Life zone and habitat disturbance do not explain the coexistence in Sturnira bat species

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Abstract

One of the key questions in ecology is to understand the mechanisms that modulate the coexistence between syntopic species. Climate and habitat perturbation gradients have been proposed as moderators of species coexistence. The first is related to time availability and the diversity of food resources. The second is related to change in habitat structure that promotes changes in plant structure and diversity that impacts the diversity of other organisms. Although there is empirical evidence that supports these mechanisms to explain coexistence, they have not been evaluated quantitatively and on a wide geographic scale. Using phytophagous bat species of the genus *Sturnira* we evaluated both mechanisms. These bats are morphologically similar and are key organisms for the seed dispersal of Neotropical Forest plants. Using systematic review protocols, we obtained data of the occurrence and relative abundance of syntopic *Sturnira* species of different Neotropical forests. We used generalized linear models to evaluate the predictor power of Holdridge's life zones and habitat disturbance type to explain the evenness of syntopic *Sturnira* species. We found a highly *Sturnira* species evenness across life zones, going from 0.68–0.92, and found life zones with a maximum of eight *Sturnira* species coexisting in the same type of forest. The life zones and the type of disturbance do not explain the variation of evenness in *Sturnira* species. These results suggest that there is not a competitive exclusion among *Sturnira* species in tropical forests, and despite their ecological niche similarity, the environment allows the coexistence among these highly related species.

Introduction

Understanding the mechanisms that modulate the coexistence between morphologically and ecologically similar species allow us to clarify biodiversity patterns, determine levels of functional redundancy in ecological communities and determine the resilience of ecosystems ultimately (Kneitel and Chase 2004; Díaz et al. 2013). The mechanisms that promote coexistence are mainly divided into two deterministic processes: limiting similarity and environmental fluctuations (Darwin 1859; Chesson and Huntly 1997; Chesson 2000). The limiting similarity establishes that there are maximum limits between the ecological niche overlap of species that can coexist on the same spatial scale. Thus, niche overlap favors competitive exclusion and in turn the coexistence of species (Macarthur and Levins 1967; Violle et al. 2011). On the other hand, environmental factors such as temperature, vegetation type, and humidity affect the coexistence of syntopic species. For example, environmental conditions filter morphological and ecological traits of species with similar niches (Chesson 1986; Chesson and Huntly 1997; Zobel 1997; Córdova-Tapia and Zambrano 2015). Another example is the intermediate disturbance, they can promote plant species diversity through the increase of diversity of pioneer plant species, resulting in an increase in animal diversity (Chesson and Huntly 1997; Clarke et al. 2005a, b; Barlow et al. 2007). Primary productivity is another environmental factor of the ecosystem that promotes food resource availability and that could favor the coexistence of closely related phytophagous species (Wright 2002). In general, these mechanisms have been evaluated at a local landscape or ecosystem scale (Kneitel and Chase

2004). However, an evaluation of its effects on a continental scale, using data coming from different populations at different times remains elusive.

An excellent biological model to evaluate the coexistence mechanisms on a continental scale are the *Sturnira* bat species of the Phyllostomidae family (Velazco and Patterson 2013). *Sturnira* bat genus contains 24 species that account for approximately 11% of the living phyllostomid bat species (Simmons and Cirranello 2022). They are key organisms in the Neotropical ecosystems because they disperse seeds of early successional stages plants (Muscarella and Fleming 2007; Mello et al. 2011), they are facultative pollinators and one of the most dominant frugivorous bat species of tropical and subtropical bat communities (Rex et al. 2008; Sánchez et al. 2012b; García-Morales et al. 2014). Therefore, these bat species are the basis for the regulation of Neotropical ecosystem functions (Galindo-González et al. 2000; Mello et al. 2008). In addition, they present a wide diversity and distribution in the Neotropics (Velazco and Patterson 2013). *Sturnira* bat species present a high niche overlap, based on diet composition, feeding behavior, morphology, and diurnal-roost ecology (Evelyn and Stiles 2003; Mello et al. 2011; Sánchez et al. 2012; Saldaña-Vázquez 2014; Cortés-Delgado and Sosa 2014; Castillo-Figueroa 2020; Fig. 1). At the same time, this genus has a diet that strongly differs from the rest of the frugivores lineages of Phyllostomidae such as Carolliinae and Stenodermatini (Sánchez and Giannini 2018). Therefore, they are ideal organisms to evaluate those mechanisms that facilitate species coexistence over a broad geographic scale.

In this study, we test the two hypotheses about the mechanisms that modulate species coexistence, using *Sturnira* bat genus on a wide spatial scale like the Neotropics. Specifically, we assess whether the differences in the vegetation type module the coexistence between syntopic species of bats. Because tropical rain forests present a greater diversity of available food, to *Sturnira* bats, compared to other vegetation types (Gentry 1988; McCain and Grytnes 2010). We hope that in tropical rainforests there will be a greater evenness of the *Sturnira* species compared with dry, temperate, and cloud forests (Barlow et al. 2007). In the same line, we hope that habitats with intermediate levels of disturbance could promote a highly coexistence of species of the *Sturnira* genus, because the early successional stages of forests promote the appearance of pioneer plants visited by *Sturnira* bats in the different patches through the fragmented forests and in selective logging systems (Clarke et al. 2005a, b), favoring the abundance of *Sturnira* species and reducing the competitive exclusion between syntopic species (Chesson and Huntly 1997; Rocha et al. 2017). Therefore, we expect a high evenness of *Sturnira* species in intermediate human-disturbed forests.

Methods

Literature search

To obtain the relative abundance of syntopic species of fruit bats of the genus *Sturnira*, in different types of forest, a systematic literature search was performed using the Google Scholar (GS) search engine and the Web of Science (WS) and Scopus (S) repositories and search engines. These engines and literature

repositories were selected since GS includes gray literature, while WS and S have a vast catalog of specialized scientific journals. In addition to the fact that previous studies have shown that WS alone does not manage to retrieve the largest amount of literature available on a topic (Beckmann and von Wehrden 2012). Combinations of the following keywords were included for searches: "bat", "Phyllostomidae", "*Sturnira*", "assemblage", "coexistence", "community", "abundance", "diversity", "species richness" (Table 1). The search was not limited to the year of publication or type of journal, was carried out in the months of October to December 2020 and in English and Spanish language. Additionally, data on theses and technical reports that were manually searched in personal literature collections were considered.

Table 1

Keywords and results of literature search. The phrase in parenthesis remarks the section of the document where the keywords were searched. The search engines used were Google Scholar (GS), Web of science (WoS), Scopus (S).

Search ID	Keywords	Search engine	Results
1	[Coexistence OR diversity OR abundance OR assemblage OR community OR species richness] AND [phyllostomid OR bats] (title)	GS	554
2	[Coexistencia OR diversidad OR abundancia OR ensamble OR comunidad OR riqueza de especies] AND [Phyllostomid OR murciélagos] (title)	GS	4
3	[Coexistence OR diversity OR abundance OR assemblage OR community OR species richness] AND [phyllostomid OR bats] (all the article)	GS	20,040
4	[Coexistence OR diversity OR abundance OR assemblage OR community OR species richness] AND [phyllostomid OR bats] (title)	WoS	301
5	[Coexistencia OR diversidad OR abundancia OR ensamble OR comunidad OR riqueza de especies] AND [Phyllostomid OR murciélagos] (title)	WoS	1
6	[Coexistence OR diversity OR abundance OR assemblage OR community OR species richness] AND [phyllostomid OR bats] (all the article)	WoS	5
7	[Coexistence OR diversity OR abundance OR assemblage OR community OR species richness] AND [phyllostomid OR bats] (title)	S	880
8	[Coexistencia OR diversidad OR abundancia OR ensamble OR comunidad OR riqueza de especies] AND [Phyllostomid OR murciélagos] (title)	S	23
9	[Coexistence OR diversity OR abundance OR assemblage OR community OR species richness] AND [phyllostomid OR bats] (all the article)	S	42

Studies selection criteria

With the studies resulting from each search, a review of titles and abstracts was made, to explore in detail those that were candidates for data extraction. It was established that the studies should meet the following criteria for data extraction: (i) the article should report at least two species of *Sturnira* captured at each study site, (ii) should report the number of individuals captured per species of *Sturnira*, (iii) the geographical coordinates or a map where the bat capture sites can be georeferenced were reported, (iv) the state of conservation or types of disturbance in the sampling sites should be described. In addition, we adopted the scientific nomenclature for species following Simmons and Cirranello (2022) to define the taxonomic identity of the species reported in each study.

Variables and data analysis

From the selected studies we obtained data on the richness and abundance of *Sturnira* species, type of vegetation disturbance and life zones. For each study, evenness was calculated using the *J* evenness index, which is based on the Shannon-Weiner diversity index, which is expressed as follows:

$$H' = \sum_{i=1}^{s} [(p_i) \times ln(p_i)]$$

H' = Shannon index value

p_i = proportional abundance of taxon i.

ln = natural logarithm

s = number of species (or taxa)

$$J = Evenness = \frac{H'}{Hmax} = \frac{H'}{lnS}$$

$Hmax$ = ln(S) = Maximum diversity possible

This index was calculated with the "diversity" function of the "vegan" package of the R programming language (Oksanen et al. 2022). To classify the type of disturbance reported in the studies we based on Carballo-Morales et al. (2021). These authors classify the disturbance of Neotropical Forest ecosystems in the following categories: Forest fragmentation, grassland, logging, secondary forest, and urban zone. The classification of each type of disturbance was based on what was reported by the authors in each document, and on the review of the study site maps of the same documents.

Holdridge's life zone system (Holdridge 1967) was used to classify the type of forest in which *Sturnira* species were observed. The coordinates of the sampling sites extracted from each study were used to locate the life zone to which they belonged, using the layer in KML (Keyhole Markup Language) format of the life zones of the FAO (2012) and the program computer Google Earth Pro (Version 7.3). The life zones in which the studies were carried out were: Warm temperate wet forest, warm temperate moist forest, warm temperate dry forest, tropical dry forest, subtropical wet forest, subtropical moist forest, subtropical dry forest, polar desert, cool temperate moist forest.

To evaluate the effect of the life zones and the type of disturbance on the evenness of *Sturnira* species, generalized linear models (GLM) were carried out where the response variable was H' and the explanatory variables were the life zones and the type of disturbance. In addition, the number of individuals of *Sturnira* captured from each study was added as an explanatory variable. After making the models, the parameters of said models were compared with a null model from an ANOVA test with statistical significance at a level of 0.05. These statistical analyzes were performed with the R software (version 3.6.3) and the "stats" package (R Core Team 2021).

Results

The search resulted in 102 studies selected for the extraction of abundance data of species of the genus *Sturnira* (Fig. 2). The database included 16 of the 24 species of the genus *Sturnira* reported to date (66.7% of the species). Which occurred in 12 life zones and up to six different types of disturbance (Fig. 3).

Life zones did not explain the variation in evenness of syntopic species of *Sturnira* (X^2 = 3.624, P= 0.104, Fig. 4). Nor did the type of habitat disturbance explain the variation in the evenness of the syntopic species of *Sturnira* (X^2 = 3.162, P= 0.08, Fig. 5).

Discussion

This study aimed to evaluate the hypothesis that postulates an effect of environmental variables as promoters of ecological changes which impact on the coexistence of morphologically similar and syntopic frugivorous species. What can generate competitive exclusion when resources are limited or, on the contrary, can promote greater tolerance between species in those environments with greater diversity and availability of resources. Specifically, we expected that life zones with more tropical climates would promote greater coexistence of *Sturnira* species, expressed as greater equity in assemblages, by containing a greater diversity of plant species. Furthermore, we expected that in temperate and cold regions assemblages would exhibit low equity with dominance of one specie. On the other hand, we expected that early successional-stage forests would promote greater species coexistence by increasing the diversity of early-successional-stage plants such as *Solanum*, which fruits that are the core of the diet of these species (Fleming 1986; Sánchez et al. 2012b; Saldaña-Vázquez et al. 2013; Sánchez and Giannini 2018). Surprisingly, our results did not support both predictions. Contrary to the first prediction of our hypotheses, we found high evenness across all life zones analyzed in both tropical and temperate forests. Being the "cool temperate moist forest" life zone the one with the greatest evenness (0.92) and richness of species presented with four coexisting species on average, which represents the highest average of *Sturnira* species for our sample.

Traditionally, attempts have been made to explain the patterns of regional diversity and abundance of bats based on environmental variables such as productivity, temperature, climatic seasonality, latitude, altitude, geographic area, and environmental energy (Lyons and Willig 1999; Willig et al. 2003; Willig and Bloch 2006; Tello and Stevens 2010; Stevens 2011; Sánchez and Giannini 2014) or by conservation of the

ecological niche over time (Ramos Pereira and Palmeirim 2013). According to these works, these factors would go down the scale, directly affecting the local diversity and complexity of the assemblages (Tello and Stevens 2010). For its part, from a biogeographical approach it is expected that the local composition of species depends on the regional set of species, which is determined by large-scale biogeographical processes. In this way, the specific composition of an assemblage or assemblage may result from the biogeographical patterns that act on the processes of speciation, extinction, and dispersion, rather than the result of a local ecological limitation (Wiens and Donoghue 2004; Wiens 2012).

An example of this is the uplift of the Andes and its role in the diversification of the Amazonian biota (Hoorn et al. 2010; Wiens et al. 2012) or the Mid-Miocene Climatic Optimum and its impact on temperatures. and rainfall on a global scale, which strongly altered the diversity of the Neotropical flora (Hoorn et al. 2010). In our case, the coexistence of species of the genus *Sturnira* in a particular region or life zone may also be the result of sympatric speciation events or post-speciation dispersal (Halas et al. 2005). This could explain our results and the high diversity we detected in the "cool temperate moist forest" life zone. In fact, biogeographical studies of the genus *Sturnira* indicate that the genus diversified in the northern region of the Andes where the "cool temperate moist forest" life zone occurs (Velazco and Patterson 2013). In addition, the colonization of lowlands in the Pacific and Mesoamerica occurred secondarily and later. Interestingly, most of the extant lineages arose recently during the Late Pliocene and Pleistocene (3.5 MY) with *in situ* speciation events (in the Andes) and with up to 40 dispersal and recolonization events (post-speciation dispersal), denoting a strong biogeographical effect on the current distribution of the species, evidencing the strong historical component of the evolution of the genus that explains the richness and co-occurrence of the species in the current assemblages (Velazco and Patterson 2013). This does not exclude the importance of proximal or local factors such as the availability and diversity of resources, which are decisive in the maintenance of the assemblages.

Although life zones and disturbance type had no effect on the evenness of *Sturnira* species, some intrinsic factors that were not evaluated in this study could explain the high evenness observed in subtropical and temperate regions. For example, the dietary nucleus of the *Sturnira* genus is made up of plants of the *Solanum* genus, which is typical of successional stages of secondary vegetation and has periods of extended fruiting (Fleming 1986; Sánchez et al. 2012b). This could generate a prolonged availability of resources that could promote the high equity that we observe. In addition, *Solanum* is a genus of plants whose center of diversity and endemism is found in the Andes (Echeverría-Londoño et al. 2020), where there is a marked and strong climatic seasonality of temperature and rainfall (Garreaud 2009). For example, *Solanum* and *Cestrum* (Solanaceae) were the most diverse and dominant genera in the understory of the evergreen cloud forest from Argentina (Giannini 1999). These plant species dominances influence the diet composition of *Sturnira* in the highest and coldest sectors of the mountain wet forest (Sánchez and Dos Santos 2015). Interestingly, the life zones "Polar desert, Subtropical dry forest, Cool temperate moist forest and Tropical dry forest" were the ones that presented the highest evenness *Sturnira* values, which could suggest a dominance of *Solanum* in these bat-plant interaction

systems and explain the equity values we find. Hence, further studies involving diet sampling and availability of resources in these life zones are necessary to test this assumption.

Other intrinsic factors that were not evaluated are the foraging and roost behavior of the species of the genus *Sturnira*. These factors, together with the high availability of food, have been proposed as variables that explain the coexistence of fruit bat species. For example, the high availability of pioneer plants of the genus *Piper*, and differential foraging behavior (a species emerges from roosts earlier) and diurnal roosting (a species perches closer to resources) are factors that promote coexistence in syntopic species of the genus *Carollia* in montane forests of Ecuador (Bonaccorso et al. 2007). The seasonal variation in the abundances of each species of frugivore that makes up the assemblages is also a factor that must be considered, since small changes in the dominance of the species throughout a year may be key to allowing the co-occurrence of similar species in the assemblages. It has been detected changes in the dominance of *Sturnira lilium* and *S. erythromos* between samples from the same site and throughout a seasonal period in the montane forests of Argentina (Sánchez et al. 2012a). Similarly, it has been detected marked monthly and seasonal differences in the dominance of the trophic guilds of phyllostomid bats in the Atlantic Forest of Brazil, showing that Neotropical bat assemblages are organized in a very dynamic way (Mello 2009).

In conclusion, the determining ecological implications in the coexistence of the sympatric species of the genus *Sturnira* on a large scale evaluated in this work, continue to be a mystery, and show the complex and multivariate set of factors that could be promoting the high evenness that we observe in the different life zones and habitats. However, it is important to deepen future studies in different perspectives such as the physiology of metabolism and the ecology of migration, considering the wide range of altitudinal ranges that these species present to minimize competition for the availability of food resources. On the other hand, climatic seasonality, and its association with plant genera with its hotspot in the Andes could be related to the high evenness of the species of the genus *Sturnira* and its response in the different life zones evaluated by minimizing temporal overlap.

Declarations

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation and analysis were performed by Esteban Mosquera-Izquierdo and Romeo A. Saldaña-Vázquez. Data collection were performed by Esteban Mosquera-Izquierdo, Mariano S. Sánchez and Romeo A. Saldaña-Vázquez. The first draft of the manuscript was written by Esteban Mosquera-Izquierdo, Mariano S. Sánchez, Federico Villalobos and Romeo A. Saldaña-Vázquez and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated and analyzed during the current study are available in the Supplementary Information of the paper.

Statements and Declarations

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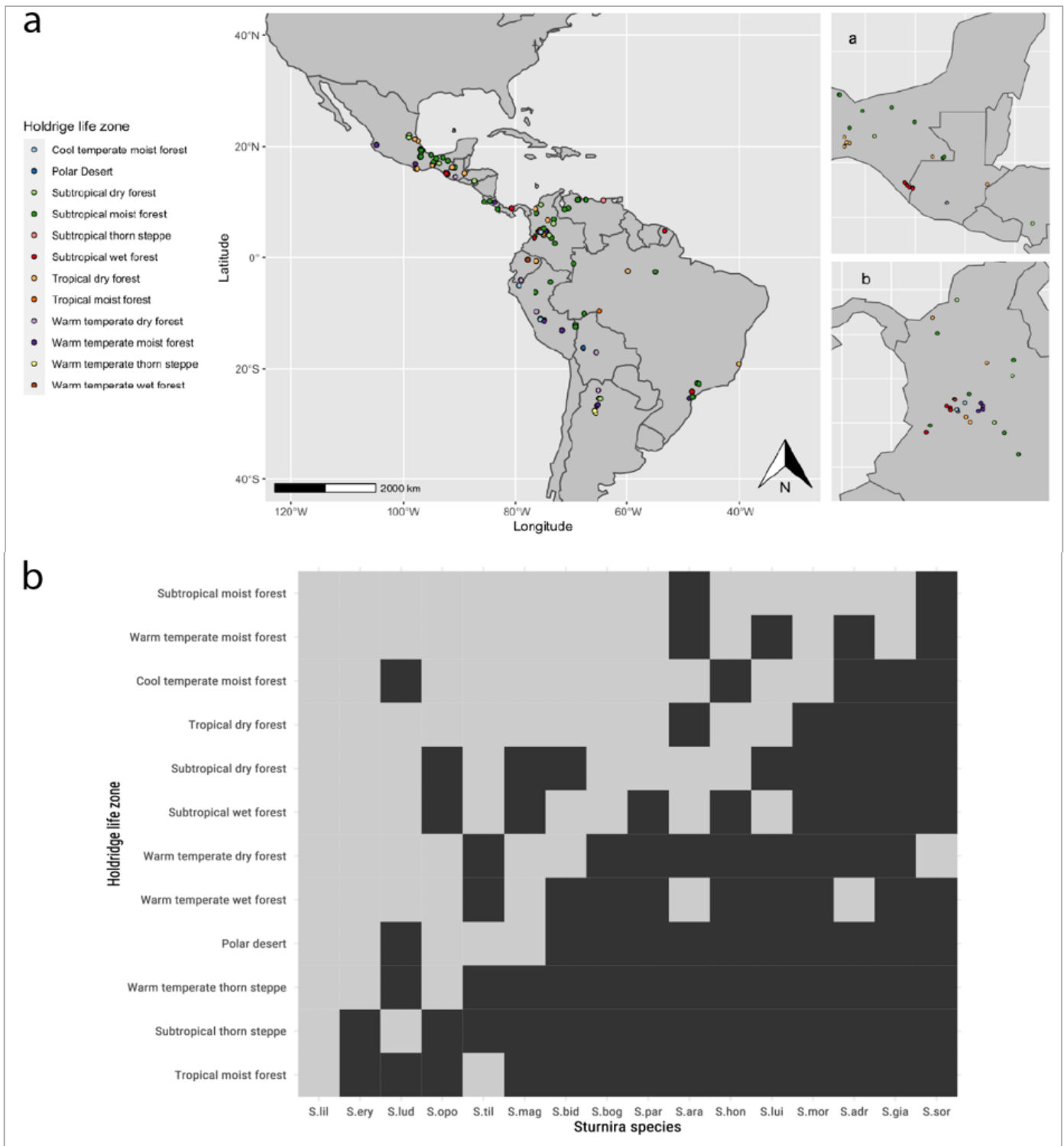
Figures

Figure 1

Species of the *Sturnira* bat genera. The species photos correspond to: a) *S. ludovici*; b) *S. parvidens*; c) *S.erythromos* ; d) *S. luisi*; e) *S.lilium*; f) *S. oporaphilium*; g) *S. aratathomasi*; h) *S. adrianae*. They present a high external morphological similarity that matches with their diet similarity, based principally on *Solanum* and *Piper* fruits. Photos by John Harold Castaño.
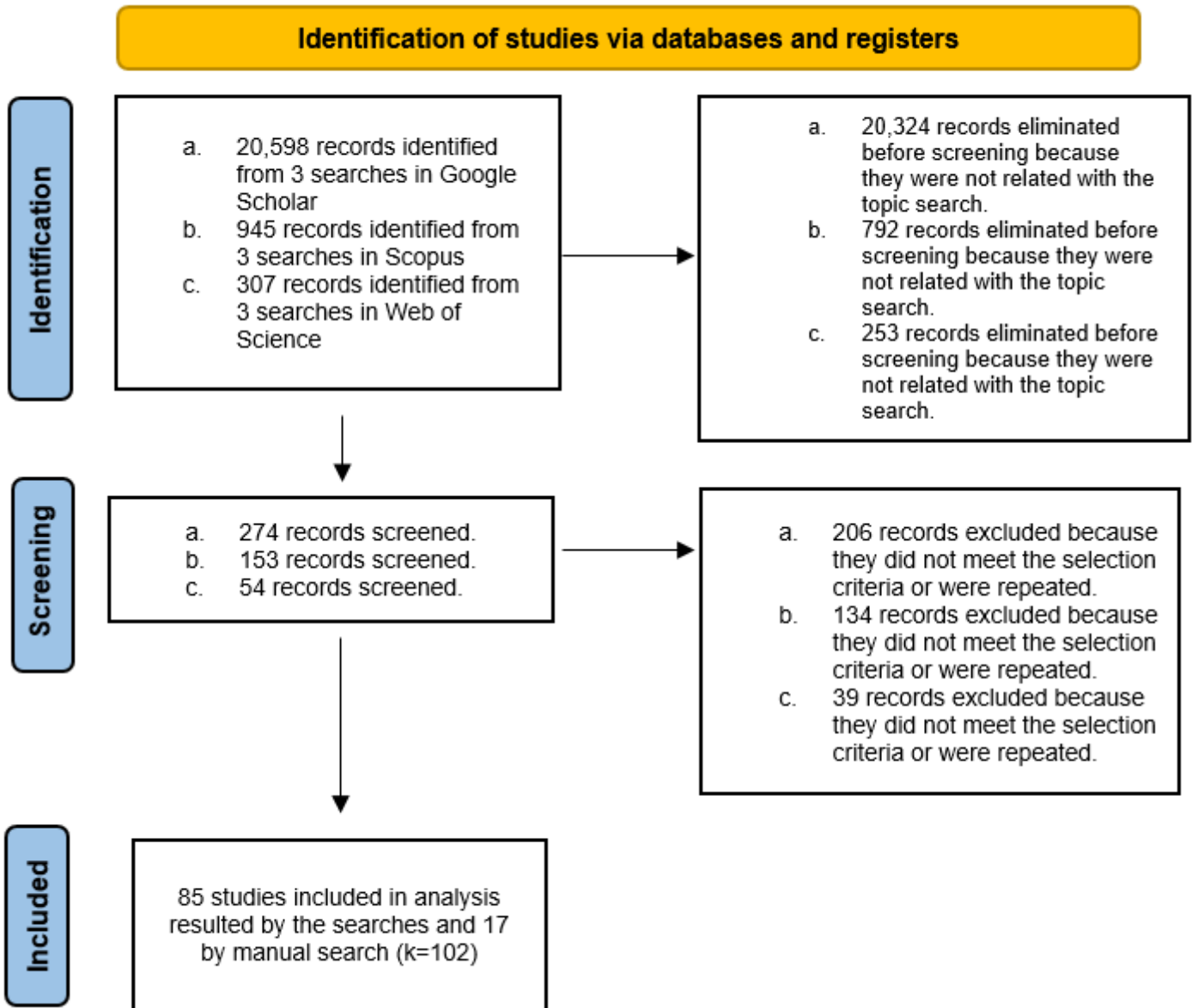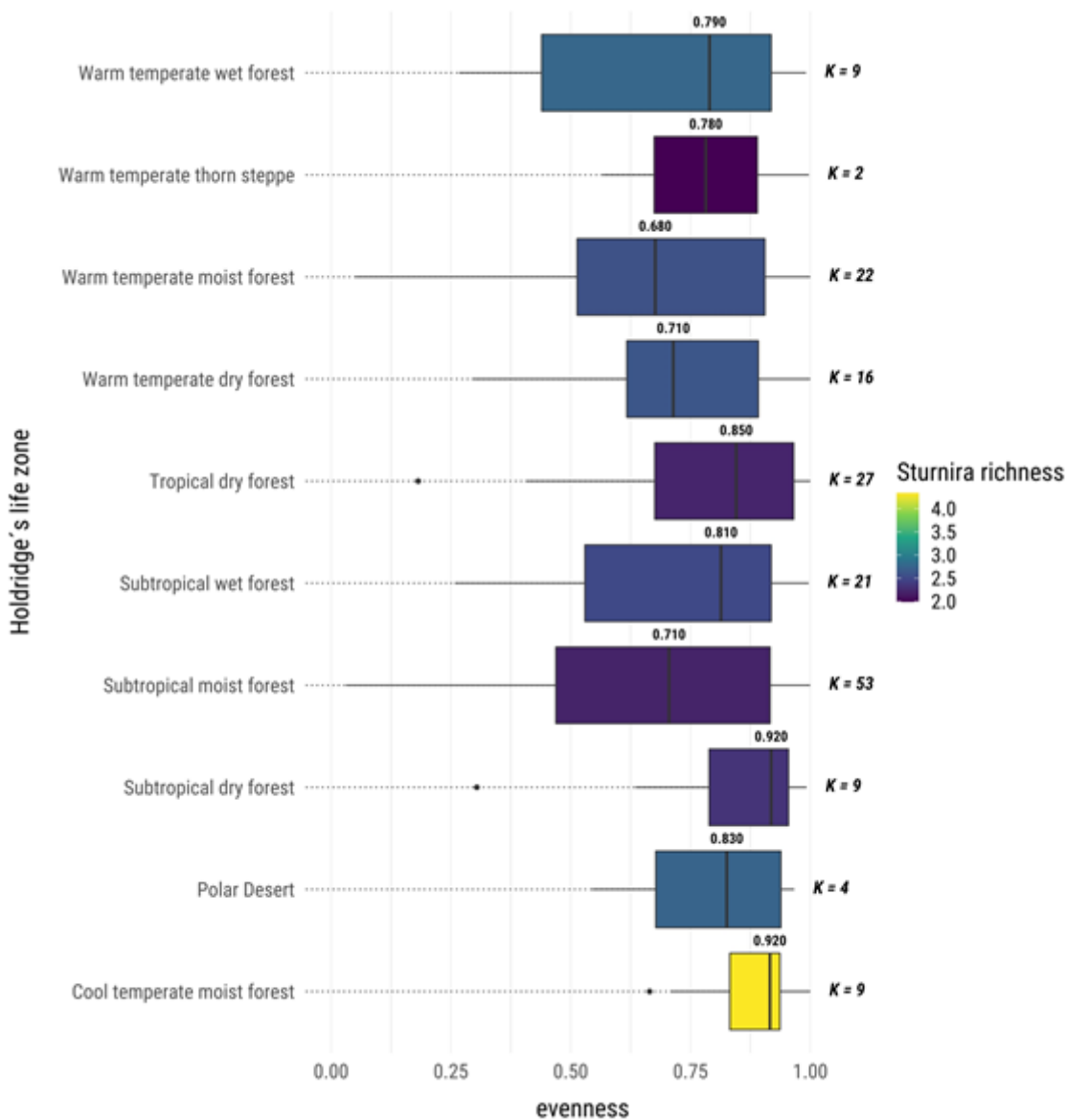
Figure 2

PRISMA flowchart of information through the different phases completed in the systematic review of the *Sturnira* species coexistence based on Page et al. (2021). Letters correspond to searches for a) Google Scholar, b) Scopus and c) Web of Science.

Figure 3

a) Study cases localities (102). The colors of marks correspond to the Holdridge life zones. Approach: a. Mexico and b. Colombia. b) Occurrence of *Sturnira* species by life zone based on the studies selected. Grey squares mean life zones occupied by *Sturnira* species: S.lil (*S. lilium*), S.ery (*S. erythromos*), S.lud (S. ludovici), S.opo (*S.oporaphilium*), S.til (*S.tildae*), S.mag (*S.magna*), S.bid (*S.bidens*), S.bog (*S.bogotensis*),

S,par (*S.parvidens*),S.ara (*S. aratathomasi*), S.hon (*S.hondurensis*), S.lud (*S.ludovici*), S.mor (*S.mordax*), S.adr (*S.adrianae*), S.gia (*S.giannae*), S.sor (*S.soranoi*).

Figure 4

Evenness variation in relation with Holdridge life zones. Colors of boxplot correspond to the maximum number of *Sturnira* species reported in each life zone. Median value of evenness is presented by the black line in each box. *K* corresponds with the total number of evaluated study cases for each life zone. No se incluyeron en el análisis zonas de vida que tenían menos de 4 estudios.
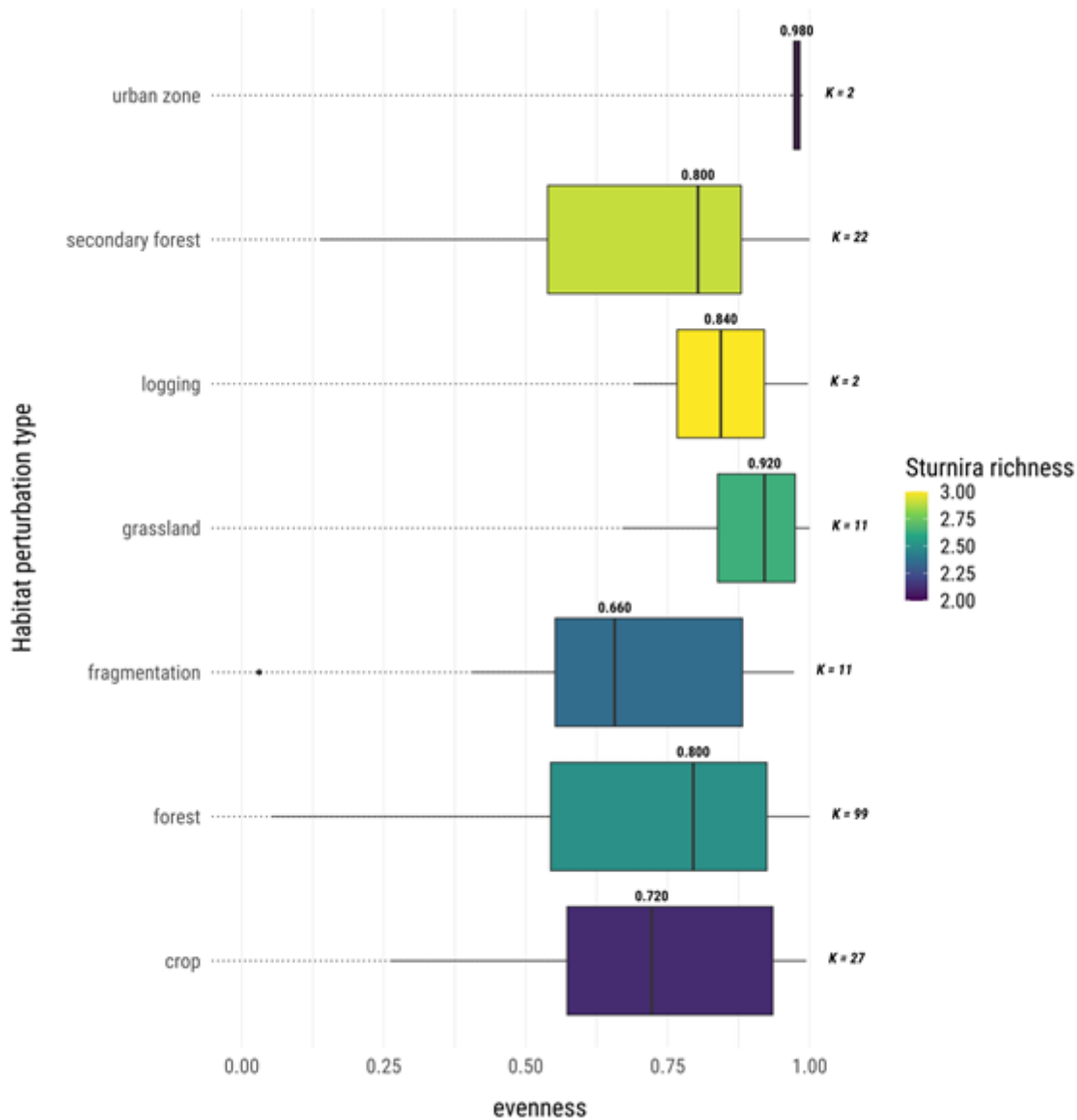
Figure 5

Evenness variation in relation with Habitat perturbation type. Colors of boxplot correspond to the maximum number of *Sturnira* species reported in each perturbation type. Solid lines in each box represent the median value of evennes. *K* corresponds with the total number of evaluated study cases for each perturbation type.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementalMaterial.xls