably higher than those of animalivorous and sanguivorous species in the four types of tree cover evaluated (Fig. 3). Overall, none of the tree cover types exhibited significant differences in two variables: (a) their capture rate frequencies ($G_W=0.484$, $P=0.99$), or (b) the richness of phyllostomid bat trophic guilds ($G_W=0.957$, $P=0.99$). The comparison between the different types of tree cover of these two variables extracted from the trophic guilds, also showed no significant differences (Table 2).

Discussion

In all types of tree covers, the most abundant phyllostomid was *Glossophaga soricina*. Prior research has indicated low capture frequencies of *G. soricina*, ranging from 0.7 to 1.5% in landscapes comprising both natural forest fragments and continuous forests¹⁸. Therefore, the elevated capture frequency in our study, in which there is an absence of natural fragments indicates that *G. soricina* may exhibit a preference for agricultural landscapes during the period of our study. The high capture rate of *G. soricina* in the four tree cover types evaluated may be attributed to the foraging opportunities and resources provided by these habitats to the species, such as food and roosts. Also, tree density could be associated positively with the capture rate of phyllostomid bats in Ecuadorian agricultural landscapes¹⁹. The other two abundant phyllostomid bat in the tree covers types were *Carollia brevicauda* and *C. perspicillata*, which are frequently recorded, as indicative of habitat alteration, in several Latin American studies²⁰. These two species belong to the group of animals responsible for the regeneration of tropical forests, by dispersing seeds which is relevant to support the dynamics of the forest²¹.

Tree cover types	No. of individuals captured		No. of species captured	
	$G_{Williams}$	P_value	$G_{Williams}$	P_value
PLF vs. MLF	0.153	0.98	0.106	0.99
PLF vs. C	0.078	0.99	0.027	0.99
PLF vs. ITP	0.274	0.96	0.411	0.94
MLF vs. C	0.023	0.99	0.216	0.98
MLF vs. ITP	0.144	0.98	0.361	0.95
C vs. ITP	0.162	0.98	0.493	0.92

Table 2. Frequency of the number of individuals and species recorded of each of the four guilds of phyllostomid bats captured in different types of tree cover. The percentage distribution of the two values, did not show significant differences, according to the G test with the goodness of fit of Williams ($P > 0.05$). $G_{Williams}$ = test G with the goodness of fit of Williams, PLF = Polyspecific live fence, MLF = Monospecific live fence, C = *Theobroma cacao* plantations, ITP = insolated trees in pastures.

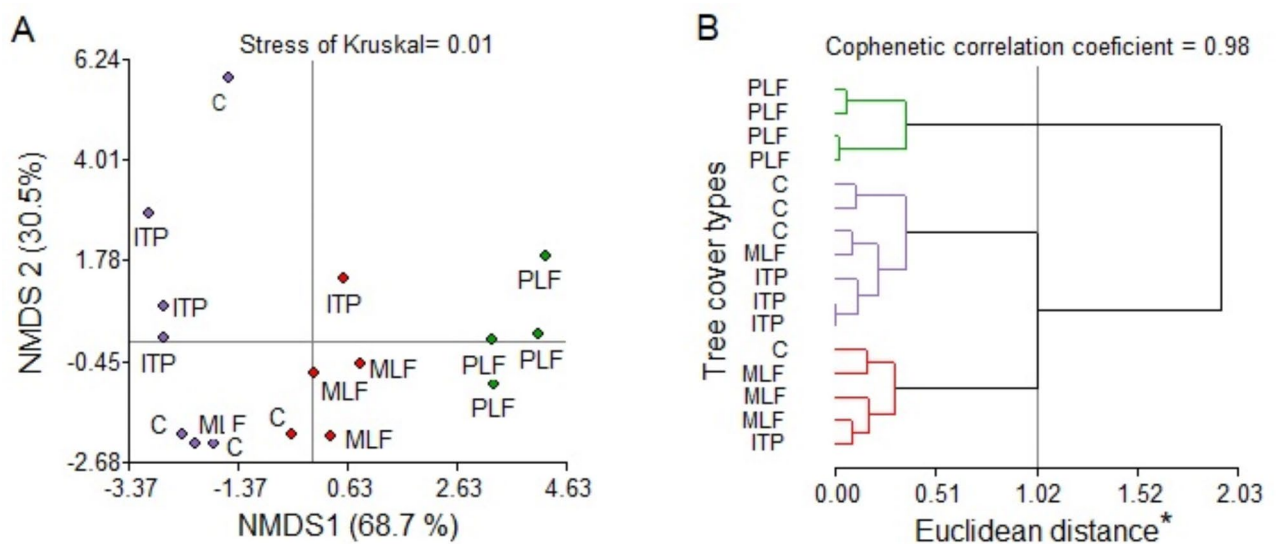


Fig. 2. Non-metric multidimensional scaling (A) and cluster analysis (B) elaborated with the indices of abundance, richness and structure (diversity and evenness) of phyllostomid bats present in the four types of tree cover. PLF = polyspecific live fences, MLF = monospecific live fences, C = *Theobroma cacao* plantations, ITP = insolated trees in pastures.

Polyspecific live fences presented the highest richness of phyllostomid bats. Harvey et al.¹¹ found that bat richness correlates positively with tree richness in agricultural landscapes which is provided by PLFs in our study. Nevertheless, the PLFs encompass a total of 26 arboreal species, while the ITPs comprise 17 species¹⁹. The ITPs display the lowest richness of bats, and thus the low richness observed in our case could be attributed to the density of trees alone. Alternatively, the low tree density typical of ITPs may be a contributing factor to the documented low bat richness, as observed by Medina¹². Despite the notable differences in richness observed between the different tree cover types, the Chao 2 estimator consistently exceeded 80%, indicating that an increase in the number of samples would not substantially alter the richness values²². These results indicate that the probability of undetected species existing within the subject tree cover is low, as demonstrated by Chao 2. Therefore, the inferences regarding bat diversity presented in this study can be considered accurate.

The findings of our study suggest that live fences formed by a variety of species of plants (PLF) are the type of tree cover that most effectively increases the diversity values of phyllostomid bats in agricultural landscapes. Some authors have proposed an association between bat diversity and plant diversity of the sites these species inhabit. Thus, it has been suggested that multi-species plantings result in an improved habitat quality and an increased availability of resources for wildlife²⁵. However, other studies have indicated a reduction in the diversity of phyllostomid bats in areas of low tree diversity^{12,24}.

As with richness, tree diversity is not considered to be the exclusive factor responsible of the increase in phyllostomid bat diversity. The living fences, regardless of their composition, support a high diversity of bat species¹², as they can be considered corridors used by bats to move between natural areas where bat richness is higher than in agricultural systems. Therefore, canopy continuity in PLFs could be a more determinant factor

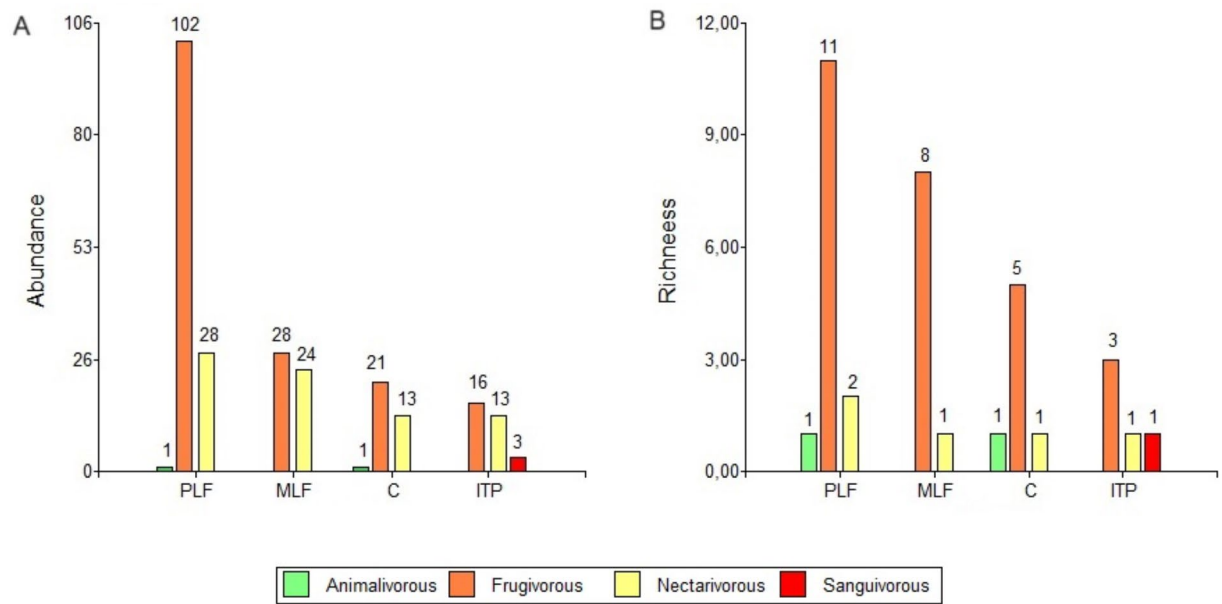


Fig. 3. Abundance and richness of trophic guilds registered in the tree cover types evaluated. PLF = polyspecific live fences, MLF = monospecific live fences, C = *Theobroma cacao* plantations, ITP = isolated trees in pastures.

than tree diversity, as in our results ITP, which also has high tree richness, is the tree cover type with the lowest phyllostomid richness. The values of evenness close to one, and the fact that no significant differences in this metric were found between the tree cover types studied, simply demonstrate that there was an equidistribution of individuals among species in each cover type.

Assessing the abundance, richness, diversity and evenness of phyllostomids with the two multivariate analyses used in this study a strict separation between the PLF and the other three cover types is demonstrated, highlighting the importance of PLFs for bat conservation in tropical agro-systems of North-western Ecuador. According to the Cox & Cox²⁵ scale, the NMDS Kruskal Stress value of 0.01 is considered 'very good'; whereas, the value of 0.98 of the co-phenetic correlation coefficient confirms a high correlation between the distances of the objects obtained in the grouping²⁶ which demonstrates that the separation of PLFs is reliable. Given that the first two dimensions of the NMDS explained 99% of the variation in the Euclidean distance matrix, we considered unnecessary to increase the number of dimensions in the analyses. It should be mentioned that NMDS is the most appropriate tool in studies of ecological communities^{27,28}, as previous studies, NMDS with low stress values, have also been used to separate phyllostomid bat assemblages from different habitats^{29–31}. The frugivorous guild is better adapted to live in farming systems than in natural forests^{4,29,32}. In the present study, the most abundant and richness guild was frugivorous, which included 67% of the individuals and 69% of richness. Frugivorous species including *Sturnira bakeri*, *Carollia brevicauda*, *C. perspicillata*, *Artibeus aequatorialis*, and *Uroderma convexum*, and the nectarivorous *Glossophaga soricina*, were the main contributors to the capture rate. In localities with different levels of habitat disturbance, frugivorous species of the genera *Artibeus*, *Uroderma*, *Sturnira*, or *Carollia* exhibit the highest abundance^{31,33}. Nevertheless, our findings indicate that the most abundant species is the nectarivorous *Glossophaga soricina* (20% of the captured individuals). In our study area corresponding to a tropical agricultural landscape without natural forest fragments, nectarivorous represented 21% of the individuals and 12% of the species recorded, i.e. they represent the second most important guild after frugivorous.

According to the literature, the frugivorous and nectarivorous guilds represent the highest abundance and richness of phyllostomid bats in agricultural landscapes supporting forest fragments^{24,34,35}. In the study area, which lacks natural habitat fragments¹⁹, the frugivorous and nectarivorous guilds combined accounted for 98% of recorded individuals and 91% of registered species. Considering the types of tree cover surveyed both tropical guilds represent an abundance of 99% in PLFs, 100% in MLFs, 97% in Cs and 90% in ITPs; whereas the combined proportion of species engaged in fruiting and nectarivory is estimated at 93% in PLFs, 100% in MLFs, 75% in Cs and 80% in ITPs. The data allow us to infer that the presence or absence of fragments of natural habitat has no effect on the prevalence of nectarivorous and frugivorous bats in agricultural landscapes. As fragmentation increases, the abundance of insectivorous and animalivorous decline^{33,36}, while the abundance of nectarivorous and frugivorous increases²⁹. We captured the animalivorous *Garderycteris crenulatum keenani* in the tree cover type with the highest tree diversity (PLF)¹⁹. Nonetheless, other animalivorous species such as *Micronycteris hirsuta* was recorded in the cacao plantations habitat. The high prevalence of frugivorous and nectarivorous species, coupled with the scarcity of animalivorous species, points to a significant level of disruption at the study site.

Phyllostomid bats in the North-west of Ecuador are grouped into 28 genera and 61 species³; hence, the records in this study represent 67% of genera and 26% of the phyllostomid bat species known to inhabit the region. The total number of individuals recorded in this study is one of the lowest in comparison to previous research conducted throughout the neotropical agricultural systems. It is important to remember that this is the first time a bat community has been studied in a site that has lost more than 80% of its original forest cover². This has resulted in the lack of natural forest fragments in our study area. Formations with conditions more similar to the original forests such as forest fragments and riparian forests favour the conservation of bat communities better than live fences in agricultural landscapes^{8,11}. It is precisely this characteristic that motivated the authors of this article to propose the study, as we sought to contribute to the knowledge of what tree cover is used by phyllostomid bats in the absence of forest fragments in agricultural landscapes.

Previous studies conducted in natural reserves in closer proximity to our study area did not report the presence of the following species³: *Chiroderma salvini*, *Lonchophylla robusta*, *Garderycteris crenulatum keenani*, *Platyrrhinus dorsalis chocoensis*, and *Vampyriscus nymphaea*. Additionally, *Trachops cirrhosus* was documented in other types of tree covers not included in this analysis (see Supplementary Information). The records of *Vampyriscus nymphaea*, *Chiroderma salvini*, and *Platyrrhinus dorsalis chocoensis* represent extensions of their respective distribution ranges³⁷, as their records are confined to localities situated further north of the study area³⁸.

The most common species in the tree covers were *Glossophaga soricina*, *Sturnira bakeri*, *Carollia perspicillata*, *C. brevicauda*, *Artibeus equatorialis*, *Uroderma convexum* and *Artibeus rufus*, which were recorded in at least three of the four types of tree cover surveyed and together accounted for over 90% of the captures. This finding corroborates the assertion that phyllostomid bats exhibiting the greatest abundance tend to be generalists, occupying a diverse range of diets and habitats³⁹. We assumed that *Desmodus rotundus* belonged to the common species group due to the presence of livestock in the study area⁴⁰; however, we only caught three individuals of the species in ITP. The low records of *D. rotundus* in the tree cover sampled may be since the study area probably does not offer suitable habitats for the species, such as dense vegetation, forest fragments, riparian forests and the presence of aquatic environments, which facilitate the movement of this species and provide resources as well⁴¹. The species *D. rotundus*, *L. robusta*, *M. hirsuta*, *G. crenulatum keenani*, *P. dorsalis chocoensis* and the species of the genus *Chiroderma* are considered to be rare species within the context of our study area, given that only one individual of each species was recorded in only one cover type.

In Ecuador, 75% of the 16 species recorded in this study are classified as “Least Concern” in the Red Book of Mammals from Ecuador, an official publication of the Ecuadorian Association of Mammalogists that provides information on the conservation status of mammals in the country⁴². *Vampyriscus nymphaea* and *Platyrrhinus dorsalis chocoensis* are classified as “Vulnerable”, and *Garderycteris crenulatum keenani* is considered “Near Threatened”⁴². It can thus be inferred that tree cover types located in these agricultural landscapes may prove beneficial for the conservation of certain threatened species.

We conclude that the most beneficial type of tree cover for promoting the abundance, richness and diversity of phyllostomid bats in northwestern Ecuadorian tropical agricultural landscapes is the live fences comprising a diverse range of plant species. Furthermore, in agricultural landscapes without natural habitat fragments, frugivorous and nectarivorous bats species increase in abundance, richness, and diversity, while the animalivorous species are negatively affected. It is known that live fences favour the availability of habitats and resources for animal species, as well as increasing the connectivity of agricultural landscapes. With the data obtained in our study, we recommend the installation of polyspecific live fences in tropical production systems to support the conservation of phyllostomid bats in North-western Ecuador. Local authorities in the field of agriculture can promote the use of live fences among local farmers. The development of agricultural management practices is crucial to raise awareness of the importance of bats to crops in agricultural areas and ensure their conservation.

Materials and methods

Study sites

The study was set in North-western Ecuador, within the provinces of Pichincha and Santo Domingo de los Tsáchilas; the life zone of the area corresponds to Tropical Rainforest⁴³. The study area is characterized by great levels of biodiversity and endemism, and it is the southernmost portion of the hotspot Choco-Darien ecoregion⁴⁴. The landscape of the study area is currently dominated by agricultural systems, responsible for the loss of more than 80% of the original vegetation cover².

We selected four sites, situated between 9 and 33 km apart, with agricultural activity for the surveys. Each site contained the four tree cover types assessed in this study. For each tree cover type we installed three sampling plots of 100 m². The distance between plots was at least of 300 m, and each sampling plot was then considered as an independent unit^{26,45} (Fig. 4).

We classified tree cover types into: polyspecific live fences (PLF: linear live fences composed of several tree species); monospecific live fences (MLF: live fences of a single tree species: *Erythrina smithiana*); cacao plantation (C: land portion of the agricultural system dedicated to the management of *Theobroma cacao*); and, isolated trees in pasture (ITP: *Brachiaria brizantha* crop where trees are distant from each other). Figure 5 shows a photographic sample of the type of tree cover evaluated.

Bat survey

At each site we set up three plots of 100 m² for each tree cover type, representing 12 per tree cover type and 48 sampled plots. In each plot we installed a mist net at ground level and reaching three m in height. These were kept open from 17:30 h until 00:30 h, and checked every 15 min, based on the period of greatest activity of phyllostomid bats^{29,46}.



Fig. 4. Example of distribution of plots by type of tree cover sampled (PLF, MLF, C, ITP, see Methods) in a map created with ArcGIS 10.5 (<http://www.esri.com/software/arcgis/arcgis-for-desktop>). Landsat image for land use combining bands 4,5,3 (orthophoto 1:5,000 NII-F3d-A4-ECW; www.geoportallgm.gob.ec.portal).

We collected information for four years (2011–2015); each year a site was sampled for five months [September, October, November (dry season), February, March (rainy season)]; two field trips per month, each trip with two effective days of capture. We spent 20 effective nights of sampling at each site (four days per month * five months), and 60 m² of mist net coverage area per tree cover type, giving a total of 19,200 m² of mist net coverage area (60 m² net per night * 20 night * four tree cover types * four sites). Trapping effort was calculated per area of mist net coverage (m²), as these data was confronted with tree density, which is expressed in area units²⁹.

Captured bats were identified, marked and released. Only one male and one female, which were difficult to identify in the field, were killed with an overdose of ketamine/xylazine (Ket-A-Xyl¹). These were preserved in ethyl alcohol (70%), following the guidelines proposed by Sikes et al.⁴⁷. The Ministry of Environment of Ecuador approved the protocols and issued scientific research authorizations 10-2013-IC-FAU-DPAP-MA and 01-2015-0-IC-FAU-DPAP-MA. The material was deposited, with a specific voucher number, at the Museo de Investigaciones Zoológicas (MIZI) of the Departamento de Ciencias de la Vida, Universidad de las Fuerzas Armadas del Ecuador as recommended by the Committee of the American Society of Mammalogists⁴⁷. Taxonomic identification of specimens was performed using dichotomous keys published in Albuja²⁰. Taxonomic names were assigned according to Wilson & Mittermeier⁴⁸. Aggregation into trophic guilds, followed the proposals of Kalko et al.⁴⁹ and Kunz et al.⁴⁶.

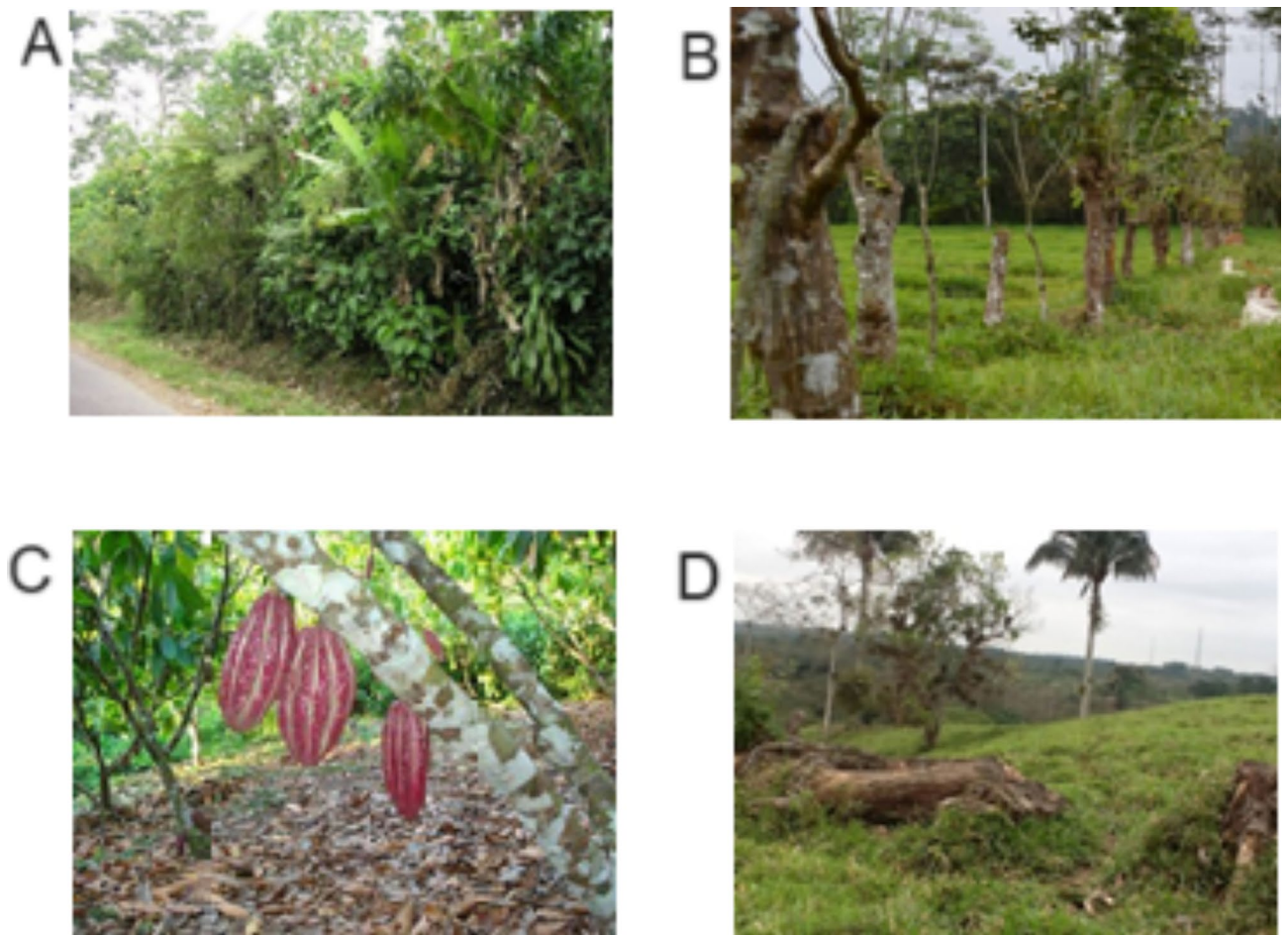


Fig. 5. Photos of the type of tree cover evaluated: (A) polyspecific live fences, (B) monospecific live fences of *Erythrina smithiana* species, (C) cocoa plantation (*Theobroma cacao*), and (D) isolated trees in pasture.

Abundance, richness, and diversity

We estimated species proportional abundance (P_i) by dividing the total number of captures of each species by the total number of individuals captured. The capture rate of phyllostomid bats by tree cover type was calculated by dividing the number of captures by the total area of the mist net (4,800 m²).

Alpha diversity was described with indices that show richness and structure in a complementary manner⁵⁰, as these two elements complement each other when properly describing biological diversity⁵¹. Following Williams-Guillen & Perfecto³² and de la Peña-Cuellar et al.^{30,31}, we used the total number of species recorded in the tree cover to represent phyllostomid bat richness. Expected species richness was obtained with Chao 2 non-parametric estimator, chosen for its low bias with small sample sizes²².

Diversity was evaluated using exponential of Shannon's index ($\exp H'$), as previously outlined by Jost⁵² and Moreno et al.⁵³. The evenness or proportion of observed diversity relative to the maximum expected diversity, was calculated with Pielou index (J')⁵¹.

Statistical analysis

The statistical program used was InfoStat⁴⁵ in interface with R⁵⁴. Capture rate, richness, diversity and evenness were also analysed using repeated measures (by plot). Generalized mixed models were used to evaluate the variation in indicators of abundance, richness, diversity and evenness among tree cover types following a randomized complete design with four replicates. Furthermore, we use the *post hoc* test of LSD ($P < 0.05$) to test for differences in the indices between tree cover types. The normality and homoscedasticity of the data were verified, respectively, by the Shapiro-Wilks test and the modelling of the independent variances.

To represent the proximity between the matrices of Euclidean distances of relative abundance and diversity variables by tree cover type in a small geometric space, we applied a non-metric multidimensional scaling. The goodness of the model was measured with Kruskal's Stress⁵⁵, which measures the differences between disparities and matrix gaps according to the following scale: excellent (0.0), very good (0.025), good (0.05), acceptable (0.1) and poor (0.2)²⁵. This multivariate method of interdependence is a useful ordination technique when variables do not conform to the normal distribution and are grouped on an arbitrary scale²⁸. For a better visualization of the groupings obtained in the non-metric multidimensional scaling, a cluster analysis was performed; the accuracy of the conglomerates was evaluated with the cophenetic correlation coefficient⁴⁵.

The homogeneity of the richness and abundance present in the trophic guilds of phyllostomid bats registered in different types of tree cover, was evaluated with the G test corrected by Williams (G_w), this test is useful to find the differences in frequency with which the values of a variable are distributed in different environments²⁶.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

“W.E.P.-R. wrote the conceptualization, methodology, and did the data collection and curation, formal analysis, writing – original draft, investigation, and discussion of the results, and S.M.S. and G.C.B. wrote – reviewed and edited the discussion of the results, and did language revision. All authors reviewed the manuscript.”

Declarations

Competing interests

The authors declare no competing interests.

Ethics statements

The original ARRIVE guidelines were adapted and approved to the specific context of free-ranging bats research. All capture and handling techniques and protocols were approved by the Ministry of Environment of Ecuador, in approval, accordance and ARRIVE guidelines⁵⁶ and with the guidelines proposed by the American Society of Mammalogists⁴⁷. This allowed obtaining research authorizations numbers 10-2013-IC-FAU-DPAP-MA and 01-2015-0-IC-FAU-DPAP-MA. No animals were left in captivity or under observation. All researchers and field assistant respected biosafety rules.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-74063-7>.

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