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Source: Acta Chiropterologica, 23(2) : 395-404

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/15081109ACC2021.23.2.009

Acta Chiropterologica, 23(2): 395–404, 2021
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2021.23.2.009

Diet composition of bats in a human-modified tropical landscape

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Human-modified landscapes are often composed of small and isolated natural habitat fragments immersed in agricultural and urban matrices. Within them, ecosystem services provided by wildlife, such as pest insect suppression, may decrease or even be lost leading to a substantial increase in agricultural production costs. Pest insect suppression by bats has been identified as an essential ecosystem service but remains poorly investigated. For example, we still lack a basic understanding of the proportion of pest insects that comprises the diet of many bat species. Here, we explored the diet composition of eight Brazilian bat species (78 individuals) in a human-modified landscape through the analysis of stable carbon (^{13}C) and nitrogen (^{15}N) isotopes. Bats were categorised into guilds: open-space aerial insectivores, narrow-space gleaning frugivores, or narrow-space gleaning nectarivores. We divided the insects collected into three groups depending on their $\delta^{13}C$ values: forest, mixed, and pest insects. We found that open-space insectivorous bats had the highest proportion of insects in total in their diet — consuming primarily from the forest group (56%) and the pest group (34%). Interestingly, narrow-space gleaning frugivores also consumed pest insects (almost 20%). The narrow-space gleaning nectarivores had traces of insects in their diet, yet the actual proportion was inconclusive. Even though bats were from different guilds, with diets consisting mainly of plants and insects, the $\delta^{15}N$ indicated that they fitted to similar trophic levels, as secondary consumers. Therefore, the trophic level of nectarivorous and frugivorous bats showed a more generalist diet than previously assumed. The proportion of forest insects in the diet of open-space aerial insectivores may indicate the importance of small forest patches as food resources for wildlife such as the ones included in human-modified landscapes. The bats' contribution to this ecosystem service could improve the economic conservation value of Neotropical bats in human-modified landscapes.

Key words: Chiroptera, crops, stable isotopes, ecosystem services, insects, carbon-13, nitrogen-15

Introduction

The expansion of agricultural areas and the increase of urbanisation is widely recognised as one of the most significant modifications humans have made to natural landscapes (Koh *et al*., 2004; Henriques *et al*., 2020; O'Connor *et al*., 2020), resulting in a variety of changes in the composition (Regolin *et al*., 2020*b*) and distribution of wildlife (Ditchkoff *et al*., 2006; Niebuhr *et al*., 2015). While some species have declined in human-modified landscapes (Bogoni *et al*., 2020), others have persisted (Tabarelli *et al*., 2010; Millan *et al*., 2015; Bovo *et al*., 2018) and may even thrive (Ditchkoff *et al*., 2006).

Human-modified landscapes (HMLs) are characterised by a combination of small and isolated forest fragments, embedded within agricultural and urban areas (Melo *et al*., 2013). Although HMLs can differ greatly from natural landscapes, they still maintain ecosystem services to regulate natural processes. Ecosystem services are defined by the benefits acquired by humans from the ecosystems (Millennium Ecosystem Assessment, 2005). For example, in urban areas trees can reduce air and noise pollution (De Carvalho and Szlafsztein, 2019); in

agricultural areas, bees can be responsible for up to 30% of the pollination of crops (Kremen, 2005), and insectivorous animals can mitigate the damage in crops by consuming arthropod pests (Kunz *et al*., 2011). Therefore, understanding the connection between land use, biodiversity, and ecological interactions in HMLs is essential because collectively, those processes benefit human well-being and the economy (Millennium Ecosystem Assessment, 2005).

Bats, in particular, play an important role in pest insect suppression (Kunz *et al*., 2011; Ghanem and Voigt, 2012), as they are often able to persist in HMLs (Bernard and Fenton, 2003; Voigt and Kingston, 2016; Regolin *et al*., 2020*a*), saving billions of dollars per year to the agricultural business that would otherwise be spent in massive amounts of pesticides (Boyles *et al*., 2011) that negatively affect wildlife (Köhler and Triebskorn, 2013). For example, bats reduce the use of pesticides in cotton production (Federico *et al*., 2008), saving farmers up to $173 per acre (Cleveland *et al*., 2006). Brazil, one of the most important food producers worldwide (BRASIL, 2015), loses approximately 25 million tonnes of food and other products, and $17.7 billion per year due to damages caused by insect pests (Oliveira *et al*., 2014). Neotropical bats have a high potential for reducing these losses as Brazil has 182 species registered so far including ranging all types of diets (e.g., carnivores, insectivores, sanguinivores, nectarivores, and frugivores — Nogueira *et al*., 2014). However, little is known about the phenology and proportion of insects in the diet of Brazilian bats. Even though the subject was a topic for systematic reviews over the past years (Boyles *et al*., 2011; Kunz *et al*., 2011; Ghanem and Voigt, 2012; Kasso and Balakrishnan, 2013; Riccucci and Lanza, 2018), the estimates on the magnitude of pest insect suppression by bats are still poor. Our study aimed at contributing to a better understanding of bat pest insect suppression in HMLs in Brazil.

To quantify the pest insect suppression services provided by bats, researchers have relied almost exclusively on morphological analysis of faecal samples (Burles *et al*., 2008), and in experiments in which the damage to the crop was compared in areas with and without bats; such experiments have been used in both natural (Kalka *et al*., 2008) and agricultural environments (Williams-Guillen *et al*., 2008). Unfortunately, the morphological analysis does not provide an accurate assessment of the bats' consumed insects' origins. However, in order to evaluate the importance of bats as pest suppressors, it is vital to determine if the insects were consumed in fact in agricultural areas and thus considered to be pests. Moreover, bats masticate their food and often do not swallow the hard parts, which are used to identify the insects, making it difficult to distinguish even the order of the insects consumed without genetic markers (Zeale *et al*., 2011; Cohen *et al*., 2020; Whitby *et al*., 2020).

Alternatively, stable isotope analysis from animal tissues is a reliable method for distinguishing an individual's foraging environment and trophic level (Fry, 2006). When analysing stable carbon isotopes ($\delta^{13}C$) of an insect's tissue, it is possible to determine the photosynthetic cycles of the plants they consumed (Layman *et al*., 2012). $\delta^{13}C$ is directly linked to the three primary photosynthetic pathways of plants: C_3 (e.g., most plants), CAM (e.g., succulents), and C_4 (e.g., grasses). Hence, a bat that consumed primarily insects that forage in agricultural areas (i.e., insects that feed on C_4 plants, hereafter referred to as 'pest insects'), would have tissues with higher $\delta^{13}C$ values compared to a bat that consumed primarily insects that forage in forests (i.e., insects that feed on C_3 plants, hereafter referred as 'forest insects') (DeNiro and Epstein, 1978). $\delta^{15}N$ in an individual's tissue also allows inferring the animal's trophic level (Kelly, 2016). $\delta^{15}N$ in consumer tissues is a way to trace the protein derived from the diet, thus it varies largely with the animal's trophic position (Vanderklift and Ponsard, 2003; Caut *et al*., 2008; Rex *et al*., 2010; Siemers *et al*., 2011) and to a lesser extent with the $\delta^{15}N$ values of local ecosystems (Hartman and Danin, 2009). N is mainly present in lipids and carbohydrates. Nitrogen accumulates at each level of the trophic chain, hence plants have tissues depleted in $\delta^{15}N$, and predators have tissues enriched in $\delta^{15}N$ (DeNiro and Epstein, 1981).

In the present study, we traced the foraging area (agricultural crop or forest) of insects consumed by different bat trophic guilds in a HML to better understand their role in pest insect suppression. We hypothesised that open-space insectivores are most likely to feed on pest insects because the crops usually have extensive open areas suitable for their wing morphology (adapted for fast flight and hunting in open areas). If they feed on pest insects, we would expect them to have tissues with higher values of $\delta^{13}C$. Additionally, we analysed the diet of narrow-space nectarivores and frugivores, which are guilds not primarily insect-eaters but are known to complement their diet with them (Oelbaum *et al*., 2019).

Materials and Methods

Data Collection and Species Identification

The present study was carried out in the campus of Escola Superior de Agricultura 'Luiz de Queiroz' (ESALQ), a peri-urban area in Piracicaba, state of São Paulo, south-eastern Brazil (22º42'30"S, 47º38'30"W). The campus is located in the Atlantic Forest biome, limited by the Cerrado biome (IBGE, 2004), with semideciduous forest fragments. Overall, it covers 914.5 ha of human-modified landscape and is composed of small patches of secondary semideciduous forest (the largest with 14 ha), pastures, crops (including corn and sugar cane), silviculture, and urban areas (Demétrio *et al*., 2000).

We captured bats for one or two days every two months from December 2013 to June 2015 at seven locations listed in Bovo *et al*. (2018, Fig. 1), repeating samples at locations with more evidence of bat activity. We opened three to six mist nets (10 × 3 m and 12 × 3 m, 2.5 mm mesh size — Ecotone Inc., Poland) each night at sunset (ca. 17:00) for six hours. The nets were placed around the urban area, near buildings where we found recent bat faeces, along the edge of forest fragments, and across trails within forest fragments.

All bats captured were identified to the finest possible taxonomic level (based on the keys by Vizzoto and Taddei, 1973; Gregorin and Taddei, 2002; Gardner, 2007). We took body measurements (forearm length and weight) and determined their sex, age class (based on the degree of ossification of their phalangeal epiphyses, following Kunz and Anthony, 1982), and reproductive status. Then, bats were classified into guilds, considering their predominant food source (fruits, nectar, or insects), foraging space (narrow or open), and foraging mode (aerial or gleaning, following (Denzinger and Schnitzler, 2013)). We followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes *et al.*, 2011), and received sampling permits from the Chico Mendes Institute for Biodiversity Conservation (SISBIO proc. no. 41352-1) and the Ethics Committee for Animal Experimentation of the Centre for Nuclear Energy in Agriculture (CENA) (protocol no. 2013-18). Specimens were identified by specialists (Dr Pamella Brennand and Dr Ayesha Ribeiro Pedrozo).

We collected potential insects prey items in pastures, cornfields, native forests, and silvicultural sampling sites using light traps: an electric lamp (yellow and UV light) placed 30 cm away from the centre of white cloth (3 × 2 m), suspended by ropes and with a folded bottom. The light trap used in the study was adequate to collect more than 30 insect families through all the sites, however, it is still possible that insects from neighbouring land use types were caught in the same trap. We were unable to capture bats in the same sites we sampled the insects, especially because in open areas (i.e., pastures and cornfields) they fly above the mist nets. The insects were identified to the family level and the families were classified by economic importance based on the literature, and we considered pests to be those that feed on or damage C_4 plants (Gallo *et al*., 2002).

To establish an isotopic baseline (Post, 2002), we collected leaves from the places where the insects were captured and also fruits usually consumed by bats (Bredt *et al*., 2012), such as *Ficus guaranitica*, *Solanum* sp., *Cecropia* sp., *Piper amalago*, *Piper* sp., as well as *Pandanus utilis*, which we have observed to be frequently consumed by nectarivores (Kruszynski *et al*., 2016). Plants were identified by comparison with vouchers deposited in the Herbarium of ESALQ.

Sample Preparation and Stable Isotope Analysis

In total, we had 78 bat fur samples, collected from the anterior dorsal region of the right scapula (about 5 mg). Hair is an inert tissue, therefore once they are formed, they carry the same isotopic composition until the next moulting event occurs (Voigt *et al*., 2016). Currently, there is no reported pattern for Neotropical bat moult, however, we have considered it to be once a year following the temperate bat pattern (Fraser *et al*., 2013).

We collected 111 insects, five leaves, and two fruits from the plants mentioned above. They were all stored in plastic tubes. We carried out all sample preparation and analysis in the Isotope Ecology Laboratory at CENA, Piracicaba, Brazil. The samples of bats, insects, and plants were washed with distilled water to remove dirt and then dried for 48 h in an oven at 60ºC. Lipids and oils of samples were not removed. Insects and leaves were ground in liquid nitrogen until pulverisation.

We weighed animal samples from 0.8 to 1.2 mg and plant samples from 2.5 to 2.8 mg in tin capsules (5 × 9 mm) with a precision scale (Sartorius Genius ME, 0.01 mg, Göttingen, Germany). Afterward, samples were processed by online combustion in an elemental analyser Carlo Erba (CHN-1110) coupled to a mass spectrometer (Finnigan Delta Plus, Germany), based on the Continuous Flow — Isotope Ratio Mass Spectrometers (CF-IRMS) methodology. Stable isotope ratios were calculated for each bat, insect, and plant sample; values are reported in standard delta notation. The standard reference materials were Vienna PeeDee Belemnite (VPDB) for C and atmospheric N_2 for N. Local sugarcane standards were inserted every 10 samples to calibrate the system and to allow posterior corrections for any drift over time. The internal standards for sugarcane leaves used were %N = 0.88% and $\delta^{15}N$ = 5.4‰. The acceptable analytical errors were 0.3 and 0.1%, for C and N concentrations, and 0.5 and 0.3‰, for isotopic values of $\delta^{13}C$ and $\delta^{15}N$, respectively.

Data Analysis

To test whether the isotopic composition varied between insects collected in the agricultural crop and the forest, we fitted a bivariate normal model. The model included the type of land use as an explanatory variable and insects' $\delta^{13}C$ and $\delta^{15}N$ values as the bivariate response variable. We estimated the model within the maximum likelihood framework, and goodness-of-fit was assessed using bivariate residual plots according to the method described in Moral *et al*. (2019). We used likelihood-ratio (LR) tests for nested models to assess the significance of the explanatory variable. These results allowed us to determine if it was possible to accurately infer the insects' foraging area, given their isotopic values.

We fitted linear mixed models to test the differences in isotopic values with $\delta^{13}C$ data for bat fur obtained from different areas, including foraging area (narrow or open) as a fixed effect, and date of collection and species as independent random effects. The significance of the fixed effects was assessed using LR tests for nested models, and goodness-of-fit was assessed using half-normal plots with a simulated envelope (Moral *et al*., 2017).

After the tests of premises described above, we were able to determine the isotopic composition of the bats' diets and from which type of land use their food sources (i.e., their prey) originated. To do that, we used a Bayesian Mixing model to fit $\delta^{13}C$ and $\delta^{15}N$ data of fur samples of each bat, with the package

MixSIAR GUI 3.1 (Stock and Semmens, 2016) in R software version 3.6 (R Core Team, 2020). We used different food sources (i.e., insects from different foraging areas) as a predictor variable and species as random effects. The analysis was done for each guild separately; specifically for frugivorous and nectarivorous bats, we also included fruits as a food source (Supplementary Table S1). Given that isotopic ratios of the sources are not transmitted directly to the bats' tissues, there is a systematic difference between the isotopic composition of their tissues and sources, i.e., the trophic discrimination factor. Their values were extracted from the literature and they varied according to the bats' guild (open-space aerial insectivores: Δ^{13}C 5.9‰, Δ^{15}N 3.4‰ (Roswag *et al*., 2015); narrow-space gleaning nectarivores: Δ^{13}C 1.56‰, Δ^{15}N 3.75‰ (Kruszynski *et al*., 2016); narrow-space gleaning frugivores: Δ^{13}C 1.0‰, Δ^{15}N 3.0‰ (Arneson and MacAvoy, 2005)). To estimate the response values, we used three Markov chains with 350,000 iterations each with the first 150,000 discarded as burn-in, and the convergence of chains was verified using the Gelman-Rubin, Heidelberger-Welch, and Geweke diagnostic tests (Heidelberger and Welch, 1983; Geweke, 1992; Gelman *et al*., 2013). All data files and R scripts are made available in the public repository (https://github.com/ rafamoral/batdiet).

Results

Isotopic Profile for Food Sources

Fruit and *Eucalyptus* leaves had significantly lower δ^{13}C and higher δ^{15}N values in relation to agricultural areas (corn plantation and grass leaves from pastures) (Supplementary Table S1 and Fig. 1), which enabled us to establish different baselines and distinguish where the collected insects foraged and consumed their food.

The insect assemblage was composed of 11 orders and 31 families, with 19 of them considered agriculture and health pests (Supplementary Table S2). From all the collected sites, only insects sampled in pastures were isotopically distinct from those of other areas (LR = 22.45, *d.f.* = 6, *P* = 0.001). In order to include the sources in the isotopic composition analysis of bats' diet, insects were required to be

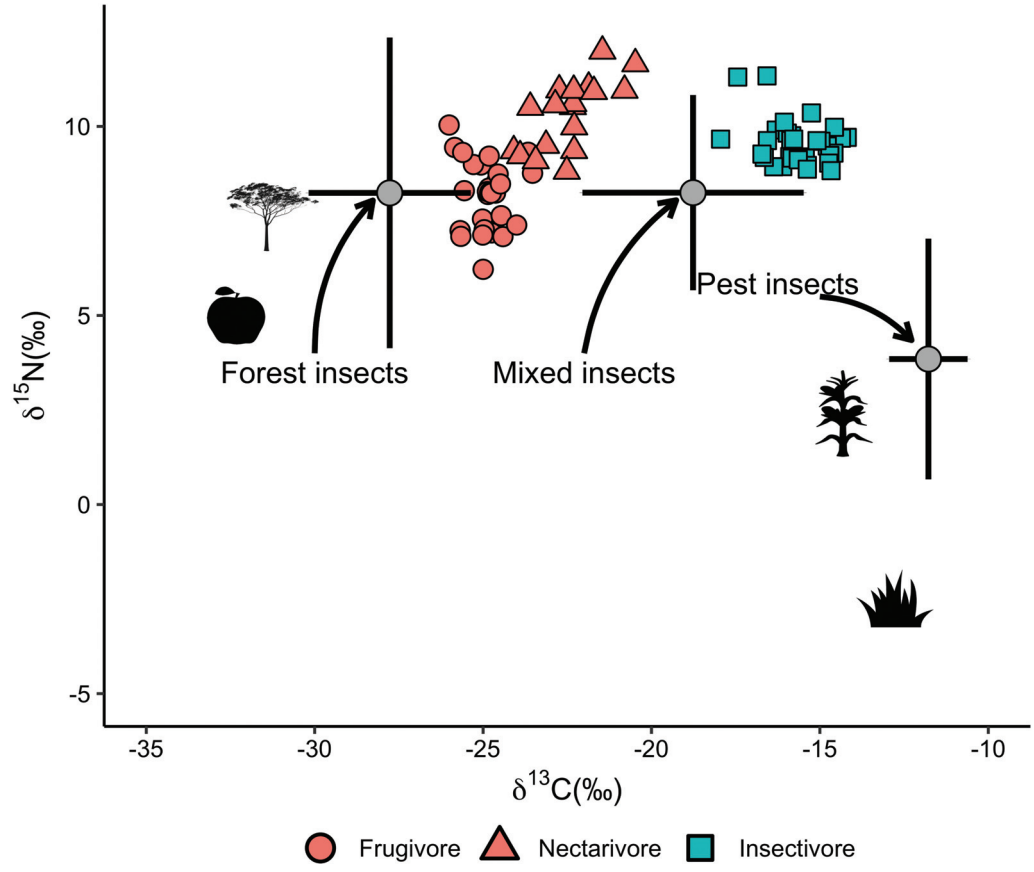

Fig. 1. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic values of bats' fur (points represent single specimens), insect groups (crosses, $\bar{x} \pm SD$) as potential food sources, and isotopic baseline (symbols, pasture, cornfield, fruits, and silviculture). Bats were classified into open-space foragers (blue) and narrow-space foragers area (red) and according to their dietary preference (indicated by different shapes). Bats were collected on the campus of Escola Superior de Agricultura 'Luiz de Queiroz' (ESALQ), southeastern Brazil. All values were corrected for the baseline [i.e., the plants in this study — *Eucalyptus* sp. (represented by tree), *Ficus guaranitica*, *Solanum* sp., *Cecropia* sp., *Piper amalago*, *Piper* sp., *Pandanus utilis* (represented by apple), corn (represented by corn), and pasture (represented by grass)]

aggregated to fit the models. Therefore, we aggregated into three artificial groups, according to the range of their $\delta^{13}C$ values: 'pest' (means: $\delta^{13}C = -11.7 \pm 1.1‰$; $\delta^{15}N = 3.8 \pm 3.1‰$; $\delta^{13}C$ range from -13.9‰ to -10.01‰), 'forest' ($\delta^{13}C = -27.7 \pm 2.4‰$; $\delta^{15}N = 8.2 \pm 4.1‰$; $\delta^{13}C$ range from -34.48‰ to -24.14‰) and 'mixed' ($\delta^{13}C = -18.7 \pm 3.2‰$; $\delta^{15}N = 8.25 \pm 2.5‰$; $\delta^{13}C$ range from -23.71‰ to -14.08‰).

Isotopic Profile for Bat Guilds

We captured 78 bats of eight species separated into three guilds: open-space aerial insectivores (*Molossops temminckii*, *M. molossus*, and *M. rufus*), narrow-space gleaning frugivores (*Artibeus lituratus*, *A. planirostris*, *Platyrrhinus lineatus*, and *Sturnira lilium*), and nectarivores (*Glossophaga soricina*) (Supplementary Table S3). The isotopic distribution of bats' fur showed that they fed on different proportions of C_4- and C_3-items and had little trophic variance between the guilds (Fig. 1). Nectarivores had the highest $\delta^{15}N$ values ($\delta^{15}N = 10.05 \pm 0.92‰$), followed by insectivores ($\delta^{15}N = 9.52‰ \pm 0.6$) and frugivores ($\delta^{15}N = 8.42 \pm 0.94‰$). We observed a significant difference between open and narrow-space bats (LR = 21.15, *d.f.* = 1, $P < 0.01$ — Fig. 2). Open-space aerial insectivores had the primary choice for insects of the forest group (56%), followed by insects of the pest group (34%) (Fig. 3). The narrow-space gleaning frugivores consumed more fruits, as expected, but almost 20% of their diet was composed of pest insects. Given the sample size, it was not possible to determine the diet of narrow-space gleaning nectarivores.

Discussion

The consumption of pest insects by wildlife is essential to reduce the use of pesticides and critical diseases that affect agricultural fields. The over-use of pesticides is still a major problem (Peng *et al*., 2008; Pimentel, 2009; Köhler and Triebskorn, 2013; Normile, 2013), and bats could reduce or even prevent its use where there is a concern for environmental and human health (Ghanem and Voigt, 2012; López-Hoffman *et al*., 2014; Maine and Boyles, 2015*a*; Puig-Montserrat *et al*., 2015; Russo *et al*., 2018). For example, when bats feed on pest lepidopterans, they may suppress larval insects and, consequently, pathogens and mycotoxins (Gallo *et al*., 2002; Maine and Boyles, 2015*b*), and even avoid infestations in crops (Maine and Boyles, 2015*a*; Puig-Montserrat *et al*., 2015; Kemp *et al*., 2019). One female corn earworm moth can lay as many as 500 eggs potentially producing 10,000 crop-damaging caterpillars and one bat can eat 20

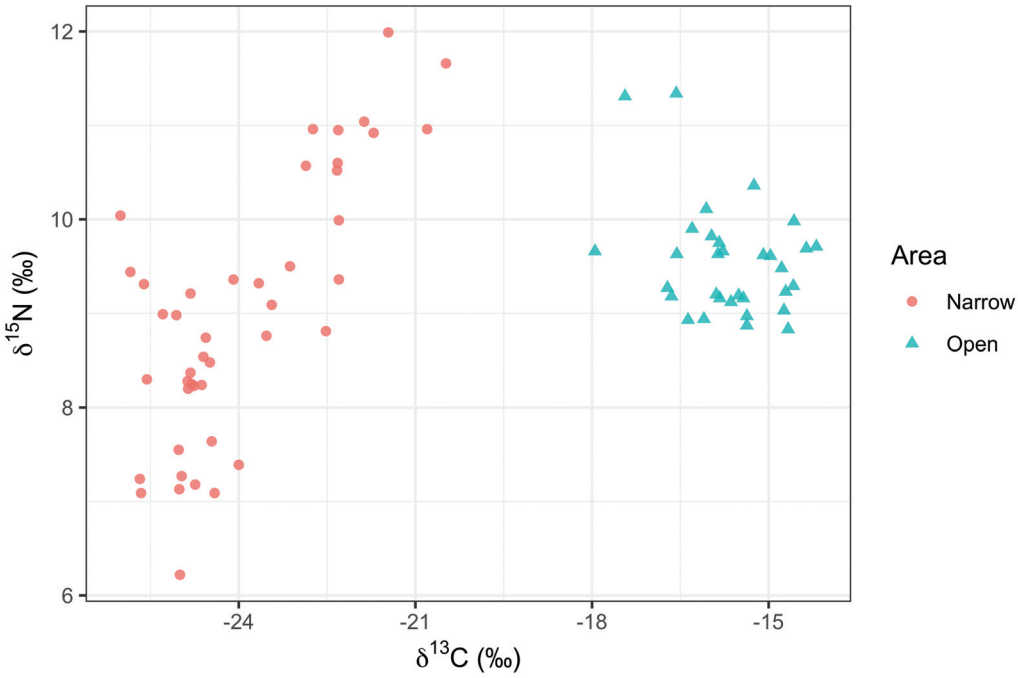

Fig. 2. Raw isotopic values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) measured in fur of open and narrow-space bats captured in the campus of ESALQ. Open-space insectivores fed in an environment more enriched in ^{13}C than the narrow-space bats. The nitrogen values of all species did not differ significantly

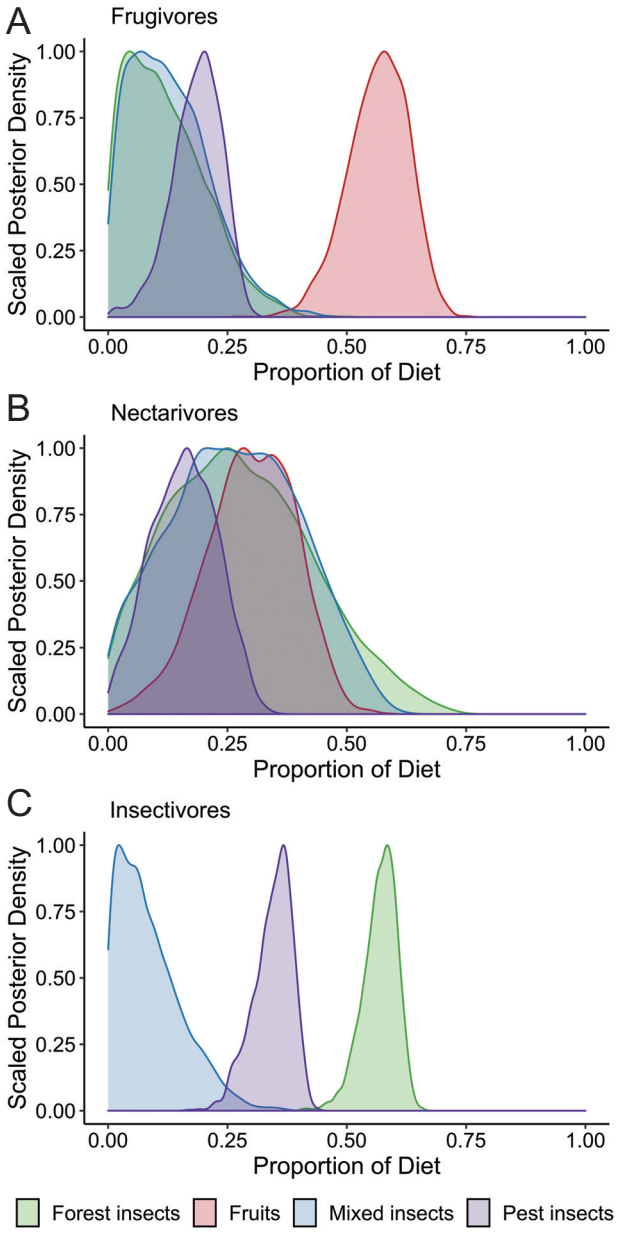

FIG. 3. Probability distributions for the proportion of each insect group (forest insects, mixed insects, and pest insects) in the diet of (A) narrow-space frugivores, (B) narrow-space nectarivores, and (C) open-space insectivores. We also included fruits as a source of diet for frugivores and nectarivores bats. The models applied stable isotope values of bat fur

adult moths in a single night (Fenton *et al.*, 1999). Consistent with our hypothesis, open-space aerial insectivores consumed more pest insects than bats of other guilds (narrow-space gleaning frugivores; narrow-space gleaning nectarivores still unknown in the human-modified landscape).

In our study area, open-space aerial insectivores consumed mainly forest insects which would indicate they forage around forest patches. Although creating artificial insect groups comes at a cost in terms of precision, we believe that it was the best solution given the purpose of our study. It is worth noting that silvicultural insects were included in the group forest even though they could also be considered pests. This could result in an underestimation of the pest insect suppression ecosystem service provided by bats therefore our grouping is rather conservative. Another grouping criterion, such as family level, would not be adequate because species from the same family occurred in more than one type of land use. For example, families of moths had $\delta^{13}C$ values indicating the consumption of both C_3 and C_4 plants, that is, they forage in agricultural and forest areas. Therefore, it is possible that the insects of the forest group also contained Eucalyptus pests because we were unable to separate them by their carbon range values. Barros *et al.* (2014) recorded high activity of Molossus bats around edges of silvicultural areas, we suggest that open-space aerial insectivores in our study could be feeding on both Eucalyptus pests and insects near forests. In fact, in HMLs insect abundance is higher in forest edges and hedgerows (Grüebler *et al.*, 2008; Froidevaux *et al.*, 2019), water bodies, and other areas with low human impacts (Wickramasinghe *et al.*, 2003; Treitler *et al.*, 2016; Froidevaux *et al.*, 2017). Thus, aerial insectivores may have difficulties locating suitable foraging areas in HMLs (Batáry *et al.*, 2015), which reinforces the importance of small and isolated forest fragments within them. Nevertheless, we would expect that they continue to forage in open-space environments due to the high metabolic costs of insect swarms search in a habitat where they have to manoeuvre (Voigt and Holderied, 2012). Their wing ratio (long and narrow) adapted for fast flights between patches (Norberg and Rayner, 1987), and their high-intensity echolocation calls (Emrich *et al.*, 2014) are favoured in this habitat as well. However, an accurate estimate of bat's efficacy as pest suppressors requires information on their trophic levels to determine if they are directly consuming pest insects or simply other predatory arthropods (Kravchenko *et al.*, 2019).

Surprisingly, narrow-space frugivores had a significant proportion of their diet that consisted of pest insects. Our finding contradicts previous records that classify them as exclusively dependent on fruits (Willig *et al.*, 1993) and corroborates with a previous study reporting a diet with more varied items (Herrera *et al.*, 2001*b*). Accordingly, frugivores bats not only are important as seed dispersers (Boyles *et al.*, 2011; Regolin *et al.*, 2020*a*) but they can also provide pest insect suppression. As for the narrow-

space nectarivores' diet, our data confirmed their flexibility in areas with fewer resources, such as human-modified landscapes. However, we cannot infer the extent to which insects were consumed by this guild in relation to plant products. Even though it has been previously indicated that the plants, or nectar, are usually routed to oxidative metabolism and could be misrepresented in tissue formation (Martínez del Rio and Wolf, 2005; Podlesak and McWilliams, 2006; Voigt and Speakman, 2007), our conclusions remain highly plausible, since insect consumption by Glossophaginae has already been recorded in other studies (Herrera *et al*., 2001*a*) and not only opportunistically (Clare *et al*., 2014). This feeding behaviour deserves further exploration, as insects could be an alternative food source where nectar flower abundance is low, as is the case in the majority of Brazilian agricultural fields (Benton *et al*., 2003). Additionally, the trophic discrimination factors used were sensible to the models and it could indicate a bias to the analysis (Auerswald *et al*., 2010).

Nectarivores had higher $\delta^{15}N$ values than insectivores and frugivores, which is consistent with the findings of other studies (York and Billings, 2009). Oelbaum *et al*. (2019) found that the trophic guilds of Neotropical bats in Belize had also significant intra- and inter-guild isotopic niches overlap. Therefore, the importance of a high diversity of bats (i.e., from different guilds) in HMLs might be higher than expected, with different guilds providing pest insect suppression even though it is not their main expected ecosystem service.

The insect sampling method we used focused on volant adult life stages of the insects and phototactic species, which could have biased the insects captured to Lepidoptera and Coleoptera. However, the sampling effort was sufficient to represent isotopically all prey items in the area. In addition, the bias towards adult sampling results in only small shifts in the isotopic signal, since fractionation during insect metamorphosis is small compared to the isotopic differences across habitats (Quinby *et al*., 2020). Therefore, we believe our conclusions are still solid. Future studies should include malaise traps and nocturnal sweep netting to comprehensively understand the insect community on the campus.

The estimation of the economic importance of bats in human-modified landscapes is challenging. We still lack basic ecological information regarding foraging behaviour and diet for many species of bats, and how this may extend to pest insect suppression services. Our results suggested that we have underestimated the role Neotropical bats can play in sustainable pest insect suppression, thus increasing the economic value of conserving these animals in human-modified areas. Moreover, the contribution of nectarivorous and frugivorous bats to pest insect suppression is probably underestimated. A concentration ratio-dependent analysis would improve these results and increase their reliability. We should, therefore, focus on exploring the ecosystem services provided by bats by developing and applying conservation efforts for their communities within human-modified areas.

Supplementary Information

Contents: Supplementary Tables: Table S1. Isotopic values measured in plants collected in the campus of Escola Superior de Agricultura 'Luiz de Queiroz' (ESALQ), University of São Paulo, Brazil; Table S2. Isotopic carbon and nitrogen values in insects collected in the campus of ESALQ. Insects are classified with their economic relevance in Pest, Forest Pest, Medical, and Predator. Groups were used to analyze their proportion in the diet of bats; Table S3. Isotopic values of carbon and nitrogen measured in the fur of bats collected in the campus of ESALQ. Supplementary Information is available exclusively on BioOne.

Acknowledgements

We thank National Council for Scientific and Technological Development (CNPq: 146315/2013-8) for the financial support to accomplish this project. M.A.R.M. was funded by the Research Dean of the University of São Paulo (PRP-USP: 18.1.660.41.7), Brazilian Council for Scientific and Technological Development (CNPq: 472372/2013-0 and 302700/2016-1), Minas Gerais Research Foundation (FAPEMIG: APQ-01043-13 and PPM-00324-15), and Alexander von Humboldt Foundation (AvH: 3.4-8151/15037). We thank Shannon E. Currie and Liam D. Bailey for reviewing the manuscript and contributing for its improvement. We also thank the Editor and four anonymous Reviewers for their comments which helped improve the manuscript.

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Received 28 January 2021, accepted 19 September 2021

Associate Editor: M. Corrie Schoeman