

# Community structure of a Neotropical bat fauna as revealed by stable isotope analysis: Not all species fit neatly into predicted guilds

Phillip J. Oelbaum<sup>1</sup>  | M. Brock Fenton<sup>2</sup> | Nancy B. Simmons<sup>3</sup> | Hugh G. Broders<sup>1</sup> 

<sup>1</sup>Department of Biology, University of Waterloo, Waterloo, ON, Canada

<sup>2</sup>Department of Biology, University of Western Ontario, London, ON, Canada

<sup>3</sup>Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York, NY, USA

## Correspondence

Hugh G. Broders, Department of Biology, University of Waterloo, 200 University Ave W, Waterloo, ON N2L 3G1, Canada.  
Email: hugh.broders@uwaterloo.ca

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## Abstract

Neotropical bat communities are among the most diverse mammal communities in the world, and a better understanding of these assemblages may permit inferences about how so many species coexist. While broad trophic guilds (e.g., frugivore, insectivore) of bats are recognized, details of diet and similarities among species remain largely unknown. We used stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) to characterize the community structure of a diverse Neotropical bat fauna from Belize to test predictions of niche theory and the competitive exclusion principle. We predicted that (1) interspecific variation in isotopic overlap would be greater within guilds than between guilds, and (2) no two sympatric populations would have isotopic niches that overlap completely, unless there is variation along some other axis (e.g., temporal, spatial). We additionally tested body size as an explanatory metric of potential overlap and predicted that larger-bodied animals would have greater niche breadths. Results suggest that while guild-level characterizations of communities are at least somewhat informative, there are multiple examples of intra- and inter-guild species pairs with significantly overlapping isotopic niches, suggesting that, counter to predictions, they may compete for resources. Understanding the trophic structure of animal communities is fundamental to conservation and management of endangered species and ecosystems and important for evolutionary studies, and stable isotope analyses can provide key insights as well as informing hypotheses of the diet of species that are not well known.

Abstract in Spanish is available with online material.

## KEYWORDS

bats, Belize, Chiroptera, diet, frugivory, niche breadth, omnivory, trophic structure

## 1 | INTRODUCTION

Hutchinson (1957) defined the ecological niche as a fundamental unit of community structure describing the “role” of a population in a community, conceptualized as an  $n$ -dimensional hyper-volume. Niche theory now has a more quantitative definition, allowing measurement of previously nebulous dimensions (defined as

niche breadth) which can be compared to characterize the role of species within a community (Bearhop, Adams, Waldron, Fuller & MacLeod, 2004; Vandermeer, 1972; Whittaker, Levin & Root, 1973). Theoretical models may predict the potential niche breadth of a species, while the realized niche breadth is the actual niche after accounting for competition and resource availability (e.g., light, food, water, roosting sites). These extrinsic factors can affect how

effectively individuals access resources (Colwell & Futuyma, 1971). When niches overlap, the competitive exclusion principle states that no two species competing for the same resource can coexist indefinitely at constant population sizes. This predicts that one species will inevitably exclude the other if they have sufficient niche overlap (Gause, 1934).

Trophic niche describes the diet of an animal—what it eats over time for both nutrition and necessary vitamins and minerals. Traditional means to characterize trophic niche breadth (e.g., observational studies or fecal analysis) can be ineffective or inappropriate when sampling some cryptic or elusive species whose feeding behavior may not be observable and where fecal collection is not possible. These methods also only offer a snapshot of what an animal ate immediately before capture (Bearhop et al., 2004). In contrast, stable isotope analysis (SIA) permits quantitative characterization of at least some components of the trophic niche of a population over time while avoiding many of the limitations of more traditional means (Bearhop et al., 2004; Layman, Arrington, Montaña & Post, 2007).

Studies using SIA to determine trophic niches infer dietary niche breadth from profiles of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) in animal tissues (Bearhop et al., 2004; Layman et al., 2007). The effectiveness of this method has been supported by experimental studies (DeNiro & Epstein, 1978, 1981). Studies in marine or aquatic systems have used sulfur ( $\delta^{34}\text{S}$ ) or hydrogen ( $\delta^2\text{H}$ ) isotopic ratios to characterize niche dynamics; however, these elements appear less effective as indicators of trophic interactions in terrestrial systems (Dalerum & Angerbjörn, 2005; McCutchan, Lewis, Kendall & McGrath, 2003; Peterson & Fry, 1987). Stable isotope ratios are the product of diet and net fractionation between what is consumed and what is incorporated into tissue (Peterson & Fry, 1987). Diet-tissue fractionation factors are calculated as the amount isotopic ratios change between the environment and tissue and are assumed to be constant though may vary by age, sex, species, body condition, or various other factors (Tieszen & Boutton, 1989).

Values of  $\delta^{13}\text{C}$  differ greatly between photosynthetic pathways ( $\text{C}_3$  or  $\text{C}_4$  plants) and the ultimate source of biological carbon may be identified in the tissues of a consumer using SIA (Peterson & Fry, 1987).  $\text{C}_3$  plants have an expected net fractionation of  $\delta^{13}\text{C}$  of approximately 21‰ from carbon uptake between the atmosphere (−7‰) and biomass (−28‰), while  $\text{C}_4$  plants have much lower fractionation approximately 6‰ (Peterson & Fry, 1987). Other inputs of carbon into natural systems may also be incorporated into tissues, and aquatic or marine sources can be identified through SIA (Broders, Farrow, Hearn, Lawrence & Forbes, 2014; Jones & Grey, 2004; Tyler, 1986; Whiticar, Faber & Schoell, 1986). There is negligible carbon isotope fractionation between consumer levels making  $\delta^{13}\text{C}$  a reliable determinant of the original source of organic carbon in an animal's tissue when the fractionation factor is known (DeNiro & Epstein, 1978). Nitrogen isotopic ratio ( $\delta^{15}\text{N}$ ) reflects rate of nitrogen gas fixation in plants, and  $\delta^{15}\text{N}$  values increase with trophic levels (DeNiro & Epstein, 1981; Peterson & Fry, 1987). Unlike  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  values of consumer tissues are, on average, 3–5‰ higher than their diet

(Peterson & Fry, 1987). This enrichment factor makes  $\delta^{15}\text{N}$  a reliable indicator of the consumer trophic level of populations within communities, such that animals at higher trophic levels will have higher  $\delta^{15}\text{N}$  (Layman et al., 2007). Stable isotope analysis allows researchers to quantify trophic niche breadth more precisely than traditional measures and better define community structure (Brewster et al., 2016; Dammhahn, Rakotondramanana & Goodman, 2015; Herrera, Hobson, Rodríguez & Hernandez, 2003; Layman et al., 2007; Rex, Michener, Kunz & Voigt, 2011).

Bat communities can be very diverse, ranging from tens to well over 100 sympatric species (Findley, 1993). Biologists have used stable isotope analysis to characterize the niche dynamics of some bat populations in different areas (Fleming, Nuñez & da Sternberg, 1993; Herrera, Fleming & Sternberg, 1998; Lam et al., 2013; Mirón, Herrera, Ramirez & Hobson, 2006; Voigt & Kelm, 2006). A significant body of literature links SIA to trophic niche in bats, but details of niche breadth and overlap in many cases remain unclear. Classification of bats into feeding guilds can simplify the situation, but does not reveal how so many species can be sympatric (Losos, 2008; Razgour et al., 2011; Webb, Ackerly, McPeck & Donoghue, 2002). Tropical bat communities are more diverse and complex than their temperate counterparts, reflecting the greater diversity, abundance, and reliability of resources (Brown, 2014; Fenton et al., 2001; Findley, 1993; Fleming, Hooper & Wilson, 1972).

In general, the dietary diversity of bats is well known and our understanding has changed little since Allen's (1939) characterization. We still lack details of what bats actually eat. Traditionally recognized feeding guilds of bats include insectivores, carnivores, piscivores, frugivores, nectarivores, and sanguivores (Allen, 1939; Arata, Vaughn & Thomas, 1967; Gardner, 1977; Humphrey, Bonaccorso & Zinn, 1983). Bats such as *Glossophaga soricina* illustrate the situation. Typically considered a nectarivore, this species regularly eats insects and fruit (Clare et al., 2014; Simberloff & Dayan, 1991). Some broad dietary guilds are inherently flawed no matter what definition is used (e.g., carnivores) because different bats take very different prey. While all carnivorous bats may eat vertebrates, there are varying degrees of carnivory, and diets of some species vary considerably across space and time depending on prey availability (Norberg & Fenton, 1988). A more fine-grained approach to understanding trophic guilds, particularly in diverse bat faunas, is necessary to effectively use guild categorizations as a tool in elucidating community structure (Rex, Czaczkas, Michener, Kunz & Voigt, 2010). We used SIA to look at these idealized bat trophic guilds from a different perspective. Examining a community as an ensemble (*sensu* Fauth, Bernardo, Camara, Resetarits & Van Buskirk, 1996), as bats share both geography and resources, allows us to better holistically characterize species interactions. We predict (a) that interspecific variation in isotopic overlap would be greater within guilds than between guilds and (b) that no two sympatric populations would have isotopic niches that overlap completely, unless there is variation along some other axis (e.g., temporal, spatial). Additionally, we examined body size as a potential explanatory metric of niche partitioning and predicted that

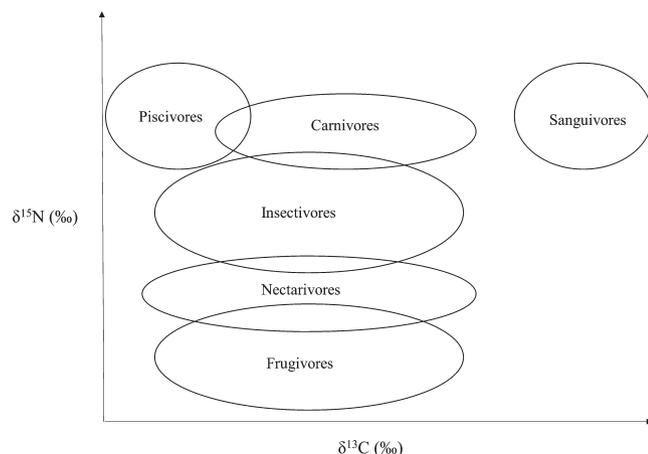
larger species would have larger niche breadths than smaller bodied species.

We examined species in a diverse community of Neotropical bats in Orange Walk District, Belize ( $\approx 40$  species). The bats represent seven families (Phyllostomidae [22 species]; Mormoopidae [4 spp.]; Vespertilionidae [5 spp.]; Emballonuridae [4 spp.]; Molossidae [3 spp.]; Noctilionidae [1 sp.]; and Natalidae [1 sp.]). Arguably, each species falls into one of six traditionally recognized trophic guilds (frugivores [13 spp.]; nectarivores [2 spp.]; insectivores [19 spp.]; carnivores [3 spp.]; piscivores [1 sp.]; and sanguivores [1 sp.]) (Allen, 1939; Fenton et al., 2001; Herrera et al., 1998). We used SIA to characterize community structure of this tropical bat community and make inferences based on predictions of niche theory (Vandermeer, 1972). While there is some information on the food items taken by many species in the community (Baker & Clark, 1987; Baker, Solari & Hoffmann, 2002; Fleming et al., 1972), the diets of many species remain unstudied, and dietary habits of populations in our study area have not been characterized. We assessed the literature on the diet and feeding habits of the sampled bat species and made predictions about expected isotopic niche patterns based on these data (Figure 1).

## 2 | METHODS

### 2.1 | Sample size and tissue selection

We captured bats in Orange Walk District, Belize. We worked in the Lamanai Archaeological Reserve and adjacent secondary forest and gardens near the Lamanai Outpost Lodge (17.75117 N,  $-88.65446$  W) and the Ka'kabish Archaeological Project (17.8147 N,  $-88.73052$  W). We were in the field for two-week periods during late April through early May 2014, 2016, and 2018 at the end of the dry season. The Lamanai locality consists of approximately 450-ha of contiguous semi-deciduous tropical dry forest including



**FIGURE 1** Prediction of positions of dietary guilds in isotope space. Predictions were based on findings of previous SIA studies and experimental studies by DeNiro and Epstein (1978, 1981). Sanguivore prediction is based on published data from the same study area (Becker et al., 2017)

habitats ranging from closed-canopy forest to clearings and secondary growth. Ka'kabish is a 45-ha forest fragment located approximately 10 km from Lamanai.

We caught bats in mist nets, harp traps, and hand nets. We identified each one to species grouped in trophic guilds based on previous dietary studies (Table 1). Guilds are inherently artificial as many of these species (particularly among frugivores and carnivores) are largely omnivorous, and species were placed according to best fit (Allen, 1939; Humphrey et al., 1983; Simberloff & Dayan, 1991). Here, we define carnivores as species which specialized feeding strategies and/or anatomical or physiological adaptations to feed on vertebrates (as opposed to species which may opportunistically feed on vertebrates (e.g., *Phyllostomus discolor* and *Micronycteris microtis*; Norberg & Fenton, 1988; Fenton et al., 1992; Cramer, Willig & Jones, 2001). Therefore, we predict their  $\delta^{15}\text{N}$  to be higher than other animalivores (i.e., obligate insectivores).

We clipped a small ( $\approx 2$  mg) sample of hair from between the scapulae of each individual. For bats with little to no hair on their back (e.g., *Noctilio leporinus* and *Pteronotus fulvus*), the sample was taken from the abdomen. Hair samples were stored dry until analysis. All research was conducted in accordance with accepted standards for humane capture and handling of bats published by the American Society of Mammalogists (Sikes et al., 2016) and approved by the Saint Mary's University Animal Care Committee (Protocol # 14-10), University of Waterloo Animal Care Committee (AUPP: 18-04) and U.S. Institutional Animal Care and Use Committee protocols (American Museum of Natural History AMNHACUC-20180123). All fieldwork was conducted under permits from the Forestry Department of Belize (Permit numbers CD/60/3/14(17), WL/1/1/16(26), and WL/2/1/18(16)).

### 2.2 | Stable isotope analysis

Tissue analysis was performed at the Stable Isotopes in Nature Laboratory (SINLab) at the University of New Brunswick, Fredericton (2014 samples) and at the Environmental Isotope Lab (EIL) at the University of Waterloo (2016 and 2018 samples), following procedures outlined in Segers and Broders (2015). Hair samples were washed three times in a 2:1 (v/v) chloroform:methanol for 10–15 min and then removed from the vial. Once washed, samples were left to air-dry overnight. At SINLab, dry samples were combusted in ThermoQuest CE Instruments NC2500 Element Analyzer (ThermoQuest Italia) and then placed into a ThermoQuest Finnigan-Mat Delta Plus Continuous Flow Mass Spectrometer (ThermoFinnigan). Stable isotope ratio measurements were recorded as  $\delta$ -values in parts per thousand (‰).  $\delta$ -values were anchored in VPBD ( $\delta^{13}\text{C}$ ) and AIR ( $\delta^{15}\text{N}$ ) scales, respectively, using international calibrated standards [International Atomic Energy Agency]. At EIL dry, samples were weighed whole to the nearest 0.001 mg and then combusted in a 4010 Elemental Analyzer (Costech Instruments) attached to a Delta Plus XL (Thermo) continuous flow isotope ratio mass spectrometer (CFIRMS). Standards used include international standards and in-house (corrected to international) standard

**TABLE 1** Number of individuals captured by species and sex from Lamanai and Ka'kabish, Orange Walk, Belize (April–May 2014, 2016, 2018) with description of diet. Primary diet reflects trophic guild while secondary diet includes any other prey material found in fecal or stomach contents analyses or notable feeding behaviors. Colors (descending order) denote guild: orange—frugivores, turquoise—insectivores, maroon—carnivores, purple—nectarivores, blue—piscivores, and red—sanguivores

Species	<i>n</i> (male, female) <sup>a</sup>	Primary diet	Secondary diet	Information source (s)
<i>Artibeus intermedius</i>	11(7, 4)	Fruit	Insects	García-Estrada et al. (2012)
<i>Artibeus jamaicensis</i>	23(11, 11)	Fruit	Insects, nectar	Heithaus et al. (1975)
<i>Artibeus lituratus</i>	27(13, 13)	Fruit	Insects, pollen	Humphrey et al. (1983), Fleming et al. (1972)
<i>Carollia perspicillata</i>	6(4, 1)	Fruit	Insects	Herbst (1986), Mello et al. (2004)
<i>Carollia sowelli</i>	21(10, 10)	Fruit	Insects	Miller et al. (2015a)
<i>Dermanura phaeotis</i>	35(18, 29)	Fruit	Insects	Herrera et al. (2002)
<i>Platyrrhinus helleri</i>	2(0, 2)	Fruit	Insects	Ferrell and Wilson (1991)
<i>Sturnira parvidens</i>	32(16, 16)	Fruit	Insects	Fleming et al. (1972), Mello et al. (2008)
<i>Uroderma convexum</i>	18(8, 10)	Fruit	Insects	Fleming et al. (1972), Herrera et al. (2002)
<i>Bauerus dubiaquercus</i>	7(4, 3)	Insects		Engstrom et al. (1987), Miller and Medina (2008)
<i>Eptesicus furinalis</i>	17(7, 10)	Insects		Aguar and Antonini (2008)
<i>Lasiurus ega</i>	2(0, 2)	Insects		Kutra and Lehr (1995)
<i>Lophostoma evotis</i>	4(4, 0)	Insects		Cajas and Miller (2008)
<i>Gardnerycteris keenani</i>	2(0, 2)	Insects	Plants, vertebrates	Humphrey et al. (1983), Giannini and Kalko (2005)
<i>Micronycteris microtis</i>	3(1, 2)	Insects	Fruit, vertebrates	LaVal and LaVal (1980)
<i>Micronycteris schmidtorum</i>	2(1, 1)	Insects	Fruit	Howell and Burch (1974)
<i>Molossus rufus</i>	19(9, 10)	Insects		Aguirre et al. (2003)
<i>Mormoops megalophylla</i>	3(2, 1)	Insects		Dávalos and Mantilla (2008)
<i>Myotis elegans</i>	24(13, 11)	Insects		Whitaker and Findley (1980)
<i>Natalus mexicanus</i>	3(3, 0)	Insects		Reid (1997)
<i>Pteronotus fulvus</i>	26(13, 13)	Insects		Howell and Burch (1974), Adams (1989)
<i>Pteronotus mesoamericanus</i>	28(14, 14)	Insects		Howell and Burch (1973), Herrera et al. (2001)
<i>Pteronotus personatus</i>	1(0, 1)	Insects		Dávalos (2006)
<i>Rhogeessa anaes</i>	16(6, 10)	Insects		Barclay and Brigham (1991)
<i>Rhynchonycteris naso</i>	15(8, 7)	Insects		Bradbury and Vehrencamp (1976)
<i>Saccopteryx bilineata</i>	22(11, 10)	Insects		Bradbury and Vehrencamp (1976)
<i>Chrotopterus auritus</i>	6(3, 2)	Vertebrates	Insects, fruit, plants	Medellín (1989), Barquez et al. (2015)
<i>Mimon cozumelae</i>	7(4, 3)	Insects	Vertebrates, fruit	Gardner (1977), Whitaker and Findley (1980)
<i>Trachops cirrhosus</i>	10(7, 3)	Insects	Vertebrates, plants	Kalko et al. (1999)
<i>Glossophaga soricina</i>	32(16, 16)	Nectar	Insects, fruit	Fleming et al. (1972), Clare et al. (2014)
<i>Phyllostomus discolor</i>	1(1, 0)	Nectar	Insects, vertebrates, plants	Willig et al. (1993), Kwiecinski (2006)
<i>Noctilio leporinus</i>	6(3, 3)	Fish	Insects	Brooke (1994)
<i>Desmodus rotundus</i>	27(21, 6)	Blood	Insects	Arata et al. (1967)

<sup>a</sup>Individuals for which sex was not identified are included in the total (*n*).

materials. Stable isotope data were then recorded as  $\delta X$  values using the formula:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where  $R_{\text{standard}}$  is equal to the isotopic ratio of VPDB or AIR (Segers & Broders, 2015). We tested a duplicate of seven samples at SINLab and EIT Lab and noted no significant difference between results. Additionally, we tested 10 unwashed hair samples and found no significant difference in isotope ratios between treated and untreated samples (single-factor ANOVAs).

## 2.3 | Statistical analysis

The Stable Isotope Analysis in R (SIAR) package and the Stable Isotope Bayesian Ellipses in R (SIBER) package were used to calculate isotopic metrics for the two stable isotope ratios for each species (Jackson, Inger, Parnell & Bearhop, 2011). R version x64 3.2.3 (R Core Team, 2015) was used for this analysis and package “devtools” (Wickham, Hester, Chang, RStudio & R Core Team, 2016). SIBER Hull Metrics (SHM; Layman et al., 2007) were calculated to test for variation between sample sites and years. These metrics include nitrogen range (dNr), carbon range (dCr), centroid distance (CD), mean

nearest neighbor distance (MNND), and standard deviation of the nearest neighbor distance (SDNND).

To test our prediction that larger animals will have larger niche breadth, average species size (forearm, mass) were calculated from field notes collected in Belize from 2010 to 2017. We used the median Bayesian corrected stable ellipse area (SEA.b) and both average mass (g) and mean forearm length (mm) for each species. We compared body size and median SEA.b both within trophic guilds and among all species using a linear regression model. We repeated this analysis excluding species which were the only representatives of their trophic guilds (*Desmodus rotundus* and *N. leporinus*) and species with sample sizes  $\leq 4$  (e.g., *Lophostoma evotis*). Stable ellipse area corrected for sample size (SEAc) was also tested, however was more relevant for shape and relative position of ellipses (Figure 3) and was less suitable for further analysis than SEA.b (Jackson et al., 2011).

To test overlap of niches, we used the package nicheROVER (Swanson et al., 2015) to calculate niche range ( $N_R$ ). Overlap was calculated as the probability that an individual from Species A would be found within the  $N_R$  of Species B, bootstrapped to  $n = 10,000$ . Only species for which we had  $\geq 3$  samples were included in species-level analysis using SEAc as ellipses cannot be drawn for smaller samples; species with sample size  $\geq 4$  were further analyzed using

SEA.b and  $N_R$  (Jackson et al., 2011; Swanson et al., 2015). Species with smaller sample sizes were included in community-wide isotope metrics (Layman et al., 2007).

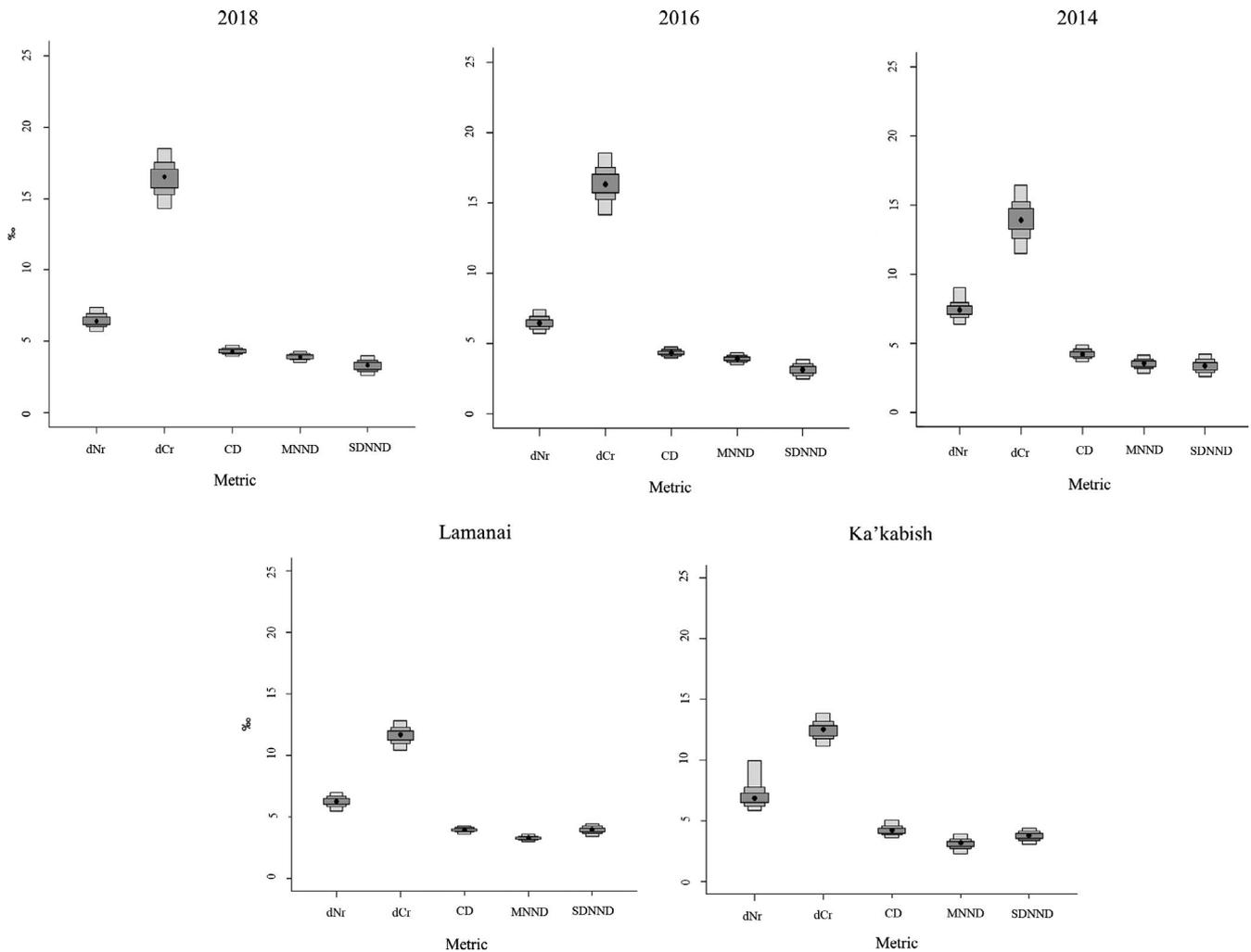
### 3 | RESULTS

We sampled 470 bats from 35 species and six *a priori* determined trophic guilds. As noted previously, these guilds represent broad groupings, and many species arranged to a guild may eat other items (e.g., many frugivores also consume insects; Table 1).

Community-wide niche metrics (Layman et al., 2007) suggested that samples from Lamanai and Ka'kabish, and those collected in 2014, 2016, and 2018 were representative of the same community (Figure 2), and therefore combined for further analysis.

Among all species the relationship between niche breadth and body size metrics were not statistically significant ( $R^2_{\text{mass}} = 0.002$ ,  $p = .873$ ;  $R^2_{\text{forearm}} = 0.013$ ,  $p = .595$ ; Table 2), even

when *D. rotundus* and *N. leporinus* were not included in the dataset ( $R^2_{\text{mass}} = 0.054$ ,  $p = .300$ ;  $R^2_{\text{forearm}} = 0.006$ ,  $p = .724$ ). Within guilds we found no statistically significant effect of body size, however among insectivores there was positive relationship ( $R^2_{\text{mass}} = 0.299$ ,  $p = .102$ ,  $\beta = 5.548 \pm 3.007$ ;  $R^2_{\text{forearm}} = 0.212$ ,  $p = .180$ ,  $\beta = 4.442 \pm 3.072$ ) and among frugivores the relationship was negative ( $R^2_{\text{mass}} = 0.309$ ,  $p = .153$ ,  $\beta = -14.951 \pm 9.135$ ;  $R^2_{\text{forearm}} = 0.212$ ,  $p = .086$ ,  $\beta = -12.360 \pm 6.019$ ). When insectivores were analyzed without *L. evotis*, the results were not statistically significant though still trending to a positive effect ( $R^2_{\text{mass}} = 0.279$ ,  $p = .144$ ,  $\beta = 6.309 \pm 3.838$ ;  $R^2_{\text{forearm}} = 0.165$ ,  $p = .279$ ,  $\beta = 4.574 \pm 3.897$ ). There was little overlap in niche areas between most guilds, and the community was largely structured as per predictions in Figure 1 (Figure 3). However, there was substantial overlap between insectivores and carnivores, probably as a result of how the carnivore guild was defined (see Discussion). As predicted, in many cases there was substantial overlap between populations of species within guilds. Surprisingly, there were several cases where



**FIGURE 2** SIBER density plot of Layman/SIBER Hull metrics (Jackson et al., 2011; Layman et al., 2007) for bat hair samples collected in 2014, 2016, and 2018 at Ka'kabish and Lamanai, Orange Walk District, Belize. X-axis values are as follows: range of nitrogen values, range of carbon values, centroid distance, mean nearest neighbor distance, and standard deviation of nearest neighbor distance. Dots represent the median value for each metric, and boxes are the distribution of values

**TABLE 2** Species-level niche breadths (SEAc and SEA.b) with body size and sample size. Ellipse data are reported in squared parts per thousand (‰<sup>2</sup>). Mean forearm length and body mass are from unpublished field notes from captures at the Lamanai and Ka'kabish study sites made between 2010 and 2017. Mean forearm and weight for *Noctilio leporinus* and *Mimon cozumelae* are from Reid (1997). Species are grouped into *a priori* assigned guilds (Colors correspond to Table 1) and sorted by median SEA.b

Guild	Species	SEA.b	SEAc	Forearm (mm)	Mass (g)	Sample (n)
<b>Frugivores</b>						
	<i>Carollia sowelli</i>	3.241	3.150	38.18	15.23	21
	<i>Dermanura phaeotis</i>	2.825	2.786	39.04	13.19	35
	<i>Sturnira parvidens</i>	2.377	2.233	38.20	14.44	32
	<i>Artibeus intermedius</i>	2.070	1.833	61.84	47.30	11
	<i>Uroderma convexum</i>	1.930	1.718	42.70	15.07	18
	<i>Artibeus lituratus</i>	1.644	1.479	68.95	57.70	27
	<i>Carollia perspicillata</i>	1.586	0.800	43.50	20.17	6
	<i>Artibeus jamaicensis</i>	1.324	1.135	60.80	38.63	23
<b>Insectivores</b>						
	<i>Lophostoma evotis</i>	4.757	2.566	50.50	18.50	4
	<i>Saccopteryx bilineata</i>	4.165	4.344	44.00	6.61	22
	<i>Molossus rufus</i>	4.138	4.154	52.25	36.16	19
	<i>Pteronotus mesoamericanus</i>	3.606	3.625	57.21	18.99	28
	<i>Eptesicus furinalis</i>	3.482	3.315	38.88	8.83	17
	<i>Pteronotus fulvus</i>	2.849	2.864	44.19	7.45	26
	<i>Rhogeessa anaeus</i>	2.367	2.278	27.73	4.20	16
	<i>Rhynchonycteris naso</i>	2.178	1.852	37.64	3.89	15
	<i>Myotis elegans</i>	2.176	2.088	32.43	3.61	24
	<i>Bauerus dubiaquercus</i>	1.880	1.335	53.90	15.07	7
<b>Carnivores</b>						
	<i>Mimon cozumelae</i>	5.362	4.438	57.00	20.00	7
	<i>Chrotopterus auritus</i>	1.463	2.106	83.64	80.40	6
	<i>Trachops cirrhosus</i>	1.422	1.992	59.64	27.56	10
<b>Nectarivores</b>						
	<i>Glossophaga soricina</i>	1.655	1.794	35.39	9.20	32
<b>Piscivores</b>						
	<i>Noctilio leporinus</i>	4.009	4.244	85.50	63.50	6
<b>Sanguivores</b>						
	<i>Desmodus rotundus</i>	8.004	8.531	56.75	27.46	27

the niche area of one species was fully overlapped by that of another species. For example, among frugivores the SEAc of *Carollia perspicillata* is fully within the ellipse area of *C. sowelli*. There appear to be two distinct groupings of frugivores separated along  $\delta^{13}\text{C}$ , with *Sturnira parvidens*, *Carollia perspicillata*, and *C. sowelli* constituting one group and *Artibeus intermedius*, *A. jamaicensis*, *A. lituratus*, and *Uroderma convexum* the other. *Dermanura phaeotis* overlaps with both groups. Among insectivores, there was large amount of overlap with all species within the guild with the exception of *Rhynchonycteris naso*, an insectivorous species that appears as highly disjunct in isotopic niche space, having the lowest  $\delta^{13}\text{C}$  among all species sampled.

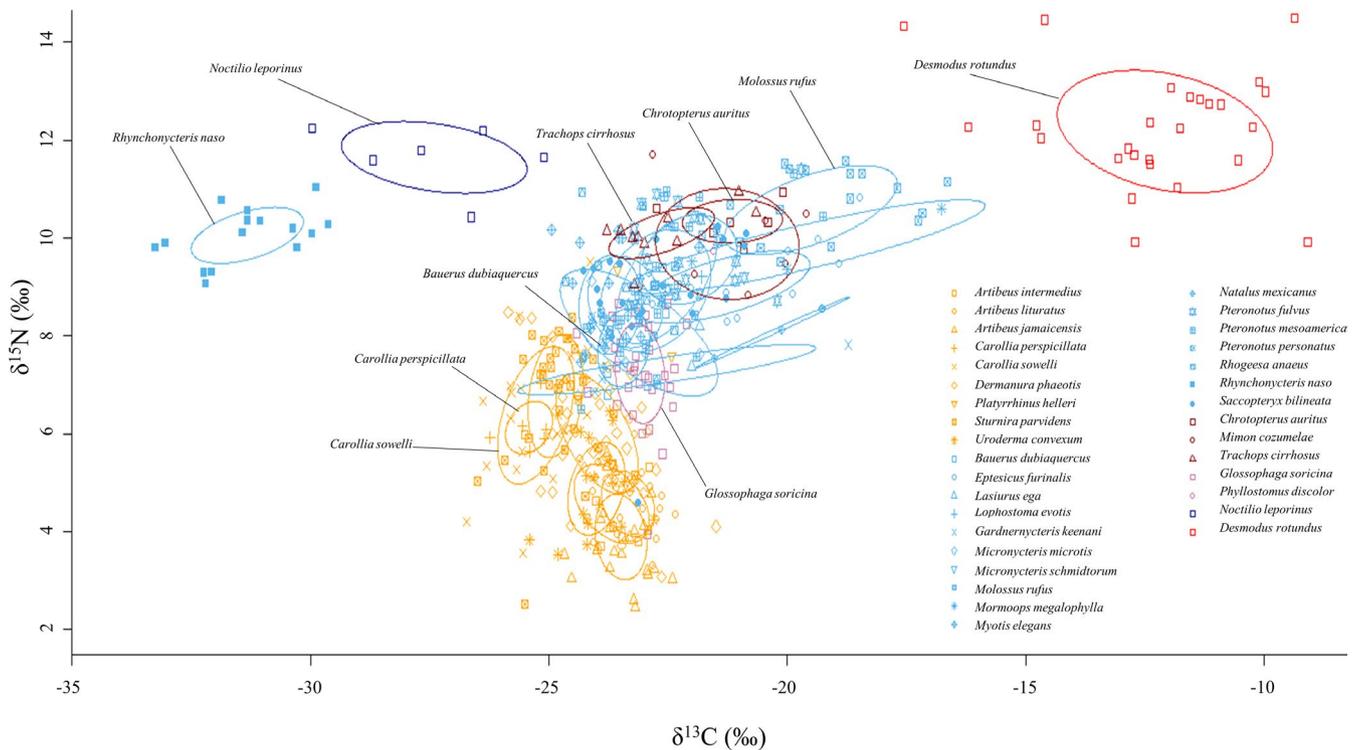
While most pairwise comparisons of species both within and between dietary guilds had little overlap (Table 3), there are cases which seemingly violate our predictions. Between guilds (black) there were no cases of >95% overlap; however, there were 4 cases involving carnivores overlapping with insectivores with >90% [*Chrotopterus auritus* – *Molossus rufus* (93.3%), *Trachops cirrhosus* – *Saccopteryx bilineata* (93.7%), *T. cirrhosus* – *Pteronotus mesoamericanus* (90.6%), *T. cirrhosus* – *P. fulvus* (90.0%)], and even more

cases by >75%. While we expected species within the same guild to overlap to some degree greater than inter-guild comparisons, we noted four cases where >95% overlap occurred [*Carollia perspicillata* – *C. sowelli* (99.1%), *Bauerus dubiaquercus* – *S. bilineata* (95.7%), *Rhogeessa anaeus* – *S. bilineata* (95.0%), *C. auritus* – *Mimon cozumelae* (95.9%)] (Table 3).

## 4 | DISCUSSION

### 4.1 | Community structure

The isotopic profiles of the bat fauna at Lamanai and Ka'kabish largely support our *a priori* characterization of guild structure, though there are some exceptions. Our empirical description of community structure shows that (a) while most populations overlap primarily with other species within their trophic guilds, there are cases with substantial overlap between species of different guilds, and (b) there were some cases with >95% overlap suggesting similar food selection and potentially significant competition. We found no relationship between niche breadth and body size among all species. Our results



**FIGURE 3** Species-level community structure of all individuals sampled in the bat fauna of Lamanai and Ka'kabish, Orange Walk District, Belize April-May 2014, 2016, and 2018 using stable isotope analysis of nitrogen and carbon ratios. Ellipses represent the niche breadth as sample size corrected ellipse area (SEAc) of each species with a sample size  $\geq 3$ ; points mark one individual. Colors denote groupings by guild: orange—frugivores, turquoise—insectivores, maroon—carnivores, purple—nectarivores, blue—piscivores, and red—sanguivores. Ellipses with labels are species featured in discussion

suggest that while trophic guilds may be informative for grouping species, caution should be used in making assumptions about diet and niche breadth based on guild assignments, particularly for less well-known species or those which have generalist diets.

Comparing the organization of trophic groups in our results to our predictions of community structure at the guild level (Figure 1), we can note few deviations. Our predictions for both the piscivorous species *N. leporinus* and sanguivorous *D. rotundus* match the results obtained; both species have feeding strategies that are unique in the fauna and appeared clearly distinct in our stable isotope plots. We predicted that nectarivorous *Glossophaga soricina* would have higher  $\delta^{15}\text{N}$  than frugivorous species due to the high proportion of insects in their diet as noted by Fleming et al. (1972) and Clare et al. (2014). We found more overlap of *Glossophaga* with insectivores than with frugivores. This suggests that at least during the period of hair growth, these “nectarivorous” bats have a significant insect contribution to their diet (Clare et al., 2014; Voigt & Matt, 2004). Insectivorous *Rhynchonycteris naso* had the lowest  $\delta^{13}\text{C}$  recorded and was isolated from all other insectivores in our sample, probably due to feeding on aquatic insects as does its nearest neighbor in our isotope plot, *N. leporinus* (Becker et al., 2018; Broders et al., 2014). Notably, carnivores were expected to have the highest  $\delta^{15}\text{N}$  because they represent a higher trophic level; however, the carnivores in our sample overlapped considerably with several insectivorous species. This is likely because most of the “carnivores” in

our study (e.g., *M. cozumelae* and *T. cirrhosus*) may in fact be eating predominantly non-vertebrate prey (Arroyo-Cabrales, Miller, Reid, Cuarón & de Grammont, 2015; Cramer et al., 2001). These gleaning animalivores probably represent an intermediate between species that rely almost entirely on vertebrate prey (e.g., *C. auritus*) and aerial insectivores which never consume vertebrates.

#### 4.2 | Niche breadth and body size

Across all species there was no statistically significant relationship between niche breadth and body size. There was however a trend toward a positive relationship for insectivorous species and a negative trend for frugivores between median niche breadth (SEA.b) with both forearm length and weight. Community-wide metrics of body size are likely less relevant to resource availability as many bats within the fauna vary significantly in feeding strategy. From an energetics perspective, larger bats may require more time to forage, though this may not reflect a larger niche breadth; some species may be specialists searching for ideal food sources (Esbérard & Bergallo, 2008; Peters, 1983). Barclay and Brigham (1991) argued that body size does not limit prey type as much as does detection method, noting the high abundance of small generalist aerial insectivores that detect prey via echolocation, whereas bats that listen for prey-generated sounds and glean their prey off the ground or vegetation tend to be larger and less common.

**TABLE 3** Mean probability values (%) that an individual from Species A (row labels) will be found within the Niche Region of Species B (column labels), sorted alphabetically by guild. All individuals were captured at Lamanai and Ka'kabish, Orange Walk, Belize in April–May 2014, 2016, and 2018. Values were calculated in NicheRover (Swanson et al., 2015) and bootstrapped to  $n = 10,000$ . All values over 90% overlap are underlined. Colors (descending order) denote guild: orange—frugivores, turquoise—insectivores, maroon—carnivores, purple—nectarivores, blue—piscivores, red—sanguivores, and black—inter-guild overlap

Species	Ai	Aj	Al	Cp	Cs	Dp	Sp	Ub	Gs	Bd	Ef	Le	Mr	Me	Pf	Pm	Ra	Rn	Sb	Ca	Mc	Tc	Nl	Dr
<i>A. intermedius</i>	NA	76.6	79.0	4.6	24.0	87.4	27.8	77.3	12.2	2.5	0.1	0.7	>0.1	1.9	>0.1	3.6	0.7	>0.1	4.5	>0.1	0.3	>0.1	>0.1	>0.1
<i>A. jamaicensis</i>	91.4	NA	88.2	0.8	9.3	94.4	11.5	76.8	20.7	2.3	>0.1	0.2	>0.1	1.6	>0.1	2.5	0.7	>0.1	4.0	>0.1	0.3	>0.1	>0.1	>0.1
<i>A. lituratus</i>	80.1	72.0	NA	0.5	6.5	71.7	8.0	66.1	7.5	1.1	>0.1	0.1	>0.1	0.8	>0.1	1.2	0.4	>0.1	1.8	>0.1	0.1	>0.1	>0.1	>0.1
<i>C. perspicillata</i>	23.5	1.4	0.9	NA	<u>99.1</u>	72.2	93.5	12.7	1.1	3.2	2.4	15.7	>0.1	5.1	0.2	12.6	1.8	>0.1	16.1	>0.1	0.7	>0.1	>0.1	>0.1
<i>C. sowelli</i>	17.6	3.3	3.0	36.4	NA	61.2	78.5	16.5	8.3	11.1	15.9	17.8	1.4	24.4	4.8	24.6	15.7	>0.1	31.6	0.2	3.7	2.2	0.4	>0.1
<i>D. phaeotis</i>	49.2	40.5	35.1	13.7	55.3	NA	58.1	58.4	36.5	21.1	10.3	15.7	0.5	28.7	2.6	33.0	15.8	>0.1	37.0	>0.1	2.4	0.4	0.1	>0.1
<i>S. parvidens</i>	23.3	6.0	5.4	33.6	92.5	82.0	NA	25.1	12.5	17.6	23.0	21.9	1.8	38.8	6.4	38.4	24.4	>0.1	47.2	0.1	4.8	2.9	0.5	>0.1
<i>U. bilobatum</i>	78.7	64.9	68.7	3.9	34.2	83.9	40.3	NA	22.8	7.9	0.8	2.3	0.1	7.3	0.5	10.5	3.5	>0.1	11.8	>0.1	0.7	>0.1	>0.1	>0.1
<i>G. soricina</i>	8.6	8.9	5.8	0.7	21.9	55.7	18.7	26.3	NA	62.6	41.7	30.8	8.0	70.6	35.8	77.5	67.7	>0.1	82.2	0.6	20.6	3.6	0.4	>0.1
<i>B. dubiaquercus</i>	2.9	1.7	1.1	1.7	44.8	54.7	41.1	14.7	89.7	NA	66.7	30.9	11.6	92.0	50.7	94.7	87.0	>0.1	<u>95.7</u>	0.8	26.0	4.5	0.5	>0.1
<i>E. furinalis</i>	0.1	>0.1	>0.1	0.4	10.9	7.5	9.1	0.4	23.1	18.7	NA	3.4	62.6	29.8	69.4	64.7	38.4	>0.1	71.4	13.8	75.0	8.5	0.9	0.3
<i>L. evotis</i>	1.5	0.1	0.1	7.8	29.1	34.3	26.1	7.5	37.2	28.8	17.9	NA	0.6	34.6	13.1	47.0	34.6	>0.1	57.3	>0.1	16.9	>0.1	0.1	0.1
<i>M. rufus</i>	>0.1	>0.1	>0.1	>0.1	1.0	0.4	0.8	>0.1	2.4	1.9	45.0	0.2	NA	5.3	39.2	34.2	7.3	>0.1	32.8	33.5	62.3	18.1	1.4	6.6
<i>M. elegans</i>	1.2	0.7	0.5	1.2	45.8	30.7	44.4	4.7	53.6	47.5	59.2	9.9	20.7	NA	58.6	80.7	84.9	>0.1	91.0	4.1	38.6	29.4	5.4	>0.1
<i>P. fulvus</i>	>0.1	>0.1	>0.1	0.1	5.6	2.2	4.1	0.3	20.7	15.3	68.4	2.3	71.3	37.4	NA	91.0	48.8	>0.1	92.1	36.4	86.7	45.4	3.8	>0.1
<i>P. mesoamericanus</i>	1.3	0.7	0.5	1.2	16.1	14.1	14.0	3.8	39.3	31.2	63.6	8.4	52.9	52.9	79.1	NA	60.3	>0.1	91.3	24.8	69.4	35.4	3.0	>0.1
<i>R. anaeus</i>	0.5	0.3	0.2	0.6	33.1	20.0	29.8	2.9	62.5	51.4	70.0	9.6	29.0	88.1	72.2	88.6	NA	>0.1	<u>95.0</u>	5.2	49.0	28.7	3.6	>0.1
<i>R. naso</i>	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	NA	>0.1	>0.1	0.1	>0.1	7.4	>0.1
<i>S. bilineata</i>	1.3	0.7	0.5	1.3	20.5	16.5	18.3	3.8	41.5	32.4	63.9	10.1	43.4	58.7	73.4	85.8	64.6	>0.1	NA	17.3	62.3	30.6	3.5	>0.1
<i>C. auritus</i>	>0.1	>0.1	>0.1	>0.1	0.4	>0.1	0.2	>0.1	0.8	1.0	46.7	>0.1	<u>93.3</u>	7.3	87.7	83.3	10.6	>0.1	78.8	NA	<u>95.9</u>	<u>63.5</u>	4.8	0.1
<i>M. cozumelae</i>	0.1	>0.1	>0.1	0.1	2.3	1.0	1.7	1.8	0.2	5.0	58.1	2.5	71.6	16.2	71.5	67.4	21.7	>0.1	68.8	39.1	NA	33.9	4.2	0.2
<i>T. cirrhosus</i>	>0.1	>0.1	>0.1	>0.1	8.2	0.8	6.7	>0.1	9.4	6.8	30.2	>0.1	68.3	51.6	<u>90.0</u>	<u>90.6</u>	55.4	>0.1	<u>93.7</u>	<u>52.3</u>	<u>85.8</u>	NA	7.5	>0.1
<i>N. leporinus</i>	>0.1	>0.1	>0.1	>0.1	0.3	>0.1	0.3	>0.1	>0.1	0.1	0.4	>0.1	0.9	0.9	3.5	1.7	2.0	4.5	3.0	0.8	4.1	1.4	NA	>0.1
<i>D. rotundus</i>	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	0.1	>0.1	3.4	>0.1	>0.1	>0.1	>0.1	>0.1	>0.1	0.2	>0.1	>0.1	NA

Bolded values indicate cases with statistically significant overlap for  $\alpha = 0.05$  with species pairs within the same guild and  $\alpha = 0.1$  with species pairs in different guilds.

Among insectivores, the only species which seemingly contradicts Barclay and Brigham's (1991) hypothesis and supports our prediction that larger bats should have larger niche breadths is *M. rufus* (formerly *M. ater*), whose niche breadth may be explained by its wing form, flight habits, and robust skull and dentition (Fenton et al., 1998). Molossids are unusual among aerial insectivores in having high aspect-ratio wings that make them fast fliers with low maneuverability, and accordingly, they preferentially forage in open areas unlike other species in the same guild (Aldridge & Rautenbach, 1987; Fenton et al., 1998; Norberg & Rayner, 1987). Foraging over larger areas and with access to diverse insect prey of many different sizes and hardnesses, *M. rufus* may be something of a generalist in terms of prey choice.

The negative trend between niche breadth and body size among frugivores, if biologically meaningful, may be driven by the small niche breadths of *Artibeus jamaicensis* and *A. lituratus*. Both species are among the largest bats sampled, and both are known to specialize on *Ficus* spp. fruits (Humphrey et al., 1983; Ortega & Castro-Arellano, 2001). Similar to predatory bats, larger frugivores may be able to specialize more on a particular resource, perhaps because they are able to forage over a greater area than smaller bats in the guild (Laska 1990). Additional drivers of dietary specialization (as a function of niche breadth) appear to relate to dietary preference and the size, mass, and hardness of preferred sources of fruits (Saldaña-Vázquez, 2014).

### 4.3 | Overlap between guilds

While in most cases there was more overlap between species within trophic guilds than between guilds, there are several instances where this was not the case, violating our first prediction. Among carnivores, the ellipses of *T. cirrhosus* and *C. auritus* were lower in  $\delta^{15}\text{N}$  than predicted as these species overlap significantly with insectivores. We found that while these two carnivorous species did not overlap significantly with one another, both overlapped significantly with several insectivorous species.

As *C. auritus* has been described as a both generalist omnivore and generalist animalivore (Medellín, 1988, 1989), it is possible that the small ellipse area we observed is due to isotope averaging from a generalist diet (Bearhop et al., 2004). Individuals from Ka'kabish were radio tracked as a part of a recently published study (Brigham, Broders, Toth, Reimer & Barclay, 2018) which found that most individuals remained within one forested block of the Ka'kabish fragment and rarely foraged far from their roost. This suggests that these bats are likely limited to abundant prey within the habitat fragment which may consist mostly of large insects or other arthropods given the  $\delta^{15}\text{N}$  range. Similarly, *T. cirrhosus* is traditionally viewed as gleaning carnivore or insectivore; this species eats large quantities of insects and is primarily insectivorous for at least the period of hair growth sampled in our study.

Another possible explanation for the overlap observed between carnivores and insectivores seen in our data is that insectivores have higher  $\delta^{15}\text{N}$  than predicted because their prey has higher  $\delta^{15}\text{N}$ . Some insects and arachnids are known to have higher  $\delta^{15}\text{N}$  due to their diets, especially ground beetles, spiders (Girard, Baril, Mineau & Fahrig, 2011), and wasps (Hyodo, Takematsu, Matsumoto, Inui & Itoika, 2011). Particularly for larger insectivores like *P. mesoamericanus* and *M. rufus*, feeding on larger, higher trophic level insects may contribute to the significant overlap in  $\delta^{15}\text{N}$  values with the carnivorous bat species.

The isotope profiles of *Glossophaga soricina* overlapped significantly with those of *P. mesoamericanus* and *S. bilineata*. While *Glossophaga soricina* are adapted to nectar feeding, most individuals in our sample seemed to have fed at a higher trophic level and likely had a large insect contribution to their diet. This conforms with previous dietary studies that found insects occur regularly in their diet (Fleming et al., 1993, Clare et al., 2014). Notably at the time of capture for our study, the feces of *Glossophaga soricina* (collected for different projects) were mostly liquid and did not contain insect parts. However, at least during the period of hair growth, our isotope results suggest that these bats may be largely or primarily insectivorous, behavior that may correspond to periods of low nectar availability (Clare et al., 2014; Howell, 1974). Further dietary and/or stable isotope studies sampling different tissues from *G. soricina* at Lamanai might reveal if there is an observable trophic shift during different times of the year (Bond, Jardine & Hobson, 2016).

#### 4.4 | Overlap within guilds

We predicted that species would comply with the competitive exclusion principle such that no two ellipses (representing niche space) should overlap completely (>95%). However, several cases within frugivores, insectivores, and carnivores in our dataset seemingly violate this ecological principle (at least in the two niche-dimensions measured), which may imply competition between species. In all cases with significant overlap, a species with a small perceived niche breadth was completely covered by the broader isotopic ellipse of another species. As noted above, this was most prominent in *Carollia perspicillata* and *C. sowelli*. The former species is found within the niche region of the latter 99.1% of cases. *Carollia perspicillata* has been studied extensively and is well known to be a *Piper* spp. specialist (Bonaccorso et al., 2007; Herbst, 1986; Montoya-Bustamante, Rojas-Díaz & Torres-González, 2016; Thies & Kalko, 2004). Da Silva, Gaona & Medellín, (2008) found that while both *Carollia* species sampled had a strong preference for fruits of the genus *Piper* spp., *C. sowelli* had a more variable diet overall with some representation from all plant groups sampled in their study area. Similarly, York and Billings (2009), using stable isotope analysis, found that *Carollia* spp. in general tend to partition resources by consuming varying quantities of insects, with *C. perspicillata* having the lowest insect contribution and *C. sowelli* having intermediate insect consumption. While there are other potential niche axes which may be affecting the populations at

Lamanai and Ka'kabish, it is also notable that *C. perspicillata* are rare in the fauna (though they are extremely common elsewhere in the Neotropics), which may indicate that abundances are being limited by competition.

Additionally, we noted significant overlap in stable isotope space was between *B. dubiaquercus* and *S. bilineata* (95.6%). *Bauerus dubiaquercus* had the smallest insectivorous ellipse area, *S. bilineata* the largest. Contrary to what was described for *Carollia* species, there is no evidence that this overlap would indicate competitive exclusion. *Bauerus dubiaquercus* is likely a specialist feeder gleaning prey close to the forest floor (Engstrom, Lee & Wilson, 1987; White, 1969), while *S. bilineata* and *P. mesoamericanus* are generalist aerial insectivores (Bradbury & Vehrencamp, 1976; Yancey, Goetze & Jones, 1998). *Rhogeessa anaesus* also had significant overlap with *S. bilineata* (95.0%), but the diet of *R. anaesus* is largely unknown. It is unlikely that insect abundance is limiting these species, though there are seasonal peaks in insect abundance and seasonal diet switching may be occurring as was proposed by Bradbury and Vehrencamp (1976).

Among carnivorous bats, the isotope ellipse of *C. auritus* overlapped significantly with that of *M. cozumelae*. The diet and foraging behaviors of *M. cozumelae* are poorly known, though Whitaker & Findley, (1980) in a fecal analysis study found remains of insects, birds, and plant material. Body size and morphology of this species suggest that it is able to regularly include small vertebrates in its diet, and for that reason, *M. cozumelae* was grouped with the carnivores although these bats may be generalist omnivores (Fenton et al., 1992). Like *C. auritus*, most of the *M. cozumelae* in our sample were captured at Ka'kabish; however, it is possible that they are ranging further from their roosts, foraging individually, or simply eating more diverse foods than *Chrotopterus*, anyone of which might have contributed to the larger ellipse area. While both species are omnivorous to varying degrees, it is unlikely that the overlap observed here is significant in an ecological sense because both species seemingly forage opportunistically and are likely separating resources spatially or along some other niche axis.

## 5 | CONCLUSIONS

As the niche of a species in a community is  $n$ -dimensional, niche dynamics are complex and species may partition resources along other niche axes to coexist. Limitations in our analysis included that we only sampled one tissue from each individual (hair) for which molting time is not known and did not sample potential prey items which would be significant in our analyses. Additionally, we could not age the bats we sampled, and diet quality was not assessed; both factors which might influence stable isotope ratios. We believe that with larger sample size (a meta-analysis of niche breadth as relative to body size) or re-defined guilds (*sensu* Segura-Trujillo, Lidicker & Álvarez-Castañeda, 2016) we may be more likely to detect biologically relevant patterns.

We present a comprehensive and complex representation of the community structure of a Neotropical bat fauna in the two niche

dimensions we measured using stable isotope analysis. We did not find a statistically significant relationship between isotopic niche breadth and body size in bats; however, we did find indication that within guilds this relationship may be relevant. Cases of overlap between guilds should remind caution on using these broad groupings to infer diet of many of these species. We found several cases of significant overlap between species which may indicate competition; however, we only examined a two-dimensional isotopic niche and further research on other axes is required to further elucidate the species–species interactions in this fauna.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.88sf103> (Oelbaum, Fenton, Simmons & Broders, 2019).

## ORCID

Phillip J. Oelbaum  <https://orcid.org/0000-0002-9152-1658>

Hugh G. Broders  <https://orcid.org/0000-0002-6151-8079>

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