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 methods (Bearhop et al., 2004; Layman, Arrington, Montaña & Post, 2007).

Studies using SIA to determine trophic niches infer dietary niche breadth from profiles of carbon (δ13C) and nitrogen (δ15N) 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 (δ34S) or hydrogen (δ2H) isotopic ratios to characterize niche dynamics; however, these elements appear less effective as indicators of trophic interactions in terrestrial systems (Dalerum & Angerbörn, 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 δ13C differ greatly between photosynthetic pathways (C3 or C4 plants) and the ultimate source of biological carbon may be identified in the tissues of a consumer using SIA (Peterson & Fry, 1987). C3 plants have an expected net fractionation of δ13C of approximately 21‰ from carbon uptake between the atmosphere (~7 ‰) and biomass (~28 ‰), while C4 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 fractioning between consumer levels making δ13C 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 (δ15N) reflects rate of nitrogen gas fixation in plants, and δ15N values increase with trophic levels (DeNiro & Epstein, 1981; Peterson & Fry, 1987). Unlike δ13C, δ15N values of consumer tissues are, on average, 3–5 ‰ higher than their diet (Peterson & Fry, 1987). This enrichment factor makes δ15N a reliable indicator of the consumer trophic level of populations within communities, such that animals at higher trophic levels will have higher δ15N (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, Rakondrasonana & 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, McPeek & 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 sanguinivores (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, Czaczkes, 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 (= 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 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 δ15N to be higher than other animals (i.e., obligate insectivores).

We clipped a small (∼ 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 δ-values in parts per thousand (%). δ-values were anchored in VPBD (δ13C) and AIR (δ15N) 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—nectarivores, blue—piscivores, and red—sanguivores.

<table>
<thead>
<tr>
<th>Species</th>
<th>n (male, female)</th>
<th>Primary diet</th>
<th>Secondary diet</th>
<th>Information source (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artibeus intermedius</td>
<td>11(7, 4)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Garcia-Estrada et al. (2012)</td>
</tr>
<tr>
<td>Artibeus jamaicensis</td>
<td>23(11, 11)</td>
<td>Fruit</td>
<td>Insects, nectar</td>
<td>Heithaus et al. (1975)</td>
</tr>
<tr>
<td>Artibeus lituratus</td>
<td>27(13, 13)</td>
<td>Fruit</td>
<td>Insects, pollen</td>
<td>Humphrey et al. (1983), Fleming et al. (1972)</td>
</tr>
<tr>
<td>Carollia perspicillata</td>
<td>6(4, 1)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Herbst (1986), Mello et al. (2004)</td>
</tr>
<tr>
<td>Carollia sowelli</td>
<td>21(10, 10)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Miller et al. (2015a)</td>
</tr>
<tr>
<td>Dermanura phaeotis</td>
<td>35(18, 29)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Herrera et al. (2002)</td>
</tr>
<tr>
<td>Platyrhinus heteri</td>
<td>2(0, 2)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Ferrell and Wilson (1991)</td>
</tr>
<tr>
<td>Sturnira parvidens</td>
<td>32(16, 16)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Fleming et al. (1972), Mello et al. (2008)</td>
</tr>
<tr>
<td>Urodema convexum</td>
<td>18(8, 10)</td>
<td>Fruit</td>
<td>Insects</td>
<td>Fleming et al. (1972), Herrera et al. (2002)</td>
</tr>
<tr>
<td>Baueraus dasyuercus</td>
<td>7(4, 3)</td>
<td>Insects</td>
<td></td>
<td>Engstrom et al. (1987), Miller and Medina (2008)</td>
</tr>
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<td>Eptesicus furinalis</td>
<td>17(7, 10)</td>
<td>Insects</td>
<td></td>
<td>Aguiar and Antonini (2008)</td>
</tr>
<tr>
<td>Lasiusa ega</td>
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<td>Insects</td>
<td></td>
<td>Kutra and Lehr (1995)</td>
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<td>Lophostoma evotis</td>
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<td>Insects</td>
<td></td>
<td>Cajas and Miller (2008)</td>
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<td>Gardnericyctes keenani</td>
<td>2(0, 2)</td>
<td>Plants</td>
<td>vertebrates</td>
<td>Humphrey et al. (1983), Giannini and Kalko (2005)</td>
</tr>
<tr>
<td>Micronycteris microtis</td>
<td>3(1, 2)</td>
<td>Insects</td>
<td>Fruit, vertebrates</td>
<td>LaVal and LaVal (1980)</td>
</tr>
<tr>
<td>Micronycteris schmidtorum</td>
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<td>Insects</td>
<td>Fruit</td>
<td>Howell and Burch (1974)</td>
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<td>Molossus rufus</td>
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<td>Insects</td>
<td></td>
<td>Aguirre et al. (2003)</td>
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<td>Mormoos megallaphylla</td>
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<td>Insects</td>
<td></td>
<td>Dávalos and Mantilla (2008)</td>
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<td>Natalus mexicanus</td>
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<td>Insects</td>
<td></td>
<td>Reid (1997)</td>
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<tr>
<td>Pteronatus mexicanusus</td>
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<td>Insects</td>
<td></td>
<td>Howell and Burch (1973), Herrera et al. (2001)</td>
</tr>
<tr>
<td>Pteronatus personatus</td>
<td>10(1)</td>
<td>Insects</td>
<td></td>
<td>Dávalos (2006)</td>
</tr>
<tr>
<td>Rhogeza anaeus</td>
<td>16(6, 10)</td>
<td>Insects</td>
<td></td>
<td>Barclay and Brigham (1991)</td>
</tr>
<tr>
<td>Rhynchochyticus naso</td>
<td>15(8, 7)</td>
<td>Insects</td>
<td></td>
<td>Bradbury and Vehrencamp (1976)</td>
</tr>
<tr>
<td>Saccopteryx bilineata</td>
<td>1(1, 2)</td>
<td>Insects</td>
<td></td>
<td>Bradbury and Vehrencamp (1976)</td>
</tr>
<tr>
<td>Chrotospiter aurita</td>
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<td>Vertebrates</td>
<td>insects, fruit, plants</td>
<td>Medellin (1989), Barquez et al. (2015)</td>
</tr>
<tr>
<td>Trachops cirrhosus</td>
<td>10(7, 3)</td>
<td>Insects</td>
<td>Vertebrates, plants</td>
<td>Kalko et al. (1999)</td>
</tr>
<tr>
<td>Glossophaga soricina</td>
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<td>Nectar</td>
<td>Insects, fruit</td>
<td>Fleming et al. (1972), Clare et al. (2014)</td>
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<td>Phylllostomus discolor</td>
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<td>Nectar</td>
<td>Insects, vertebrates, plants</td>
<td>Willig et al. (1993), Kwiecinski (2006)</td>
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<td>6(3, 3)</td>
<td>Fish</td>
<td>Insects</td>
<td>Brooke (1994)</td>
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<td>Desmodus rotundus</td>
<td>27(21, 6)</td>
<td>Blood</td>
<td>Insects</td>
<td>Arata et al. (1967)</td>
</tr>
</tbody>
</table>

*Individuals for which sex was not identified are included in the total (n).

Stable isotope data were then recorded as δX values using the formula:

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

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 ≤ 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 (Nc). Overlap was calculated as the probability that an individual from Species A would be found within the Nc of Species B, bootstrapped to n = 10,000. Only species for which we had ≥ 3 samples were included in species-level analysis using SEAc as ellipses cannot be drawn for smaller samples; species with sample size ≥ 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 ($R^2_{mass} = 0.002, p = .873; R^2_{forearm} = 0.013, p = .595; Table 2$), even when $D. rotundus$ and $N. leporinus$ were not included in the data set ($R^2_{mass} = 0.054, p = .300; R^2_{forearm} = 0.006, p = .724$). Within guilds we found no statistically significant effect of body size, however among insectivores there was positive relationship ($R^2_{mass} = 0.299, p = .102, \beta = 5.548 \pm 3.007; R^2_{forearm} = 0.212, p = .180, \beta = 4.442 \pm 3.072$) and among frugivores the relationship was negative ($R^2_{mass} = 0.309, p = .153, \beta = -14.951 \pm 9.135; R^2_{forearm} = 0.212, p = .086, \beta = -12.360 \pm 6.019$). When insectivores were analyzed without $L. evotis$, the results were not statistically significant though still trending to a positive effect ($R^2_{mass} = 0.279, p = .144, \beta = 6.309 \pm 3.838; R^2_{forearm} = 0.165, p = .279, \beta = 4.574 \pm 3.897$). 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.
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 δ¹³C, 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 δ¹³C 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% [*Chrototterus auritus* – *Molossus rufus* (93.3%), *Trachops cirrhous* – *Saccopeterx bilineata* (93.7%), *T. cirrhous* – *Pteronotus mesoamericanus* (90.6%), *T. cirrhous* – *P. fulavus* (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%), *Rhogeesa anaeus* – *S. bilineata* (95.0%), *C. auritus* – *Mimon cozumelae* (95.9%)] (Table 3).

### TABLE 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Frugivores</th>
<th>Insectivores</th>
<th>Carnivores</th>
<th>Nectarivores</th>
<th>Piscivores</th>
<th>Sanguivores</th>
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<td>Forearm (mm)</td>
<td>3.241</td>
<td>2.825</td>
<td>2.777</td>
<td>2.070</td>
<td>1.930</td>
<td>1.644</td>
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<td>Mass (g)</td>
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<td>2.233</td>
<td>1.833</td>
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<td>Sample (n)</td>
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<td>39.04</td>
<td>38.20</td>
<td>61.84</td>
<td>42.70</td>
<td>68.95</td>
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<tr>
<td>Species</td>
<td><em>Carollia sowelli</em></td>
<td><em>Dermanura phaeotis</em></td>
<td><em>Sturnira parvidens</em></td>
<td><em>Artibeus intermedius</em></td>
<td><em>Uroderma convexum</em></td>
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<td>SEA.b</td>
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<td>Forearm (mm)</td>
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<td>Mass (g)</td>
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### 4 | DISCUSSION

#### 4.1 | Community structure

The isotopic profiles of the bat fauna at Lamanai and Ka’akibish largely support our *a priori* characterization of guild structure, though there are some exceptions. Our empirical description of community structure of 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...
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 $\delta^{15}N$ 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 $\delta^{13}C$ 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 $\delta^{15}N$ 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 (Arrroyo-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.

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**Note:** 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.

### 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 $\delta^{15}N$ 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 $\delta^{15}N$ range. Similarly, *T. cirrhosus* is traditionally viewed as a gleaner 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 δ¹⁵N than predicted because their prey has higher δ¹⁵N. Some insects and arachnids are known to have higher δ¹⁵N due to their diets, especially ground beetles, spiders (Girard, Baril, Mineau & Fahrig, 2011), and wasps (Hyodo, Takematsu, Matsumoto, Inui & Itioka, 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 δ¹⁵N 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%). Bauersus 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. Bauersus 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, Goetz & Jones, 1998). Rhogeesa anaeus also had significant overlap with S. bilineata (95.0%), but the diet of R. anaeus 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 Chiropterus, 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 metaanalysis 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

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