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Synthesis of knowledge of the plant diet of nectar-feeding bats of México

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The interaction between bats and plants is key to the stability of ecosystems and economically important industries, such as tequila and mezcal in México. For these reasons, it is important to determine the current state of knowledge about the plant diet of nectar-feeding bats. In this study, we conducted a systematic review of the literature on plants that have been reported as sources of food for nectar-feeding bats (subfamily Glossophaginae) in México. Based on this information, we identified bat species with the best-documented knowledge of their diet, the most consumed plant genera, and the territories with information gaps in the country. The literature search on the diet of nectar-feeding bats was carried out in the Web of Science database, Google Scholar, and digital collections of universities. We constructed rarefaction curves for bat diet richness, a heat map of the plant genera consumed by each, and a map of food localities in the different biogeographical provinces of México. This information served to explore whether knowledge of the diet of bats was related to variables such as the presence of chiropterophilous plants or the richness of nectar-feeding bats. In México, nectar-feeding bats feed mainly on plants of the genera *Agave* spp., *Pseudobombax* spp., and *Ceiba* spp., which, according to the literature, provide food to more than 75 % of nectar-feeding bats in Mexican territory. *Leptonycteris yerbabuenae* is the species with the most information on its diet in México, while *Lichonycteris obscura* is the species with the least information. None of the bat species reached a value greater than 65 % of the expected richness. Localities where the plant diet of nectar-feeding bats has been studied correspond to provinces in the Neotropical region of México. Knowledge about the diet of nectar-feeding bats in México is far from complete. The distribution of diet localities is biased over a large part of its geographic range and is positively correlated with areas with higher nectar-feeding bat species richness.

La interacción entre los murciélagos y las plantas es clave para la estabilidad de los ecosistemas y para industrias económicamente importantes, como la del tequila y mezcal en México. Por ello, es importante determinar el estado del conocimiento de la dieta vegetal de los murciélagos nectarívoros. En este estudio hicimos una revisión sistemática de literatura sobre las plantas que se han reportado como alimento de las especies de murciélagos nectarívoros glosofaginos de México. A partir de ello, identificamos las especies de murciélagos con mayor completitud en el conocimiento de su dieta, los géneros de plantas más consumidos y los territorios con vacíos de información para el país. La búsqueda de literatura sobre dieta de glosofaginos se realizó en la base de datos Web of Science, en el buscador Google Scholar y en acervos digitales de universidades. Construimos curvas de rarefacción de riqueza de la dieta de los murciélagos, un mapa de calor de los géneros consumidos por especie, así como un mapa de las localidades de dieta en las diferentes provincias biogeográficas de México, para saber si el conocimiento de la dieta vegetal de estos murciélagos estaba relacionado con variables como presencia de plantas quiropterofílicas o riqueza de especies de murciélagos. La dieta de los murciélagos se concentró en los géneros *Agave* spp., *Pseudobombax* spp. y *Ceiba* spp., los cuales proveen de alimento a más del 75 % de las especies de estudio. *Leptonycteris yerbabuenae* es la especie con mayor información sobre su dieta vegetal en México, mientras que *Lichonycteris obscura* es la especie con menos información. Ninguna especie de murciélago alcanzó un registro mayor al 65 % de la riqueza esperada. Las localidades donde se ha estudiado la dieta de estos murciélagos se concentran en provincias biogeográficas correspondientes a la región Neotropical del país. El conocimiento sobre la dieta de nectarívoros glosofaginos en México está lejos de estar completado. La distribución de localidades de dieta está sesgada en una gran parte de su distribución geográfica y parece relacionarse positivamente con áreas de mayor riqueza de especies de murciélagos.

Keywords: Biogeography; Chiroptera; conservation; plant-animal interaction; research bias.

Introduction

The food resources of animals are key to their survival and reproductive success. The diet can vary widely between species and landscapes, impacting the different consumption webs and causing cascading effects on ecosystem productivity and functioning (Cusser *et al.* 2019). An animal can be a generalist, *i. e.*, having several food sources, or specialized, feeding preferentially on a particular resource type. In the latter case, the relationship between the animal and the resource can become very close and mutually dependent (Muchhala 2006). An example is zoopollination, in which the animal feeds on the plant while contributing to its sexual reproduction (Fontaine *et al.* 2006). There is a diverse group of zoopollinators that includes bees, flies, bumblebees, beetles, butterflies, reptiles, and mammals, including bats (IPBES 2016).

The New-World nectar-feeding bats, which are specialized in nectar consumption, belong to the family Phyllostomidae, subfamily Glossophaginae (Rojas *et al.* 2016; Muchhala and Tschapka 2020). They comprise a diverse group that shows morphological, physiological, and behavioral adaptations to feeding on pollen and flower nectar (Tschapka *et al.* 2008; Ayala-Berdon *et al.* 2011; Muchhala and Tschapka 2020). These species have ecological attributes that make them particularly susceptible to extinction by anthropogenic causes (Arita and Santos del Prado 1999; Ortega-Garcia *et al.* 2020).

México is home to 12 of the 25 species of nectar-feeding bats belonging to the subfamily Glossophaginae, including two species (*Musonycteris harrisoni* and *Glossophaga morenoi*) and one genus (*Musonycteris*) endemic to the country (Ramírez-Pulido *et al.* 2014). In addition to their biological diversity and specialization, these mammals play socially and economically important roles for Mexicans by pollinating plants used in the production of alcoholic beverages such as *pulque, bacanora, mezcal*, and tequila — an industry that generated export profits of US$1.2 billion in 2015 (Trejo-Salazar *et al.* 2016). Additionally, plants that produce edible fruits such as pitaya (*Stenocereus queretaroensis*) and that are also pollinated by bats yield profits in excess of US$2,500/ha/year (Tremlett *et al.* 2020).

Given the ecological and economic importance of nectar-feeding bats, multiple studies have addressed their diet in México (Sánchez-Casas and Álvarez 2000; Sánchez and Medellín 2007; Caballero-Martínez *et al.* 2009). However, we still ignore which are the plant genera most consumed by each bat species and the degree of completeness of their dietary richness. This information is relevant for determining the key plant species in the diet of these mammals and promoting new research agendas on their ecological interactions. On the other hand, the projection of this information in the Mexican territory may contribute to evaluating whether the patterns of diet localities are related to the diversity patterns of both plants and nectar-feeding bats. This may foster conservation strategies in areas with high levels of bat-plant interactions in México.

Therefore, the objective of this study was to summarize the information on the degree of completeness of the plant diet of nectar-feeding bats and construct maps including information on the diversity of chiropterophilous plants and the distribution of nectar-feeding bats. This will promote new research agendas on the ecology of bat-plant interactions in México, especially in areas where further exploration is needed, focusing on species that are vulnerable due to the lack of knowledge of their diet.

Materials and methods

Data search. We conducted a comprehensive search of scientific literature on the Google Academic Platform (GA) and the Web of Science (WoS) database, as well as in digital thesis repositories of different universities (UNAM https://tesiunam.dgb.unam.mx; BUAP https://repositorioinstitucional.buap.mx; UV https://cdigital.uv.mx; UDG http://biblioteca.udgvirtual.udg.mx; UAEM http://ri.uaemex.mx; UANL https://cd.dgb.uanl.mx; INECOL https://inecol.repositorioinstitucional.mx). The keywords used in the search were the scientific name of each nectar-feeding bat species in the subfamily Glossophaginae distributed in México (*e. g*., *Leptonycteris nivalis*) together with the words "nectar", "diet", "pollination", "frugivory". This search was conducted in Spanish and English. Keywords were searched in the title, abstract, and keywords of the documents; the search covered from 1955 to December 2020.

Once all references were collected, any duplicate documents were removed. All documents were then evaluated according to the following inclusion criteria: 1) The study species should be nectar-feeding bats currently distributed in México, belonging to the subfamily Glossophaginae (Rojas *et al.* 2016). Documents that provided no certainty as to which bat species visited the plant were excluded. Since some of our study species, such as *Leptonycteris yerbabuenae* and *Glossophaga mutica*, had recent taxonomic changes (Simmons and Wetterer 2002; Calahorra-Oliart *et al.* 2021), the collection sites reported in these cases were reviewed and assigned to the species according to the recent taxonomic proposals. 2) The study should mention the genus of the plant used as source of nectar by the bat. 3) The document should include the collection locality. Records of nectar, pollen, seeds, fruits, and plant visits were included in the database as part of the plant diet of bats. The records used came from sources such as stomach contents, stools, hair, video records, and sightings, among others. The literature search yielded 3,200 documents. After applying the inclusion and exclusion criteria described above, 80 documents were considered for the study (Supplement 1).

A database of plant species in bat diets was constructed (see below). If studies reporting the same interaction met all criteria, the oldest was included for being the first record of the interaction. Once the database of all the plants visited by the bat species studied was gathered, it was homogenized according to the nomenclature of TROPICOS (2021) and POWO (2020).

Analysis of plant genera reported in the plant diet of nectar-feeding bats in México. Once all records of the interaction between a bat species and a plant genus in a locality were obtained, a heat map was constructed from a matrix of plant-bat interactions. This matrix contained bat species in columns and the plant genera consumed by bats in rows. The number of unique species recorded in the literature for that genus was noted in each cell. The matrix was used to construct the rarefaction curves of the species observed, to identify whether the information on the plant diet is representative for each bat species.

Species rarefaction curves were constructed with the Hill numbers corresponding to the diversity of order 0 (taxonomic richness of species). The extrapolation and rarefaction of each curve were constructed with a 95 % confidence interval, allowing extrapolating to twice the number of observations recorded. These analyses and graphs were performed using the R iNEXT V. 2.0.20 package and pheatmap (Kolde 2015; Hsieh *et al.* 2016; R Development Core Team 2021).

Since the search in GA and WoS allowed us to access information on the diet of species of nectar-feeding bats distributed in and outside the Mexican territory, we could compare the number of plant genera in the diet reported for México with the data for the rest of the geographic range of each bat species. *Musonycteris harrisoni* and *Glossophaga morenoi* were excluded from this analysis for being species endemic to México. *Choeronycteris mexicana* and *Lichonycteris obscura* were also excluded from this analysis since, according to the inclusion/exclusion criteria, records were found only within or outside México, respectively.

Spatial analysis of diet localities. We performed the following procedures to understand whether the distribution of plant diet localities reviewed and selected in this study is related to variables such as chiropterophilous plant richness or nectar-feeding bat richness. From each document selected in the search, we obtained unique geographic locations mentioned as study sites by the authors. In cases where the locality was mentioned, but not the geographic coordinates, these were estimated using a georeferencing calculator (Wieczorek and Wieczorek 2021).

To determine the areas of highest chiropterophilous plant richness, we requested the authors of a recent spatial modeling study (Ureta *et al.* 2021) to provide the localities of the plant species that are most common in the bat diet (according to our search), which corresponded to the genera *Agave*, *Pseudobombax,* and *Ceiba*. These localities represented the most complete and homogeneous source of plant presence information that could be obtained in relation to the bat species studied. The localities represented 17.8 % of the species of the genus *Agave* recorded in this study (5 species), 50 % of the species of the genus *Pseudobombax* (1 species), and 20 % of the species of the genus *Ceiba* (1 species). To obtain the areas of highest richness where these three genera of plants are found, localities were classified by sector in the Mexican territory using a grid created with ESRI ArcGIS © version 10 (Redlands, CA 1999–2010). In this sector classification, all species of a given genus were included on the same map. The resulting maps of each plant genus were combined; then, this richness map was overlapped with the plant diet localities. Since this analysis was conducted for México, plants with reported diet localities outside of the country were excluded.

The areas with the highest bat richness were determined using the distribution maps elaborated by the International Union for the Conservation of Nature (www.uicnredlist.org). The maps of the twelve bat species were combined to identify the areas with a higher richness of nectar-feeding bats. This map was overlapped on diet localities. All spatial analyses were conducted using ESRI ArcGIS © version 10 (Redlands, CA 1999–2010). Last, the biogeographical provinces of México (Morrone *et al.* 2017) were used to link and delimit the spatial distribution of diet localities and the results of both geographic overlays according to regions.

Results

The diet of nectar-feeding bats in México and the rest of their geographic range. A total of 443 plant diet records were obtained from nectar-feeding bats throughout their geographic range, corresponding to 298 plant genera (Tropicos.org. Missouri Botanical Garden; Supplement 2). Trends in records outside and within México differed between species (Figure 1), but, on average, there were a higher number of records within the country (33.1) than outside of it (8.3).

Choeroniscus godmani, Leptonycteris yerbabuenae, *L. nivalis, Glossophaga leachii*, and *G. mutica* had most of their records in México (83, 97, 90, 95, and 98 %, respectively). *G. commissarisi* had a similar number of records within and outside of México (54.8 % and 45.1 %, respectively), whereas *Anoura geoffroyi* and *Hylonycteris underwoodi* had a higher number of records outside of México (64 % and 63 % respectively).

In México, we found 370 records of plants consumed by nectar-feeding bats, corresponding to 237 genera (Tropicos.org. Missouri Botanical Garden). These plant records were attributed to 11 of the 12 species of nectar-feeding bats in México. A single record of the genus *Lonchocarpus* was obtained for the bat *Lichonycteris obscura*, but its geographic location could not be established; therefore, this bat species was excluded from the analysis. The genera *Agave* and *Pseudobombax* were recorded for the 11 bat species, followed by the genus *Ceiba* for 10 (Figure 2). The completeness of the plant diet inventory for each nectar-feeding bat species ranged from 15 % to 65 % (Figure 3). The effective number of species calculated with Hill's number did not reach an asymptote for any bat species.

Spatial analysis of diet localities. The total number of unique plant diet localities was 160. Of these, 88 % localities

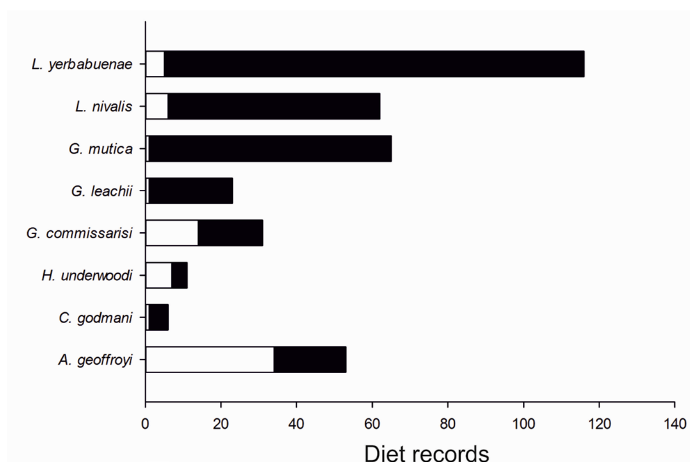

Figure 1. Comparison of the number of plant diet records in Mexico (in black) with the rest of the geographic distribution (in white) for eight nectar-feeding bat species. The rationale for the exclusion of the other study species in this chart is detailed in the Material and Methods section.

Figure 2. Dendrogram based on similarities of plants consumed by nectar-feeding bats of Mexicoand heat map of plant diet records: Matrix cells show the plant-bat pairs (rows and columns corresponding to each bat species and the plant genus with which it interacts) for which an increase (red) or decrease (blue) occurs in the number of interactions. Plant genera are ranked according to the family to which they belong. For details of each species by genus and family, refer to Supplement 2.

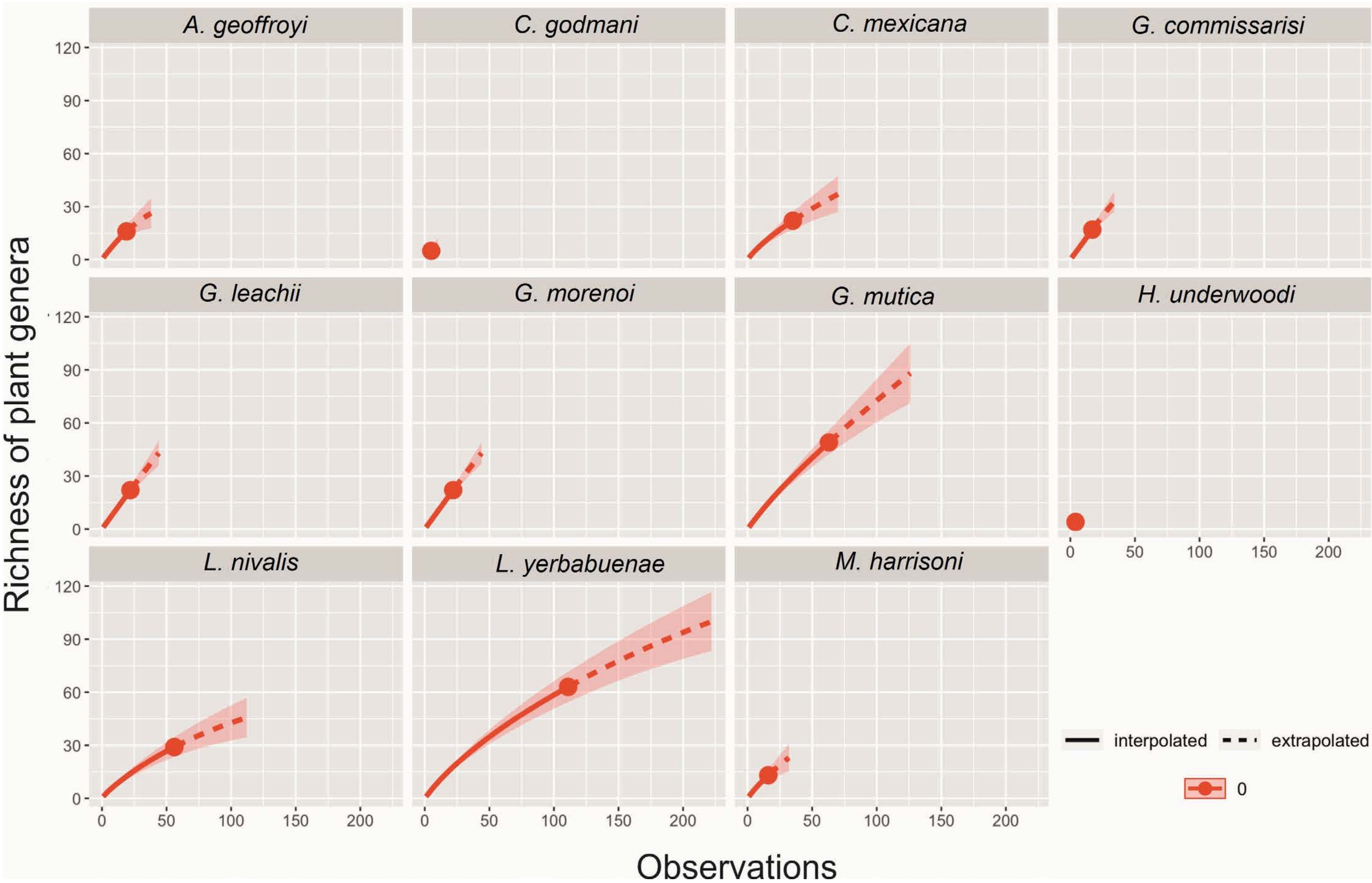

Figure 3. Rarefaction curves for eleven species of nectar-feeding bats in Mexico in relation to the number of plant genera visited. To note, the extrapolation curve does not reach the asymptote for any of the bat species. The rationale for the exclusion of *L. obscura* in this chart is detailed in the Material and Methods section.

were found in the Mexican Transition Zone, which includes the Sierra Madre del Sur, Trans-Mexican Volcanic Belt, Sierra Madre Oriental, and Chiapas Highlands biogeographical provinces, in addition to the Neotropical region, including the Pacific Lowlands, Veracruzan and Balsas Basin provinces (Morrone 2019). In turn, these provinces corresponded to the biogeographical provinces with the highest richness of nectar-feeding bats (Figure 4). The highest richness of consumed plant genera was concentrated in the northern part of the Pacific Lowlands province, the Trans-Mexican Volcanic Belt, and the Balsas Basin. These last two provinces showed the greatest overlap between the richness of plant genera and plant diet localities (Figure 5).

Discussion

The plant diet of nectar-feeding bats in México and the rest of their geographic range. The diet records of *Leptonycteris yerbabuenae*, *L. nivalis*, and *Glossophaga mutica* found are located mainly in Mexican territory, probably because these species are distributed mainly in México (Pfrimmer and Wilkins 1988; Cole and Wilson 2006; Calahorra-Oliart *et al.* 2021). Diet records of *Choeroniscus godmani* and *Glossophaga leachii* were also found mainly in México, although these species are also distributed in Central America and, in the case of *C. godmani*, in northern South America (Arita 2005).

Glossophaga commissarisi had a similar number of records within and outside of México, although the plant genera recorded for both areas were different. In México, the records correspond to the genera *Agave*, *Ceiba*, and *Cordia*; in the rest of its geographic distribution, records correspond to *Piper*, *Markea*, or *Mucuna*.

Anoura geoffroyi and *Hylonycteris underwoodi* have more records outside of México, and the recorded plant genera are different within and outside the country. For *A. geoffroyi*, the plant genera recorded most frequently in México were *Agave*, *Ceiba*, and *Ipomea*, while *Burmeistera* was the most recorded genus in the rest of the geographic range of this bat species. Separately, *H. underwoodi* has records of *Conostegia*, *Pseudalcantarea,* or *Spondias* in México, and of *Marcgravia*, *Markea,* or *Mucuna* in the rest of its distribution. The difference in the plant genera consumed by *A. geoffroyi, G. commissarisi*, and *H. underwoodi* within and outside of México may be due to the change of species in their plant diet throughout their geographic distribution. This pattern has also been observed in fruit bat genera distributed throughout the American continent (Saldaña-Vázquez *et al.* 2013).

Our results showed that the diet of *L. obscura* is poorly known across its distribution range, so further studies are needed to broaden the knowledge of this species. The analysis of plant diet is incomplete for all the species stud-

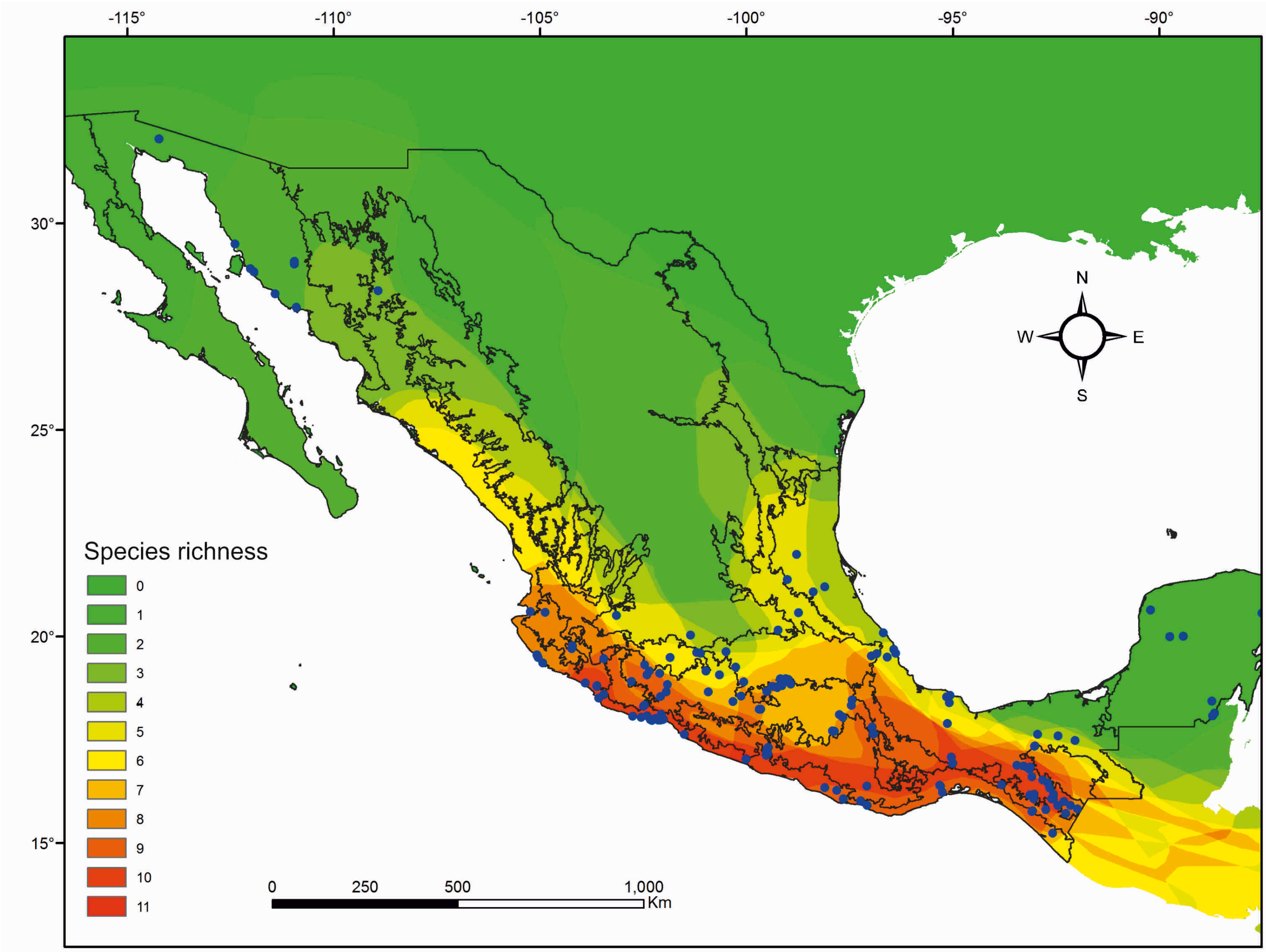

Figure 4. Map of unique plant diet localities (blue dots) in relation to the biogeographical provinces of Mexico (for further details of the provinces, refer to Morrone 2019), and the species richness of nectar-feeding bats in Mexico, shown in a decreasing (green) or increasing (red) gradient. Modified from Ortega Garcia 2018.

ied, but this study shows that there has been a greater effort to determine the plant diet of *Leptonycteris*, *Glossophaga*, and *Choeroniscus* in México than in any other country within their distribution area. In the case of *A. geoffroyi* and *H. underwoodi*, there is a need to increase the knowledge of these species in México relative to the rest of their geographic distribution.

Fleming *et al.* (2009) studied the evolution of bat pollination, including a list of 360 species of angiosperms visited by nectar-feeding bats of the family Phyllostomidae. The present study recorded 64.7 % of the plant species listed by Fleming *et al.* (2009). This suggests that the knowledge produced in México to date is significant. However, at the species level, our completeness results show that the dietary information is still limited for most nectar-feeding bats in the country.

The present study of the plant diet of Glossophaginae nectar-feeding bats also found records of fruit consumption (Supplement 2). Of the twelve species studied, only two had frugivory records: *L. yerbabuenae* and *H. underwoodi.* This may be due to various causes, such as the relative low frequency of frugivory in this group of nectar-feeding bats, or that these habits have been poorly studied. The available information shows that fruits are important elements in the diet of *L. yerbabuenae* (Rojas-Martinez *et al.* 2012); however, the contribution of fruits to the diet of the other species is unknown.

The knowledge of the plant diet of nectar-feeding bats summarized in this paper highlights the absence of research on key dietary habits for our ecosystems, especially in northern México.

Spatial analysis of diet localities. This study shows the information gaps in the plant diet of nectar-feeding bats in México. To understand the existence of these information gaps in México at the geographic level, we first tested whether the distribution of diet localities was associated with the presence of chiropterophilous plants, since a close relationship between some bat species and the plants on which they feed has been reported (Aguilar-Rodriguez *et al.* 2019). Our analysis of some species of the most consumed plant genera by these nectar-feeding bats showed a geographic overlap with the Trans-Mexican Volcanic Belt and

Balsas Basin provinces, but not with other high-richness areas such as the northern part of the Pacific Lowlands province.

The genus *Agave* is associated mainly with the Nearctic zone of México and the Valley of Tehuacán-Cuicatlán (Garcia Mendoza 2007; Morrone 2019), but most of the diet localities were found in the Neotropical region, where the Tehuacán-Cuicatlán Biosphere Reserve is also located. However, the number of unique localities in the Reserve is lower than in to other areas of the Neotropical region, as shown on the map (Figure 5).

This study did not find a geographic overlap in all sites with a high richness of these plant genera, and this finding may be because the association between bats and the plants on which they feed is not specialized in all the nectar-feeding bats in México. Plant-bat mutualism has been observed mainly for the bats *L. nivalis, L. yerbabuenae*, and *C. mexicana* (Arizaga *et al.* 2000; Arias-Coyotl *et al.* 2006), so an analysis by bat species may yield results differing from those reported herein. Additionally, the lack of overlap between diet localities and areas of high plant genus richness may be associated with a low research effort in these areas of high genus richness of chiropterophilous plants.

The superposition of the map of nectar-feeding bat richness with diet localities (Figure 4) showed a great degree of geographic overlap between the biogeographical regions with the highest number of diet localities and the areas with the highest richness of nectar-feeding bats, mainly associated with the Neotropical region. The relationship between the species richness of nectar-feeding bats and diet localities may be because the high coexistence of bat species leads to a greater number of plant-bat interactions, reflected in a greater number of plant diet localities reported. An exception to this pattern was observed in two regions of the country. One is located in the Yucatan Peninsula province and the second is in the Nearctic region, associated mainly with the Sonora province. As observed in other studies (refer to Guevara *et al.* 2015; Suárez-Castro *et al.* 2021), there are challenges in obtaining random samples, such as the range of activities of the researcher or the proximity to accessible areas, which bias the data distribution. Alternatively, the larger number of diet localities in sites with a high richness of nectar-feeding

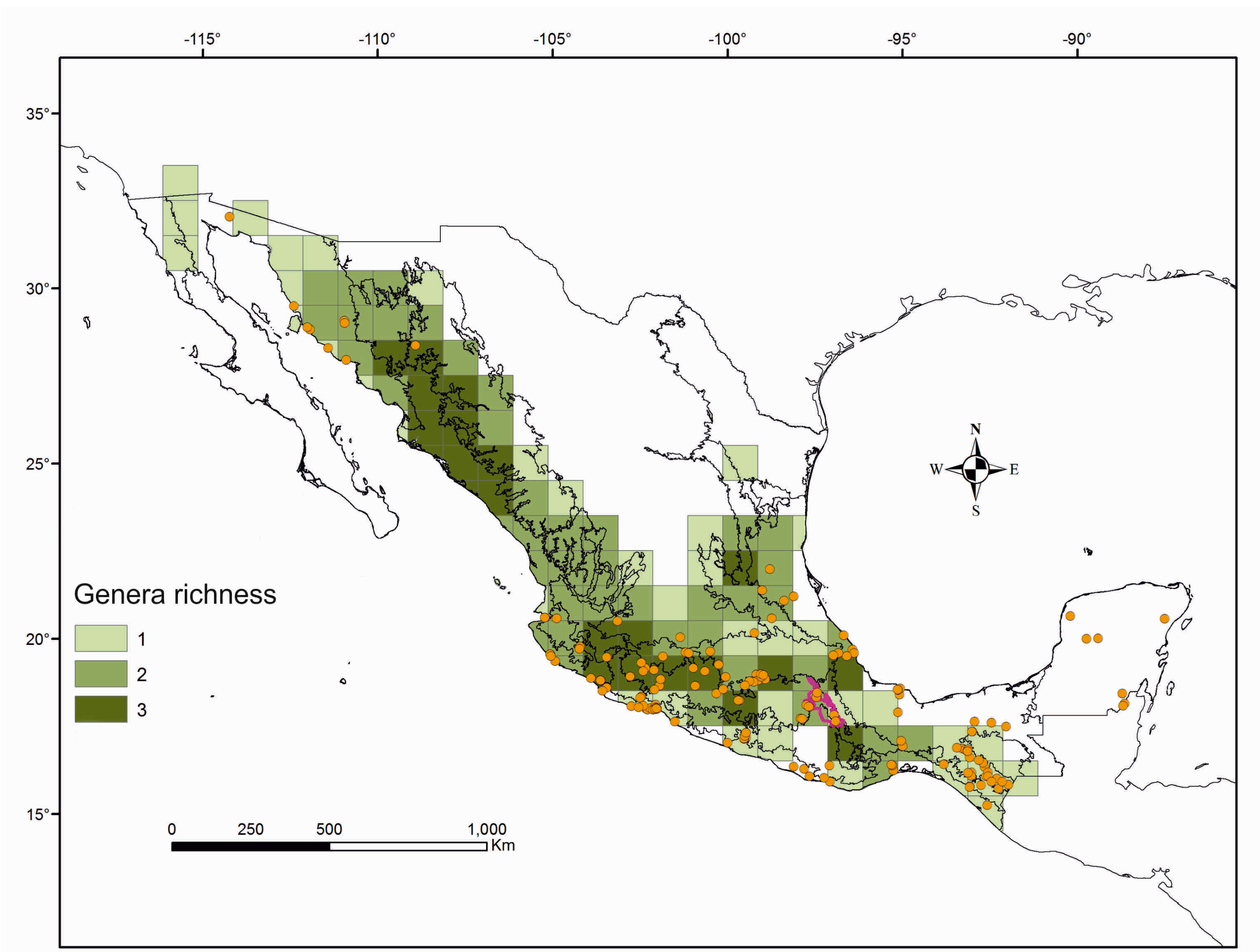

Figure 5. Map of unique plant diet localities (orange dots) in relation to the biogeographical provinces of Mexico (for further details of the provinces, refer to Morrone 2019), and the species richness of the genera *Agave*, *Ceiba,* and *Pseudobombax* in Mexico, shown in a decreasing (light green) or increasing (dark green) gradient. The Tehuacán-Cuicatlán Biosphere Reserve is marked in pink.

bats may be associated with the preference (or need) of many researchers to work in areas of high biodiversity. Therefore, the bias in the present knowledge of bat diet in these two areas is likely related to logistical rather than biotic variables.

In conclusion, the spatial analysis of the geographic distribution of plant diet localities showed that in the Trans-Mexicana Volcanic Belt and Balsas Basin, variables such as richness of plant genera consumed by bats and richness of nectar-feeding bats are importantly related to this plant-bat interaction, while in the rest of the territory, the presence of these localities is more closely related to the richness of nectar-feeding bats. However, the distribution of plant diet localities is also likely biased by logistical factors and a low research effort.

This study showed that the current knowledge of the diet of Glossophaginae nectar-feeding bats in México is far from complete, particularly for *L. obscura*, *H. underwoodi*, and *C. godmani*. We know that there is a decreasing trend in the occurrence and diversity of pollinators in northeastern Europe and North America, along with a lack of information on wild pollinators in several regions of the world, including Latin America (IPBES 2016). Pollinator decline has been linked to factors such as intensive agriculture, land-use change, and climate change, among others. For instance, Zamora- Gutierrez *et al.* (2021) used different future scenarios to analyze how co-occurrence patterns between pollinating bats and the plants pollinated could be disrupted due to the last two factors. These authors found that, in general, the number of plant-bat interactions may decrease between 34.1 % and 47.1 %, on average, under the pessimistic scenario for México.

The loss of pollinators has short- and long-term consequences (Ashworth *et al.* 2009). In the short term, there is a decrease in the food supply; in the long term, there are cascading effects related to the decline of plant diversity, air and water purification, nutrient cycling, and disease control, among others (Ashworth *et al.* 2009). If we are to preserve the permanence of bats, the plants they visit, and the ecosystem services they provide, advancing their study will guide us toward more effective conservation strategies.

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