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On the development of a trait-based approach for studying Neotropical bats

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Abstract. New World bats are involved in key ecological processes and are good indicators of environmental changes. Recently, trait-based approaches have been used in several taxa to better understand mechanisms underlying species assemblages, biotic interactions, environmental relationships and ecosystem functions. However, despite the relevance of bats on ecosystem dynamics, so far, there is no conceptual framework that relies on the measurement of bat traits to address functional studies. Here, we present a set of 50 bat biological traits, which are suitable to assess environmental stressors and can potentially affect ecological processes. Several examples were provided to show the applicability of this framework in the study of Neotropical bat ecology. We suggest some considerations regarding trait-based approach including the importance of intraspecific variation, correlations between traits, response-effect framework, global dataset, and future directions to assess the reliability of functional relations across species and Neotropical regions by using traits. This could be helpful in tackling ecological questions associated with community assembly and habitat filtering, species diversity patterns along environmental gradients, and ecological processes. We envision this paper as a first step toward an integrative bat functional trait protocol held up with solid evidence.

Keywords. Chiroptera; Ecosystem functions; Functional traits; Morphology; Life-history.

INTRODUCTION

Global biodiversity loss is a major concern that has motivated ecologists to explore the links between biodiversity and ecosystem functioning (Gross *et al.,* 2017), especially under different scenarios of human impact (García-Morales *et al.,* 2016). The necessity to transfer this knowledge into management planning is critical, as the massive loss of biodiversity is threatening the ecosystem services from which humans depend on (Millennium Ecosystem Assessment, 2005). Accordingly, several approaches have been conducted to monitor biodiversity, of which measures of taxonomic diversity (*i.e.,* species richness, evenness, diversity) are the most widely used ones (Cadotte *et al.,* 2011; Mayfield *et al.,* 2010; García-Morales *et al.,* 2016). However, taxonomic diversity indices (*e.g.,* Shannon, Simpson) ignore species differences in ecological roles (Villéger *et al.,* 2010; Córdova-Tapia & Zambrano, 2016). Alternatively, functional diversity approach has been a core topic research in community ecology and conservation biology over the last decades (García-Morales *et al.,* 2016; Gross *et al.,* 2017), due to the inclusion of ecological attributes of species associated to ecosystem functioning (Gómez-Ortiz & Moreno, 2017). In line with this, functional diversity provides a comprehensive framework of causes, consequences, and mechanisms in the relations between species diversity and ecological processes (Córdova-Tapia & Zambrano, 2016).

Moving from ecological studies based on the taxonomic structure of communities to investigations that include functional diversity measures and relationships with ecosystem processes requires, mainly, a functional trait-based approach. Functional traits are traditionally defined as any morphological, physiological, behavioral, or phenological characteristic that, in addition to impact the fitness of an organism (Violle *et al.,* 2007), reflects interactions with the environment either by mirroring the impact on some ecosystem process (effect traits) (Lavorel & Garnier, 2002; Luck *et al.,* 2012) and/or by responding to environmental changes (response traits). Values measured by a functional trait in the same spatio-temporal dimension are called functional attributes (Lavorel *et al.,* 1997). Thus, functional trait-based approach is a promising tool to address plenty of ecological questions that contribute to biodiversity conservation (Castillo-Figueroa, 2018a; Jung & Threlfall,

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2018). For example, several studies show that functional traits explain the impact of human-made landscapes on ecological groups of animals (Castillo-Figueroa & Pérez-Torres, 2018), the influence of climate change on species distributions and phenology (Robbirt *et al.,* 2011), the effect of chemical elements on community assembly (Rubach *et al.,* 2011; Van den Brink *et al.,* 2013), and the distribution of functional diversity at macro-ecological scale (McGill *et al.,* 2006; Hortal *et al.,* 2015; González-Maya *et al.,* 2017), to name a few examples.

The concept of functional traits has been, however, criticized because of its vague meaning, as all the traits of an organisms affect, at least indirectly, the fitness of an individual (Mlambo, 2014). Focusing on functionality rather than the performance of the organism seems to be a more comprehensive definition of functional trait. Hence, real functional traits are those that modulate ecological processes, whereas the other traits can be categorized as biological ones (Mlambo, 2014). In this sense, before reaching functional traits is essential to list, describe and study biological traits that can potentially be functional.

Plant communities are the main biological group in which functional trait-based approach has been widely developed (Cornelissen *et al.,* 2003; Hortal *et al.,* 2015). Plant ecologists have been able to conceptualize the linkages between individual plant traits and ecosystem processes, including mechanisms and ecological factors such as competition, intra- and inter-specific variation, and environmental filtering across several ecosystems (Siefert *et al.,* 2015). This field has advanced in the last few years with global databases like TRY (Kattge *et al.,* 2020), LEDA (Kleyer *et al.,* 2008) Global Wood Density (Chave *et al.,* 2009), as well as handbooks and protocols (Cornelissen *et al.,* 2003; Salgado-Negret *et al.,* 2015). Undoubtedly, plant functional trait-based approaches have been a successful model that animal ecologists have adopted in handbooks and frameworks of traits in zoological groups such as terrestrial invertebrates (Moretti *et al.,* 2017), fishes (Zamudio *et al.,* 2015), birds (López-Ordoñez *et al.,* 2015), and amphibians (Cortés-Gómez *et al.,* 2015). Nevertheless, so far, there is no such protocol for mammalian traits, mainly due to the challenge of developing a single handbook that integrates the striking ecological complexity of this group. Although several but isolated investigations using functional traits have been conducted in mammals, it is necessary to start selecting biological traits of mammal groups to accomplish a complete and solid functional trait handbook.

Chiroptera is one of the most ecologically important taxa among mammals. Accounting for 1,411 recognized species (Mammal Diversity Database, 2020), bats represent a fifth of mammalian diversity (Hutson *et al.,* 2001; Frick *et al.,* 2019), with many opportunities for investigating ecological questions in a comparative framework (Brokaw & Smotherman, 2020). New World bats, in particular, consist of 400 species (Arita *et al.,* 2014) and display a variety of morphological (Findley *et al.,* 1972; Santana *et al.,* 2011a, 2012; Castillo-Figueroa, 2020a), ethological (Vandoros & Dumont, 2004; Voss *et al.,* 2016; Castillo-Figueroa *et al.,* 2018), physiological (Schondube *et al.,* 2001; Saldaña-Vázquez *et al.,* 2015; Tschapka *et al.,* 2015), and reproductive traits (Fleming *et al.,* 1972; Kerth, 2008; Vela-Vargas *et al.,* 2016; Stukenholtz *et al.,* 2018). Moreover, this group has a high diversity of feeding habits (Wilson, 1973), trophic niches (Giannini & Kalko, 2004), and habitat use (Kalko *et al.,* 2008; Denzinger & Schnitzler, 2013; Voss *et al.,* 2016), which are reflected in their multiple ecological roles in the ecosystems they inhabit (Lacher *et al.,* 2019; Castillo-Figueroa, 2020b). Even though ecological studies using traits have long been conducted in bats (Findley & Wilson, 1982; Norberg & Rayner, 1987; Fleming, 1991), recently some investigations have focused on functional diversity measures based on traits (Pereira *et al.,* 2018; Mancini *et al.,* 2019; Pereira *et al.,* 2019; Farneda *et al.,* 2019; Ramírez-Mejía *et al.,* 2020), many of which have lacked an ecological criterion to select the most suitable functional traits. Because the success of trait-based approaches depends on trait selection (Hortal *et al.,* 2015), conceptual frameworks that define the ecological relations of traits becomes imperative to better apply this approach into functional ecology studies. Here, we present a synthetic conceptual framework which emphasizes in the main biological traits of Neotropical bats by defining an extensive set of features. We then show how our framework might aid to perform different studies on bat ecology through several examples from literature that includes: trait-related responses to habitat fragmentation, land use management, elevational gradients, seasonal changes and seed dispersal networks. We also emphasize the importance of testing, either empirically or experimentally, these biological traits in order to discover the real functionality of each trait. Finally, we discuss issues regarding trait-based approach in Neotropical bats encompassing intraspecific variation, correlations between traits, response-effect framework, global dataset, and future directions regarding their application in functional ecology and biodiversity conservation.

MATERIAL AND METHODS

Functional ecology and trait selection

Neotropical bats play key ecological roles in arthropod suppression, vertebrate predation, seed dispersal, pollination, and fertilization (Kasso & Balakrishnan, 2013; Castillo-Figueroa, 2020b). Furthermore, bats have broad geographical ranges and can be affected by several environmental gradients including habitat fragmentation (Meyer *et al.,* 2008, 2016; Rocha *et al.,* 2017), agricultural management (Castillo-Figueroa & Pérez-Torres, 2018), urbanization (Jung & Threlfall, 2018), climate change (Sherwin *et al.,* 2012), among others. In fact, bats have been considered as bioindicators of disturbance due to idiosyncratic responses to environmental variation (Fenton *et al.,* 1992; Medellín *et al.,* 2000; Jones *et al.,* 2009a). Consequently, effect and response traits may reflect the relations with ecological processes and the impact of environmental conditions on this group, yet there are few studies using functional traits and, in most cases, the selection seems to be arbitrary because of the absence of functional interpretations of traits. Easy measurable traits are usually chosen, rather than traits more related to functional components (Raunkiaeran Shortfall *sensu* Hortal *et al.,* 2015).

We selected 50 bat biological traits according to studies that directly relate traits to environmental conditions, but we also included traits potentially linked to, either directly or indirectly, individual performance and ecosystem process (Table 1). However, more research is needed to clarify direct linkages with ecosystem functioning as the available information that relates traits with ecological processes is very scarce. This paper, therefore, helps to provide a list of potential traits that need to be investigated in-depth for an understanding of their functionality.

The selected traits were grouped into two main types of traits: Morphological (21 traits) and Life history traits (29 traits) (Fig. 1). The former includes six functional complexes (size, wings, pollex, hindlimbs, head, and tail) and the latter is divided into six functional dimensions following the proposal of Gómez-Ortiz & Moreno (2017): reproductive, physiological, behavioral, trophic niche, spatial niche, and echolocation (Table 1). We focused on the selection of traits that can be measured directly and quantitatively, but we also presented categorical traits, which have been extensively used in several ecological studies (Cisneros *et al.,* 2016; Castillo-Figueroa & Pérez-Torres, 2018; Farneda *et al.,* 2019; Ramírez-Mejía *et al.,* 2020). In all the traits we indicated the pertaining group (functional complex or functional dimension), the value of the trait (attribute), the way to measure (description), and the source of information where the trait can be obtained (trait obtaining). We also present the ecological information of each trait based on an extensive literature revision of bat ecology.

Study cases from literature

We reviewed the available information that employed the usage of trait-based approach in Neotropical bats by searching in Scopus and Google scholar databases (consulted the 25/09/2020) with the terms "Neotropical Bats" OR "New World bats" AND "Trait-based approach". We obtained 135 document results from Scopus and 541 from Google Scholar. After reviewing carefully each one of the documents we obtained a total of 19 study cases that employed this approach. For each case we recorded location, morphological and natural history traits, and the application of the study. Five of those cases were illustrated to show the type of research questions that can be pursued under trait-based approach.

RESULTS

Morphological Traits

Size complex

Body size is probably one of the most informative traits, and it is also one of the easiest features to measure in bats (MacNab, 2007; Safi *et al.,* 2013; Giannini *et al.,* 2012). In the past few years, body size has been the core of ecological and evolutionary studies (Safi *et al.,* 2013;

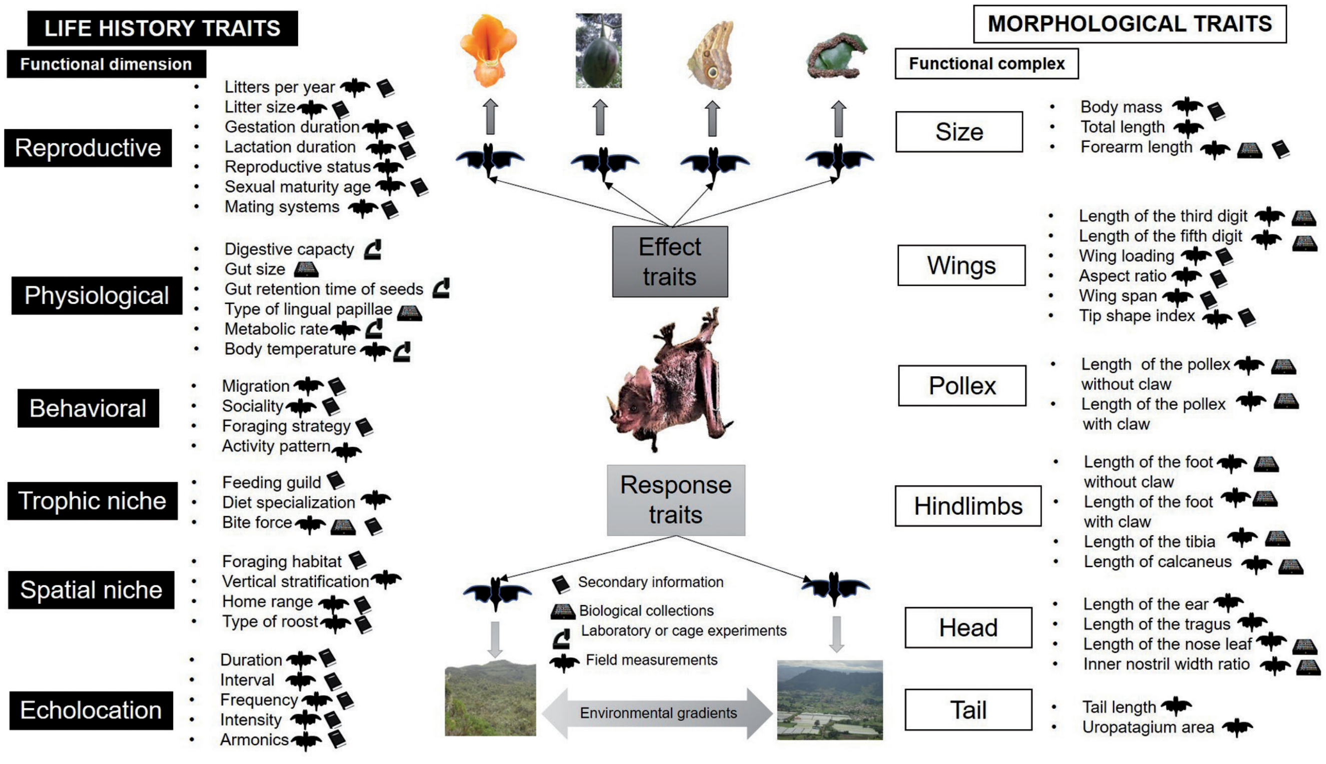

Figure 1. Schematic model of biological traits of Neotropical bats. Life history traits in black boxes whereas morphological traits are depicted in white boxes.

Table 1. Biological traits of Neotropical bats. Morphological traits are grouped into six functional complexes and life history traits are classified into six functional dimensions. In trait obtention: SI = secondary information, FM = field measurement, BC = Biological collections, LE = laboratory or cage experiments.

Trait type	Complex or functional dimension	Trait	Attribute	Trait obtention	Description of the trait
Morphological	Size	Body mass	Value of the trait in grams (g)	SI, FM	Based on weight
		Total length	Value of the trait in millimeters (mm)	FM	Measurement from the tail (if any) to the head (tail + body + head). If there is no tail, the measurement encompasses the lower end of the body to the head
		Forearm length	Value of the trait in millimeters (mm)	SI, FM, BC	Measurement from the base of the elbow (tip of the olecranon process) to the distal region of the forearm where it joins the carpus
	Wings	Length of the third digit	Value of the trait in millimeters (mm)	FM, BC	In biological collections the trait is the result of the sum of the metacarpus and its three phalanges. The metacarpus is measured from the joint with the phalanx to the junction with the carpus. The phalanx is measured as the maximum distance between the joints. In the field, the trait is measured from the junction of the metacarpus with the carpus to the tip of the third phalanx
		Length of the fifth digit	Value of the trait in millimeters (mm)	FM, BC	In biological collections the trait is the result of the sum of the metacarpus and its two phalanges. The metacarpus is measured from the joint with the phalanx to the junction with the carpus. The phalanx is measured as the maximum distance between the joints. In the field, it is measured from the junction of the metacarpus with the carps to the tip of the second phalanx
		Wing loading	Value of the trait in Newtons/m^2	FM, SI	Wing loading (Wl) is body mass in kg times acceleration of gravity (Mg) divided by its wing area in m^2 (S); *gravity acceleration = 9.8 m/s^2; Wl = Mg/S (N/m^2)
		Aspect ratio	Adimensional (numerical)	FM, SI	Aspect ratio (A) is the result of the wing span squared (m^2) (B) divided by wing area (m^2) (S); $A = B^2/S$
		Tip shape index	Adimensional (numerical)	FM, SI	Tip shape index (I) is the tip area ratio (Ts) divided by tip length ratio (Tl) minus Ts; I = Ts/(Tl-Ts)
		Wing span	Value of the trait in millimeters (mm)	FM, SI	Measurement taken from tip to tip of the extended wings held along to the long axis of the body
	Pollex	Length of the pollex without claw	Value of the trait in millimeters (mm)	FM, BC	Measurement from the beginning of the phalanx of finger to the beginning of the claw
		Length of the pollex with claw	Value of the trait in millimeters (mm)	FM, BC	Measurement from the beginning of the phalanx of the thumb to the tip of the claw
	Hindlimbs	Length of the foot without claw	Value of the trait in millimeters (mm)	FM, BC	Measurement from the joint with the tibia to the beginning of the claws
		length of the foot with claw	Value of the trait in millimeters (mm)	FM, BC	Measurement from the tibia joint to the tip of the claw
		Length of the tibia	Value of the trait in millimeters (mm)	FM, BC	Measurement from the joint with the femur to the joint with the foot
		Length of calcaneus	Value of the trait in millimeters (mm)	FM, BC	Measure from the base of the calcaneus to the tip of it
	Head	Length of the ear	Value of the trait in millimeters (mm)	FM	Measure from the base of the ear to its most apical region
		Length of tragus	Value of the trait in millimeters (mm)	FM	Measure from the base to the tip of the structure
		Length of nose leaf	Value of the trait in millimeters (mm)	FM, BC	Measurement from the base of the nasal horseshoe to the tip of the lancet
		Inner nostril width ratio	Adimensional (numerical)	FM, BC	Ratio of the cranial width to the inner nostril width
	Tail	Tail length	Value of the trait in millimeters (mm)	FM	Measurement from the insertion of the tail in the body to its distal end
		Uropatagium area	Value of the trait in area (m^2)	FM	Measurement of the surface area of the intrafemoral membrane
Life history	Reproductive	Litters per year	Mean number of litters during a year	FM, SI	Number of litters produced per year
		Litter size	Mean number of pups per litter	FM, SI	Number of pups produced per litter
		Gestation duration	Mean days in pregnancy	FM, SI	Length of the pregnancy expressed in days
		Lactation duration	Mean days in lactation	FM, SI	Length of the lactation expressed in days
		Reproductive status	For females the frequencies or population averages of each stage: Proestrus. Estrus. Metestrus. Anestrus. For males the frequencies or population averages of: Scrotted males Non-scrotted males	FM	Reproductive stage that involves hormonal concentration (progesterone and estradiol peaks) and physiological changes in females (corpus luteum and ovarian follicle). Vaginal smears can reveal superficial nucleated cells (proestrus), superficial non-nucleated cells parabasal (estrus), intermediate cells (metestrus) and parabasal cells (anestrus) in bat females. Females can be considered reproductive when they presented a dominance in proestrus, estrus, and metestrus. By contrast, non-reproductive females are when the dominant stage is anestrus. This can be measured individually and can also be expressed in frequencies or population averages of each stage. For males, reproductive status can be determined by examining testes (scrotted or not), thus obtaining frequencies or population averages of each condition.
		Sexual maturity age	Mean number of years	FM, SI	Age at first reproductive event (adult)
		Mating systems	Monogamic; Polygyny; Polyandry; Promiscuty	FM, SI	All the potential combinations between bats to find mate and copulate during reproductive season
	Physiological	Digestive capactiy	Food intake response	LE	Bat capacity to obtain nutrients when consumption item differ in nutrient quality. Food intake response is defined as the relationship (following power function) between volumetric food intake and nutrient concentration
		Gut size	Mean surface area (cm^2)	BC	Gut area of the total gut
		Gut retention time of seeds	Mean number of time (minutes)	LE	Time that the seeds are retained inside the gut of the bat until is expelled by feces

Trait type	Complex or functional dimension	Trait	Attribute	Trait obtention	Description of the trait
		Type of lingual papillae	Gustative, including vallate and fungiform, or mechanical comprising basal, postero-median, scalelike, filiform, foliate, conical, and horny	BC	Shape of the papillae in tongue
		Metabolic rate	Mean energetic expenditure (kcal/day)	FM, LE	Energy unit per time required by an individual to maintain its basal physiological functions
		Body temperature	Mean and ranks of body temperature (°C)	FM, LE	Individual capacity to survive at a specific temperature, either hot or cold temperatures
	Behavioral	Migration	Resident; Migratory	FM, SI	Species movement according its life history
		Sociality	Solitary; Society; Group; Colony; Aggregation	FM, SI	Clustering of individuals
		Foraging strategy	Gleaning foragers; Aerial foragers; Trawling foragers	SI	Behavioral strategy that is used to obtain food
		Activity pattern	Number of recording events per time hour	FM	Activity period of bat species within nocturnal time. Commonly spanned from 18:00h to 6:00h
	Trophic niche	Feeding guild	Necterivore; Frugivore; Carnívore; Omnívore; Sanguinivore; Insectívore; Piscívore	SI	Based on the food item that is consumed mainly for a large part of bat life
		Diet specialization	Value of the niche breadth index selected (*e.g.,* Levin, Morisita, etc.) ranging from low values (specialist) to high values (generalist)	FM	Based on the percentage of the contribution of each food item to the total diet the species. Levin index as well as Morisita index can estimate dietary specialization
		Bite force	Maximum bite force (Newtons)	FM, BC, SI	Is the result of the interplay between the teeth, the masticatory muscles, the mandible, the maxillae, and temporomandibular joints. Bite force can be measured *in vivo* with an isometric Kistler force transducer or can be estimated with assessments of muscular and bony morphology from skulls using algorithms
	Spatial niche	Foraging hábitat	Background space; Uncluttered space; Highly cluttered space	SI	It is the space where the bat is found most of the time, especially when searching for food. Resource availability and conditions limit foraging habitat
		Vertical stratification	Capture rate (individuals per mist-net hour) in each strata: Understory; Canopy	FM	Based on the proportion of bat capture rate in ground (shrubs) and canopy nets (treetops). Bats can also use both strata (no preference)
		Home range	Mean surface area traveled during a period of time (km^2)	FM, SI	Area of available habitat over which an individual does its daily activities. There are several ways to estimate home range such as minimum convex polygon, minimum area probabilities, areas of kernel, etc.
		Type of roost	Animal burrow or hole; Termite ant/nest; Cavity in fallen tree; Cavity in standing tree; Exposed on standing tree; Foliage, leaf tent; Foliage, unmodified foliage; Rocks, crevices, or caves; Under fallen tree; Undercut earth bank	FM, SI	Diurnal roosts used by bats
	Echolocation	Duration	Time (ms)	FM, SI	Time span of the call emitted by the bat
		Interval	Time (ms)	FM, SI	Time between one call to another emitted by the bat
		Frequency	Pitch of a sound (Khz)	FM, SI	Number of pressure waves of the call emitted by the bat that pass by a reference point per unit time. This can include the start of the call (initial frequency), the end of the call (final frequency) and the maximum amplitude of the call (maximum frequency)
		Intensity	Strength of the tone signal (db)	FM, SI	Height of the sound pressure wave emitted by the bat
		Harmonics	Number or harmonics (if any)	FM, SI	Wave that is a multiple of the fundamental frequency emitted by the bat

Giannini *et al.,* 2012; Arevalo *et al.,* 2020). Size has remarkable implications in essential functions such as aerodynamic performance (Norberg & Rayner, 1987; Arevalo *et al.,* 2020), echolocation (Barclay & Brigham, 1991; Jones, 1999; López-Cuamatzi *et al.,* 2020; Arevalo *et al.,* 2020), basal metabolic rate (MacNab, 2003), biomechanical properties (Swartz & Middleton, 2008), dietary habits (Norberg & Fenton, 1988), foraging habitats (Muscarella & Fleming, 2007) and other life history traits (Safi *et al.,* 2013). Body measurements, therefore, can be a reliable proxy for general size, being informative regarding environmental changes and ecosystem functions as well (García-Morales *et al.,* 2016; Castillo-Figueroa & Pérez-Torres, 2018).

Body mass: related to morphometric structures including skull size (Aguirre *et al.,* 2002), length of the digestive tract (Bonaccorso, 1979), biomechanics structures of postcranial skeleton (Swartz & Middleton, 2008) and wings (Norberg & Rayner, 1987). Body mass is also linked to other functions associated to wingbeat frequency (Jones, 1999; Norberg & Norberg, 2012), pulse duration (Jones, 1999), peak frequency (Jones, 1999; Thiagavel *et al.,* 2017; López-Cuamatzi *et al.,* 2020), bite force (Aguirre *et al.,* 2002), basal metabolic rate (Kleiber, 1947; Soriano *et al.,* 2002), quantity, quality and time invested in food handling (Fleming, 1991; Gómez-Ortiz & Moreno, 2017), hardness and size of the food (Aguirre *et al.,* 2003), and niche partitioning (Willig *et al.,* 2003). In frugivorous bats, body mass is positively related to foraging height (Rex *et al.,* 2011), food transit time (Laska, 1990), and the consumption of large-sized and low-quality fruits (low concentration of sugars and proteins), with a longer time in handling, processing and intestinal transit (Fleming, 1991; Saldaña-Vázquez, 2014a). Large species are more likely to disperse heavier fruits (López & Vaughan, 2004), colonize and dominate urban environments (Saldaña-Vázquez & Schondube, 2016; Jung & Threlfall, 2018) as well as other human-dominated landscapes (*e.g.,* coffee plantations) (Frank *et al.,* 2017), but are prone to be more vulnerable to habitat loss (Martínez-Ferreira *et al.,* 2020) and fragmentation (Farneda *et al.,* 2015). Body size also determines the foraging habitats of frugivorous bats (Muscarella & Fleming, 2007); that is, small bats with low wing loading and low aspect ratio can potentially forage both in the understory and canopy of forests because of their greater maneuverability. Conversely, larger species with high wing loading and high aspect ratio are less maneuverable and tend to forage in the canopy (Norberg & Rayner, 1987; Muscarella & Fleming, 2007). It has been found that body mass is positively correlated with colony size, which is associated with lower individual predation risk and with certain morphological features such as the absence pelage markings (Santana *et al.,* 2011b). Also, to some extent, body size seems to be positively related to home range in some fig-eating stenodermatines (Kalko *et al.,* 1996).

Total length: this trait comprises the length from the tail, if any, to the head. Total length is associated to body size, developmental stage, and the amount of resources and energy required by bats (Gómez-Ortiz & Moreno, 2017).

Forearm length: a reliable proxy for body size (Dietz *et al.,* 2006; Safi *et al.,* 2013; Thiagavel *et al.,* 2017). In phyllostomid bats, forearm length is positively related to nose leaf length (Arita, 1990). Studies conducted in silvopastoral agricultural systems have shown an increase of forearm length because of the availability of food and roosting sites (Ballesteros-Correa, 2015; Castillo-Figueroa & Pérez-Torres, 2018; Chacón-Pacheco & Ballesteros-Correa, 2019). This trait can be converted to a categorical variable, and the species may be classified in three groups, according to Muñoz (2001) as follows: small (< 40 mm), medium (40 mm-60 mm) and large (> 60 mm). Maneuverability is also related to size; small bats are more likely to perform a better flight performance in highly cluttered habitats than large and fast-flying bats (Thollesson & Norberg, 1991; Stockwell, 2001; Denzinger *et al.,* 2016). Particularly, for insectivorous bats, forearm length is a significant predictor of peak frequency and wing morphology; that is, small species with low wing loadings and low aspect ratios tend to emit higher frequency calls, whereas large species with high wing loading and high aspect ratio are characterized by emit lower frequency signals (Norberg & Rayner, 1987; Thiagavel *et al.,* 2017; Núñez *et al.,* 2019). It has been also found a positive correlation between forearm length and prey size (Houston *et al.,* 2004). For stenodermatinae bats, species that use leaf tents as diurnal roosts display short forearm length than bats that use other type of roosts (Garbino & Tavares, 2018).

Wing complex

Wings are the idiosyncratic structures that distinguish bats from other mammals (Camargo & Oliveira, 2012; Castillo-Figueroa, 2018b). The development of this multivariate flight apparatus was paramount in bat adaptative radiation (Cooper & Sears, 2013), allowing the colonization of several niches in their evolutionary history (Sears *et al.,* 2006). As such, bat wings consist of modifications of forelimbs, characterized by a membrane of skin, known as dactylopatagia, which is stretched between elongated digits (digits II-V) (Wang *et al.,* 2010). Besides the explicit relationship of wings with locomotion and flight performance (Norberg & Rayner, 1987), this structure plays a major role in thermoregulation (Makanya & Mortola, 2007), food handling (Vandoros & Dumont, 2004), habitat use (Marinello & Bernard, 2014; Castillo-Figueroa, 2020a), foraging mode (Marinello & Bernard, 2014), vertical stratification (Olaya-Rodríguez *et al.,* 2019), assistance in delivery of pups and male-male aggression (Swartz & Middleton, 2008).

Length of the third digit: measure of hand-wing length. A high ratio between third digit length and forearm length indicates long wings and thereby fast flights and low energy expenditure (Dietz *et al.,* 2006; Castillo-Figueroa, 2020a). Lower values of length of the third digit in relation to length of the fifth digit indicate short wings adapted to a slow flight in narrow habitats (Dietz *et al.,* 2006; Castillo-Figueroa & Pérez-Torres, 2018). Altogether with forearm length and length of the fifth digit, this trait is a good proxy of wing morphology (Findley *et al.,* 1972).

Length of the fifth digit: measure of the wing width. A high ratio between the length of the fifth digit and forearm length indicates wide wings with high maneuverability and hovering capacity (Dietz *et al.,* 2006; Castillo-Figueroa, 2020a), slow flights and low wing loading (Lisón, 2012). A high ratio between the length of the third digit and the fifth digit indicates long wings, adapted to fast flight in uncluttered habitats and open areas (Dietz *et al.,* 2006). This measure together with forearm length and length of the fifth digit is a good proxy of the wing morphology (Findley *et al.,* 1972).

Wing loading: defined as the relationship between weight and wing area, wing loading reflects the flight speed and the ability to load items during the flight (Giannini & Brenes, 2001). Small bats have low wing loadings (Norberg & Rayner, 1987; Thollesson & Norberg, 1991), whereas large bats that carry heavier fruits, preys and pups (in the case of reproductive females), usually have higher wing loadings (Norberg & Rayner, 1987; Thollesson & Norberg, 1991). This trait is positively related to higher heart mass, thus compensating for the energy expenditure generated by rapid flights (Rodríguez-Durán & Padilla-Rodríguez, 2008). Bats with high wing loadings are suitable to better exploit uncluttered habitats with few dodges and obstacles, whereas in highly cluttered areas bats with low wing loadings are more likely to use efficiently these habitats (Norberg & Rayner, 1987; Kalcounis & Brigham, 1995; Marinello & Bernard, 2014). Due to this, bats with high wing loading are more tolerant to urban and suburban areas because this trait favor high-speed flight at low-energy cost, allowing for the exportation of open environments which are quite common in cities (Jung & Threlfall, 2018; Ramírez-Mejía *et al.,* 2020). Wing loading is also related to echolocation traits. Bats with high wing loading and high aspect ratio are likely to produce long-duration signals and low frequency calls (Norberg & Rayner, 1987; Jones, 1999). By contrast, bats with low aspect ratio and low wing loading are more likely to generate echoes characterized by high frequency and short-duration signals (Norberg & Rayner, 1987; Jones, 1999). High wing loading in frugivorous bats also indicates higher flexibility in the use of space and a higher ability to move between fragments (Farneda *et al.,* 2015; Frank *et al.,* 2017), contrary to species with low wing loading which are prone to be negatively affected by habitat loss and fragmentation (Frank *et al.,* 2017; Martínez-Ferreira *et al.,* 2020).

Aspect ratio: reflects the wing width in relation to the body (wing narrowness) and is positively related to flight efficiency and flight speed (Norberg & Rayner, 1987; Thollesson & Norberg, 1991) and inversely related to flight energy expenditure (Giannini & Brenes, 2001). Species with a higher aspect ratio have constant and high-speed flights at low-energy costs generally in upper strata (Blood & McFarlane, 1988; Saunders & Barclay, 1992), as well as long commuting flights (Giannini & Brenes, 2001). By contrast, species with lower values in aspect ratio have slower but more maneuverable flights generally in low strata (Blood & McFarlane, 1988; Thollesson & Norberg, 1991; Saunders & Barclay, 1992). Species that forage in open and uncluttered areas, like many aerial insectivores, have high aspect ratios, whereas species typical of cluttered spaces such as forest interiors have low aspect ratios (Norberg & Rayner, 1987). Bats with high aspect ratio and high wing loading tend to produce echolocation calls of low frequency and long duration, whereas bats that display low aspect ratio and low wing loading are more likely to emit calls of high frequency and short duration (Norberg & Rayner, 1987; Jones, 1999). In frugivorous bats, low aspect ratio explains higher diversity of fruits consumed because of slow and highly maneuverability flights that allow to forage in all forest strata (Laurindo *et al.,* 2020). It has been found that bats with low aspect ratio tend to be negatively affected by habitat loss and fragmentation (Martínez-Ferreira *et al.,* 2020), whereas bats with high aspect ratio seems to be more tolerant to human-made landscapes such as urban and suburban areas, since they are able to exploit open environments (Jung & Threlfall, 2018).

Tip shape index: wingtip shape estimates wingtip geometry (Norberg & Rayner, 1987) and indicates maneuverability within dense vegetation (Findley & Wilson, 1982). Tip shape varies depending on the forest strata used by particular species, being higher in understory vegetation (Olaya-Rodríguez *et al.,* 2019). According to this index, wingtips can be triangular (I = 0), rounded (I > 0), or pointed (I < 0) (Norberg & Rayner, 1987; Norberg, 1990, 1994). Bats with large tip shape index (rounded) perform low flight speed, whereas bats that display small tip shape (pointed) can make flights with high roll acceleration (Thollesson & Norberg, 1991). Tip shape index is also related to echolocation traits. Pointed wingtips are related to calls with low frequency and long duration, whereas rounded wingtips are associated to echoes characterized by high frequency and short duration (Norberg & Rayner, 1987). In the case of insectivorous bats, rounded wings are related to generalist diet because of higher maneuverability that allow to exploit a high diversity of habitats and prey items, whereas pointed wings are related to specialist diet as a consequence of less maneuverable flights that restrict bat foraging to a narrow range of habitats and preys (Magalhães de Oliveira *et al.,* 2020).

Wing span: measure showing the amplitude of the extended wings over the long axis of the body (Thollesson & Norberg, 1991). Higher flight speed is common in bats that present shorter wing span and thinner body, whereas lower flight speed is common in bats that display longer wing span and large wing area (Thollesson & Norberg, 1991). Similar to birds, this trait can be related to size, dispersion capacity and flight performance (Claramunt *et al.,* 2012).

Pollex complex

The pollex (thumb) is the only structure of the forelimbs that has not been drastically modified for powered flight in bats (Granatosky, 2018). However, the pollex is very important in other functions such as terrestrial quadrupedal locomotion (Granatosky, 2018), food manipulation, perching and climbing over several types of substrates (Walldorf & Mehlhorn, 2013). The length of the pollex can vary from being vestigial (Furipteridae), very small (Thyropteridae) to very developed (*e.g., Desmodus rotundus*). This body complex is probably, one of the less investigated in terms of ecological variations.

Length of the pollex without claw: related to food handling and locomotion. This trait is not integrated into the membrane and therefore has a function to grip, hold and scale (Walldorf & Mehlhorn, 2013). The pollex varies considerably in size across guilds. Species that use the pollex to manipulate food, move or perch, display longer pollex length (Myers *et al.,* 2016). In the case of blood-eating bats and particularly in *Desmodus rotundus,* longer pollex allows them to propel themselves from the ground to fly.

Length of the pollex with claw: related to food handling, including fruits (Uieda & Vasconcellos-Neto, 1984) leaves (Pereira *et al.,* 2017), and flowers (Vieira & Carvalho-

Okano, 1996; Tschapka, 2003; Sazima *et al.,* 2003). Claws are also useful in climbing ability and defend from other bats (Myers *et al.,* 2016).

Hindlimbs complex

Depending on the guild, the legs can be involved in key roles including prey capture (Fish *et al.,* 1991), walking on the ground (Dietz, 1973), and food handling (Vandoros & Dumont, 2004). The claws have a key function saving energy expenditure by perching with the tendon locking mechanism in roosting sites (Quinn & Baumel, 1993).

Length of the foot without claw: related to the perching behavior, the capture of some preys and locomotion. The foots are useful in food-handling behaviors and are related to the type of suspension during food consumption (Vandoros & Dumont, 2004).

Length of the foot with claw: related to the absolute drag force (air resistance) and the type of prey consumed (Fish *et al.,* 1991). Higher values of the length of the foot with claw generate more absolute drag force but allow the capture of larger preys such as fishes and other vertebrates. Piscivorous bats have large foots, long and sharp claws (Denzinger *et al.,* 2016) that can rotate 180 degrees to hook the slippery fishes they catch from the water (Fish *et al.,* 1991). In nectarivorous bats that rely on landing on the flowers/inflorescences as foraging strategy, claws are useful in resource exploitation of flowers (Vieira & Carvalho-Okano, 1996; Tschapka, 2003; Sazima *et al.,* 2003). Large claws also are used in the manipulation of fruits (Uieda & Vasconcellos-Neto, 1984) and preys (Fish *et al.,* 1991).

Length of the tibia: measurement related to size (Swartz & Middleton, 2008; Giannini *et al.,* 2012). This trait has been poorly studied, but it is likely related to moving on surfaces such as foliage, soil, woods, among others. In bats with developed uropatagium, the width and maneuverability of this membrane is related to the length of the tibia.

Length of calcaneus: process that articulates with the posterolateral surface of the proximal region of the calcaneus (tarsal bone) (Adams & Thibault, 1999). The calcaneus helps the uropatagium to change its curvature giving rigidity and flexibility simultaneously, thus being important in the aerodynamics of the flight by avoiding wind resistance, and improving maneuverability and hovering (Adams & Thibault, 1999). In the case of insectivorous species, the calcaneus has a key role in prey capture, as it helps to stretch the uropatagium to catch insects and take them to the mouth (Webster & Griffin, 1962).

Head complex

The head integrates the bulk of sensory functions in bats. Particularly, New World bats have a broad spectrum of morphological adaptations in the olfaction, which in some species are important for detecting resources such as ripe fruits (Mikich *et al.,* 2003; Bianconi *et al.,* 2007) insects (Hurtado *et al.,* 2015), shelter and mates (Brokaw & Smotherman, 2020). Indeed, external nasal morphology is strongly related to diet and foraging ecology (Brokaw & Smotherman, 2020). Echolocation is a key feature for bats to detect and track preys and avoid obstacles as well. By doing so, the external ears receive the echoes of the environment and the tragus filters this information for localizing auditory targets (Chiu & Moss, 2007). Thus, ear and nose traits are key to the acquisition of food, spatial orientation, and intraspecific and interspecific communication.

Length of the external ear: main structure of the acoustic system of bats that maximize the distance in which they can receive sound signals. This trait allows to locate potential preys, members of the same species (Balcombe & Fenton, 1988), and detect predators (Fenton, 1980). Larger ears contribute to detect low auditory threshold of ultrasonic uptake, amplify incoming soundwaves from its surrounding, and improve the sensitivity of echolocation and directionality (Obrist *et al.,* 1993; Huihua *et al.,* 2003; Håkansson *et al.,* 2017). Large ears may also hamper aerodynamic performance as they generate wind resistance during the flight (Gardiner *et al.,* 2011a), precluding high-speed aerial acrobatics (Razak, 2018). During slow flights, however, large ears contribute to lift generation (Håkansson *et al.,* 2017). Importantly, ear size is also related to foraging strategy and foraging habitats; that is, gleaning bats with large ears use them for passive listening and detecting preys, whereas bats with small ears usually fly faster in uncluttered habitats (Norberg & Rayner, 1987; Gardiner *et al.,* 2011a; Håkansson *et al.,* 2017). Therefore, length of the ear size is associated to the composition of preys consumed, which may affect the ability of each species to regulate particular group of arthropods.

Length of tragus: this structure is a skin flap located lateral to the ear canal that is likely to affect the incoming acoustic signal, but also may generate spectral cues for vertical sound localization (Chiu & Moss, 2007). The tragus has a functional contribution to the directivity patterns (Müller, 2004), and to elevation-dependent spectral cues which enable successful prey capture performance (Chiu & Moss, 2007). The degree of inclination aids in detecting and processing acoustic signals (Müller, 2004). For gleaning animalivores, the tragus is more developed, providing gain for frequencies (10-20 kHz) to capture preys more efficiently (Müller, 2004; Razak, 2018).

Length of nose leaf: typical structure of phyllostomid bats. This trait is mainly related to nose-emitted echolocation (King *et al.,* 2013), and the length of the nasal spear correlates with the length of the forearm (Arita, 1990). Larger leaf-nose can be potentially associated with an increased ability to direct sound during echolocation in the vertical plane, allowing thus a more precise detection of food items in the dense foliage such as insects, fruits, and nectar (Martínez-Ferreira *et al.,* 2020). This because a more developed leaf-nose favor a higher directionality of sonar beam, which gives two principal advantages to the species by, firstly, reducing the echoes from the periphery of the bat, minimizing thus the information that should be processed to detect objects and, secondly, enhancing the detection range by focusing the sound energy into an specific target (Martínez-Ferreira *et al.,* 2020). Species that use hearing to locate roost or food have more developed nose leaf spears as is the case of species of Phyllostominae (Arita, 1990) and Lonchorhininae subfamilies (Brokaw & Smotherman, 2020). Conversely, species that use vision or smell to locate the food, do not have large nose leaves, as is the case of Desmodontinae species (Arita, 1990). Secondary sexual dimorphism has been found in this structure in Phyllostominae bats (Hurtado *et al.,* 2015), probably because females forage more intensely during pregnancy and breastfeeding, so they have developed significantly larger nose leaves than males to improve their foraging efficiency (Hurtado *et al.,* 2015). In response to environmental conditions, leaf nose manipulation modulates the shape of the sound beam by adjusting the directionality (Martínez-Ferreira *et al.,* 2020). For example, in structurally complex vegetation the leaf nose can modify frequency and intensity of the emitted sound, thus adjusting the search volume and the perception of vegetation structure, which ease the navigation in clutter habitats (Arita, 1990). In this sense, forest loss affect negatively species with large leaf-nose that forage in the dense foliage (Martínez-Ferreira *et al.,* 2020).

Inner nostril width ratio: reflects the separation between receptors in bats (nostrils). Considering that the maximum separation of the nostrils is restricted by the cranial width (Stoddart, 1979), lower values of the inner nostril width ratio indicate wider nostrils and higher values entails narrow nostrils (Brokaw & Smotherman, 2020). Wider separation between nostrils increase the effective area and the ability to detect different chemical signals from the environment (Stoddart, 1979). Diet, foraging habitat, foraging strategy, and echolocation are related to nostril separation (Brokaw & Smotherman, 2020). Insectivorous bats that use uncluttered habitats, exhibit aerial foraging, and employ the oral mode of echolocation, show lower inner nostril width ratio (Brokaw & Smotherman, 2020).

Tail complex

Although the structures of forelimb are mainly responsible for flight performance, the structures that support the tail membrane (uropatagium) are important for aerial locomotion, especially in maneuverability and thrust during horizontal takeoffs (Gardiner *et al.,* 2011b; Adams *et al.,* 2012). Moreover, uropatagium performs a key role in prey capture for insectivorous bats (Webster & Griffin, 1962; Saunders & Barclay, 1992; Kalko, 1995), carrying pups during the reproductive season (Adams & Thibault, 1999), and in thermoregulation through blood perfusion (Reeder & Cowles, 1951).

Tail length: the tail and the surrounding membrane (uropatagium) are involved in flight performance by providing greater maneuverability (Gardiner *et al.,* 2011b). These structures also provide thrust and horizontal displacement during the flight (Adams *et al.,* 2012). Species with tails and larger uropatagia have better flight control (Gardiner *et al.,* 2011b).

Uropatagium area: as a membrane structure, the uropatagium is an aerodynamic surface related to wing loading and should be included in flight performance assessments (Marinello & Bernard, 2014). Larger uropatagium improves flight agility (Gardiner *et al.,* 2011a, 2011b; Adams *et al.,* 2012) and prey capture (Kalko, 1995). Species that consume evasive flying preys, such as moths, have a larger uropatagium (Saunders & Barclay, 1992). Similarly, other bat guilds including piscivores and animalivores also have a large uropatagium area (Marinello & Bernard, 2014). The uropatagium is also useful when carrying pups during the reproductive season and its manipulation is largely controlled by the calcaneus (Adams & Thibault, 1999). Also, it has been proposed that nectar-eating bats uropatagium serves to transport pollen from one flower to another (Aguilar-Rodríguez *et al.,* 2019).

Life History Traits

Reproductive dimension

Bats have a diversity of mating systems and reproductive strategies in response to environmental conditions (Crichton & Krutzsch, 2000). Many of the reproductive traits are heavily determined by the distribution of food resources through time and space as well as ambient temperature (McGuire & Boyle, 2013; Saldaña-Vázquez *et al.,* 2020). In the Neotropics, reproductive patterns of many species can be synchronized with rainy seasons (Mello *et al.,* 2004; Kunz *et al.,* 2009), due to the increase of resources, mainly fruits and insects (Altringham, 2011). Nonetheless, with some exceptions, reproductive traits are poorly investigated in New World bats and the effects of habitat perturbation on reproduction are still unknown.

Litters per year: reflects reproductive output (Barclay & Harder, 2003), availability and demand of trophic and spatial resources (Gómez-Ortiz & Moreno, 2017). Bats tend to employ different reproductive strategies to produce offspring in favorable environments during specific times of the year (Fleming *et al.,* 1972; Mello *et al.,* 2004). For example, there is a correspondence between fruit abundance and arthropod biomass with rainfall, thus influencing reproductive timing for frugivorous and insectivorous bats, respectively (Crichton & Krutzsch, 2000). It is important to highlight, however, that food availability rather than climatic factors underlies the timing of reproductive events in Neotropical bats (Crichton & Krutzsch, 2000).

Litter size: related to bat fecundity (Barclay & Harder, 2003). Litter size is influenced by several characteristics such as maternal body mass, pup mass and food intake (Speakman, 2008). In the case of insectivorous bats, dietary characteristics including the capacity to obtain calcium may constrain litter size (Barclay, 1994).

Gestation duration: reflects the demand of trophic and spatial resources (Gómez-Ortiz & Moreno, 2017). The length of the pregnancy is a key period in bat reproduction (Crichton & Krutzsch, 2000), which is influenced by availability of food, and environmental factors. Bats with long gestation periods are unable to react faster to short-term environmental fluctuations, thus their reproduction strategy lies into predictable seasonal changes to maximize reproductive success (Crichton & Krutzsch, 2000).

Lactation duration: this is the most energetically costly period (Speakman, 2008), in which bats increase the consumption of food during the early weeks of lactation to milk production and export (Kunz *et al.,* 1995). Therefore, food availability is a key factor in determining the ability of females to obtain nutrients for reproduction (Gómez-Ortiz & Moreno, 2017). Bats display a correspondence between lactation, or at least a part of it, and the peak of food availability (Crichton & Krutzsch, 2000).

Reproductive status: related to fertility and timing of pregnancy (Stukenholtz *et al.,* 2018) and can be influenced by environmental conditions (Vela-Vargas *et al.,* 2016). Rather than temperature cycles (Crichton & Krutzsch, 2000), rainfall seasonality may be the critical factor in Neotropical bat reproduction by influencing either directly reproductive activity or indirectly the availability of food resources (Mello *et al.,* 2004; Montiel *et al.,* 2011). During oestral cycle, hormone concentrations, mainly progesterone and estradiol, determine reproductive status in bats (Stukenholtz *et al.,* 2018). Based on the monitoring of the reproductive status of males and females, four basic reproductive patterns of Neotropical bats can be distinguished: (1) reproduction all the year (*e.g.,* Desmodontinae), (2) a long reproductive period with a short period of reproductive inactivity (*e.g.,* Vespertilionidae) (3) bimodal seasonal polyoesstry defined by two reproductive peaks during the year (*e.g.,* frugivorous from Phyllostomidae) and, (4) seasonal monoestry characterized by a single reproductive period during the year (*e.g.,* Noctilionidae) (Fleming *et al.,* 1972; Mello *et al.,* 2004).

Sexual maturity age: the more time needed to reach adult age, the more demand for trophic and spatial resources (Gómez-Ortiz & Moreno, 2017). This trait is also related to demography. Thus, generalist bats that become adults in a short time (*e.g.,* four months) are more likely to have a higher abundance of adults in bat colonies (Mello & Fernandes, 2000).

Mating systems: related to reproductive success, the protection of the offspring and the demand for trophic and spatial resources (Gómez-Ortiz & Moreno, 2017). Mating systems are a consequence of bat that live in groups, where all the possible combinations to find a mate during reproduction are included (Davies *et al.,* 2012). These systems entail intraspecific interactions where antagonistic reactions can occur in both sexes (*i.e.,* sexual conflicts) (Davies *et al.,* 2012). More broadly, mating systems can be classified into monogamic when male mates with only one female and the parental investment is the same for both sexes or polygamic when different combination between males and females can occur during breeding season (*i.e.,* polyandria, polygyny, promiscuity). Species such as *Vampyrum spectrum* are monogamous, *Carollia perspicillata, Artibeus lituratus* and the bulk of the bats are polygynous, and *Eptesicus fuscus* are promiscuous (Altringham, 2011).

Physiological dimension

Physiological traits are among the most important in terms of the relationships with ecosystem processes. The way in which bats obtain the maximum amount of energy has remarkable effects on the interaction with their environment (Ayala-Berdon *et al.,* 2013). Due to the experimental difficulties of their measurements but also the key information provided, these measurements are considered as "hard traits" (*sensu* Hodgson *et al.,* 1999). Bat ecology is constrained by different environmental factors that encompass mean atmospheric temperature and humidity (McCain, 2007), as well as the availability of food resources (Montiel *et al.,* 2011). Hence, several adaptations in physiological functions including echolocation, digestion, flight, thermoregulation and movement have been accomplished in the natural history of this mammal group.

Digestive capacity: directly related to diet diversity (Saldaña-Vázquez *et al.,* 2015). In nectarivorous bats, rates of hexose assimilation as well as affinity of sucrase for its substrate affect the food quantity that an individual is capable to digest (Ayala-Berdon *et al.,* 2013). Bats with higher digestive capacities can maintain a constant nutrient intake independently of diet quality (Ayala-Berdon & Schondube, 2011; Saldaña-Vázquez & Schondube, 2013). Also, high digestive capacity of bats to acquire and store energy from food intake can confer the ability to survive at montane and cold environments efficiently (Ayala-Berdon *et al.,* 2013; Cruzblanca-Castro *et al.,* 2018; Ortega-García *et al.,* 2020). This means that physiological capacities to process energy are likely to influence spatial distribution of bats (Ayala-Berdon *et al.,* 2013; Cruzblanca-Castro *et al.,* 2018).

Gut size: gut plays a central role in diet diversity, especially in frugivorous bats (Saldaña-Vázquez *et al.,* 2015). Larger gut size increases energy intake in low-quality food items (Karasov *et al.,* 2011; Cruzblanca-Castro *et al.,* 2018), enabling their digestion and potential germination of pioneer plants (Saldaña-Vázquez, 2014a), but also may reduce viability of other seed species (Traveset, 1998). By contrast, shorter gut size contains a greater amount of lymph in the tissues which represents rapid assimilation of nutrients (Oliveira & Lemes, 2010). Gut size may also limit food intake volume in nectarivorous bats (Ayala-Berdon & Schondube, 2011).

Gut retention time of seeds: the time that seeds remain in the gut of an animal can prompt heavily effects for plant reproduction (Traveset, 1998). Retention of seeds may influence plant fitness through dispersal distance and gene flow (Murray *et al.,* 1994; Shilton *et al.,* 1999), recruitment of new individuals to plant populations (Schupp *et al.,* 2010), and the seed germination (Baldwin & Whitehead, 2015); therefore, the role of this trait may be pivotal in effective seed dispersal. Optimum retention time enables seed scarification (Jacomassa & Pizo, 2010) and decreases minimum imbibition time, thus increasing germination probability of seeds, especially in dry ecosystems (Naranjo *et al.,* 2003). Nevertheless, depending on the ecological context (the seeds, the dispersers, and environments), longer gut retention time can enhance seed germination (cleaning the pulp and with seed scarification) or, conversely, can reduce seed viability (damaging the seed with the acid environment of the gut) (Traveset, 1998). Overall, Neotropical bats present shorter food transit times, usually less than 1 h (Fleming, 1988; Baldwin & Whitehead, 2015), which may be the best strategy to maximize energy gain in frugivorous bats, when eating a low-quality diet (Laska, 1990). Some studies have shown that gut retention time in bats can increase germination success but does not influence germination speed (Baldwin & Whitehead, 2015). It is important to highlight that gut retention time is not only determined by intrinsic morphological and physiological features of the disperser animal, but also by extrinsic factors related to the food ingested such as nutrient composition, secondary compounds, consistency, mass, hardness and amount ingested (Laska, 1990; Cipollini & Levey, 1997; Traveset, 1998; Baldwin & Whitehead, 2015).

Type of lingual papillae: lingual physiology can be useful in elucidating dietary preferences and evolutionary patterns of feeding habits (Gregorin, 2003). Variations in papillae shape and distribution on the tongue are related to the way of capturing prey, the ingestion, and the diet (Pastor *et al.,* 1993). For instance, in frugivorous bats that are not able to swallow big fruits, they can absorb the juice and avoid the fiber by using the mechanical and gustatory papillae (Gunawan *et al.,* 2019), whereas nectivorous bats can perform nectar extraction by using a tongue with hair-like papillae or tongues with lateral grooves (Fleming *et al.,* 2009; Tschapka *et al.,* 2015; Lacher *et al.,* 2019). The different types of lingual papillae may also vary at intra-specific level and between habitats or geographical locations (Gunawan *et al.,* 2019).

Metabolic rate: related to the demand for trophic resources, energy expenditure (Gómez-Ortiz & Moreno, 2017) and body mass (Kleiber, 1947; Soriano *et al.,* 2002; MacNab, 2003). Variations in metabolic rate can also be related to feeding habits; that is, highest rates of metabolism are likely to be found on nectarivores, followed by frugivores, intermediate rates in frugivorous-insectivorous, and the lowest rates in hematophagous and insectivorous guilds (Soriano *et al.,* 2002). Several environmental factors can affect metabolic efficiency such as rain through increasing the energy cost in bat flight (Voigt *et al.,* 2011), ambient temperature via thermoregulation at lower and higher temperatures, elevation in which phytophagous bats can increase metabolic rate with increasing altitude (Soriano *et al.,* 2002), and food quality that affect food volumetric ingestion and therefore energy intake (Ortega-García *et al.,* 2020).

Body temperature: stress can elicit changes in body temperature (Muise *et al.,* 2018; Ortega-García *et al.,* 2020). Increasing rapidly body temperature may be critical to escape predators while roosting during day (Muise *et al.,* 2018). The reduction of metabolic rate is related to a subsequent decreasing in heart rate and body temperature, which is strongly related to ambient temperature (O'Mara *et al.,* 2017). For example, nights with rains, high winds and low ambient temperatures increase the use of torpor as a consequence of less energy intake (Klug & Barclay, 2013; Ortega-García *et al.,* 2020). Other factors such as poor foraging condition may increase the use of torpor, and reproduction (*e.g.,* lactation and early development) may influence the thermoregulatory strategies employed by bats to control body temperature (Klug & Barclay, 2013). Body mass is also related to body temperature given that large bats can better regulate their temperature than small bats regardless the guild (Soriano *et al.,* 2002).

Behavioral dimension

Behavioral traits in New World bats are poorly known, mainly because of their cryptic lifestyles. Behavioral information is the cornerstone for many essential aspects of bats such as demography, ecological constraints, intra- and interspecific interactions (Kerth, 2008). Moreover, behavioral changes are useful indicators of human-made habitat modification, as they may be an appropriate measure of sensitivity to disturbances other than traditional measures of species richness or abundance (Presley *et al.,* 2009; Montaño-Centellas *et al.,* 2015).

Migration: migration events during the reproductive season are necessary for some bats. Females' migrations to warmer sites improve prenatal development, thus enhancing breeding success (Saldaña-Vázquez *et al.,* 2020). During migration bats flight over long distances and thereby this trait is linked to the demand for trophic and spatial resources, torpor, lethargy and temporary segregation (Esbérard *et al.,* 2011; Gómez-Ortiz & Moreno, 2017). Furthermore, altitudinal migration over shorter distances can be performed by bats because of seasonal variation in food resources across elevational gradient

(McGuire & Boyle, 2013), but also to find appropriate sites for breeding (Saldaña-Vázquez *et al.,* 2020). This altitudinal movement may constitute an important factor affecting bat interactions with plant species they disperse and/or pollinate (Saldaña-Vázquez *et al.,* 2020), or insects they prey at different periods thought the year.

Sociality: bat aggregation may reduce energetic expenditure due to thermoregulatory demands in lactating mothers and juveniles (Agosta, 2002; Klug & Barclay, 2013). Ecological factors such as roost or shelter limitation could forces bats to aggregate, even in contexts where group living is detrimental (Kerth, 2008). Moreover, physiological demands, demographic predispositions including philopatry, longevity and overlapping generations influence sociality in bats (Kerth, 2008). Depending on whether bats forage in a group or solitary could influence individuals' movement paths and spatial patterns of seed rain.

Foraging strategy: the way to capture the food allows species to take advantage of habitat heterogeneity and generate a higher resource partition in ecosystems (Patterson *et al.,* 2003). It has been suggested that the more forage strategies, the more resources and habitats can be used by bats, which may be linked to a greater number of ecological processes (Mora-Fernández *et al.,* 2013). Foraging strategy is related to diet; for example, insectivorous bats obtain their food primarily as aerial foragers but can also present a gleaning behavior; carnivorous, omnivorous and hematophagous bats consume some animals or parts of them (*e.g.,* blood) that are captured in the foliage or some surface by employing different senses to locate their food (Kalko *et al.,* 2008). Frugivorous bats can be canopy or understory since vertical stratification is associated to resource allocation because in each of these strategies there are differences in the quantity and quality of fruits they consume (Bonaccorso, 1979; Soriano, 2000). Also, foraging strategy in frugivorous bats are related to displacements performed per night to obtain the fruits and in the associations with the fruiting patterns of the plants (*Big bang* for canopy bats or *Steady state* for understory bats) (Bonaccorso, 1979; Soriano, 2000). Foraging strategy is also related to foraging habitat, since uncluttered areas (and in some cases background) are suitable places for aerial foragers, whereas narrow habitats are suitable for bats that gather their food on the foliage (Kalko *et al.,* 2008), in the canopy or at understory level (Bonaccorso, 1979; Soriano, 2000). In the case of nectarivorous bats, trap-lining foraging contributes to efficiency as pollen dispersers over long distances, promoting outcrossing in plants (Muchhala & Thomson, 2010). These foraging strategies are likely to influence plants distribution patterns.

Activity pattern: bat activity represents an important niche dimension because indicates how species exploit the environment (Presley *et al.,* 2009). The optimization of activity times is critical for the species survival (Di Blanco *et al.,* 2017), and the bulk of these temporal events are associated with predatory and anti-predatory strategies as well as temporary segregation (Thies *et al.,* 2006; Gómez-Ortiz & Moreno, 2017). Environmental factors such as rain (Voigt *et al.,* 2011), humidity (Ferro-Muñoz *et al.,* 2018) and temperature (Barclay, 1985; Verde, *et al.,* 2018; Ferro-Muñoz *et al.,* 2018) may influence energy expenditure by constraining foraging activity times. Bat activity patterns may also respond to local disturbance (Montaño-Centellas *et al.,* 2015), habitat conversion (Presley *et al.,* 2009), and availability to ripe fruit in the case of frugivorous (Thies *et al.,* 2006). Other factors including moonlight intensity displays a negative relationship to bat activity, especially for those species that forages in open habitats such as water surfaces and forest canopy (Saldaña-Vázquez & Munguía-Rosas, 2013).

Trophic niche dimension

New World bats, particularly from Phyllostomidae family, show a high diversity feeding habits as well as foraging strategies to obtain their food. According to optimal foraging theory (MacArthur & Pianka, 1966; Schoener, 1971), an animal displays the best strategy to accomplish the maximum benefit with the lowest energetic cost. In line with this argument, Neotropical bats are under several ecosystem contexts in which many extrinsic and intrinsic factors influence the ability to exploit food and better maximize energetic gains (Saldaña-Vázquez, 2014a). The consequences of the interactions between bats and their food resources are reflected in ecosystem functions associated to seed dispersal, pollination, arthropod suppression, vertebrate control, and the regulation of pathogens and diseases (Kunz *et al.,* 2011; Kasso & Balakrishnan, 2013; Lacher *et al.,* 2019; Castillo-Figueroa, 2020b).

Feeding guild: reflects the strategy of resource partitioning within bat assemblages (Wilson, 1973; Giannini & Kalko, 2004). Diet is related to processes such as seed dispersal (frugivorous), pollination (nectarivorous), pest and disease control (insectivorous) (Mora-Fernández *et al.,* 2013). Dietary characteristics are related to several morphometric traits of the skull (Santana *et al.,* 2012), jaw (Monteiro & Nogueira, 2010) teeth (Santana *et al.,* 2011a), wing morphology (Marinello & Bernard, 2014), inner nostril width ratio (Brokaw & Smotherman, 2020), and bite force (Nogueira *et al.,* 2009) This trait is also a predictor of vulnerability to fragmentation (Farneda *et al.,* 2015) and is related to species sensitivity to environmental changes affecting food resources (Ramírez-Mejía *et al.,* 2020).

Diet specialization: in frugivorous bats is related to intrinsic factors including foraging behavior, mouth morphology, bite force, digestive physiology (Saldaña-Vázquez, 2014a) and body size (Saldaña-Vásquez & Schondube, 2013). Likewise, dietary specialization has shown relationships with extrinsic factors such as plant phenology (Thies & Kalko, 2004), the physical characteristics of the fruit, the non-digestible material, secondary metabolites, nutrients, fruit energy (Saldaña-Vázquez, 2014a), latitude, altitude, and ecoregion (Saldaña-Vásquez & Schondube, 2013). This trait is also a key factor that determines the structure of the bat assemblage (Saldaña-Vázquez, 2014a) and are likely related to floristic diversity and supply of resources where the species are found (Fleming, 1986; Loayza *et al.,* 2006). Considering intraspecific characteristics, dietary specialization can differ between males and females (Alviz & Pérez-Torres, 2020) and between reproductive stages (Bohlender *et al.,* 2018). Interestingly, this trait is not related to habitat fragmentation (Meyer *et al.,* 2008; Farneda *et al.,* 2015), despite that this process isolates and reduces resources for many species (Pérez-Torres, 2004). Nonetheless, narrow dietary breath is related to extinction risk in insectivorous bats (Boyles & Storm, 2007). Wing morphology seems to be related to dietary specialization. For example, frugivorous bats with low aspect ratio tend to have a high dietary breadth due to slow and highly maneuverability flights that enable to forage in all forest habitats (Laurindo *et al.,* 2020). Similarly, for insectivorous bats, individuals with more rounded wings have a more generalist diet, whereas individuals with more triangular and pointed wings present specialized diets (Magalhães de Oliveira *et al.,* 2020).

Bite force: reflects the performance of the whole organism and can be linked to the fitness (Anderson *et al.,* 2008; Davis *et al.,* 2010), because of its influence on the spectrum of available food and niche partitioning (Aguirre *et al.,* 2003). Bite force is strongly correlated to body mass (Aguirre *et al.,* 2002), food size and food hardness (Aguirre *et al.,* 2003), limiting dietary selection in bats. Importantly, bite force is also related to size gap angle and bite point (Dumont & Herrel, 2003; Santana, 2015), skull and mandibular shape (Nogueira *et al.,* 2009), as well as temporalis muscle mass, temporalis fiber length and masseter muscle mass (Herrel *et al.,* 2008).

Spatial niche dimension

Bats can occur in almost all the environments of the Neotropics, ranging from sea level to montane forests and paramos across different ecosystems with a diversity of vegetational physiognomies, habitat complexities, and landscapes characteristics (including man-made environments and structures). Accordingly, bats have developed different strategies, morphological adaptations and aerodynamic features to use the horizontal and vertical space. In doing so, bats can move genetic material (*e.g.,* pollen or seeds) between sites, promoting plant reproduction (Quesada *et al.,* 2003). Bats can also track their preys thought the space and time, being important as agents for the suppression of agricultural pests (McCracken *et al.,* 2012).

Foraging habitat: related to echolocation conditions and foraging strategy (Schnitzler & Kalko, 2001; Schnitzler *et al.,* 2003; Denzinger & Schnitzler, 2013; Denzinger *et al.,* 2016). In uncluttered habitats, insectivorous bats generally have echolocation characterized by calls with low frequency and narrow band, adapted to detect insects over long distances (Kalko *et al.,* 2008). High-frequency signals are emitted in edge areas that present a component used to detect flying insects and another component to detect oscillations (Kalko *et al.,* 2008). In these habitats are also bats that forage water surfaces (Denzinger & Schniltzler, 2013). In highly cluttered habitats, the waves emitted are short, broadband, multi-harmonic and often modulated (Kalko *et al.,* 2008). In these habitats, it is difficult to distinguish the echoes coming from the food (fruits, nectar, insects, small vertebrates) from the echoes generated by the surrounding vegetation (Denzinger & Schnitzler, 2013). To solve this, they can specialize in detecting insect flutter, by using passively foraging when using other senses (sit- and wait strategy), or employing actively foraging of conspicuous local resources, or even combining passive and active foraging which is common in phytophagous bats (frugivorous and nectarivorous) (Denzinger & Schnitzler, 2013). Foraging habitat is also related to wing and ear morphology, thereby in cluttered habitats, the predominant ecoforms are wide and short wings (Kalko *et al.,* 2008) with low wing loading and aspect ratio (Norberg & Rayner, 1987), longer length of the fifth digit in proportion to the length of the third digit and forearm length (Dietz *et al.,* 2006; Castillo-Figueroa, 2020a), allowing greater maneuverability and agility (Norberg & Rayner, 1987). In these habitats, bats are likely to have large ears and slow flights for passive listening to detect prey, (Norberg & Rayner, 1987; Gardiner *et al.,* 2011a; Håkansson *et al.,* 2017). By contrast, in uncluttered spaces, the predominant ecoforms are long wings (Kalko *et al.,* 2008) with high wing loading and aspect ratio (Norberg & Rayner, 1987), and smaller length of the fifth digit in proportion to the length of the third digit and forearm length (Dietz *et al.,* 2006; Castillo-Figueroa, 2020a), thus enabling fast-speed flights (Norberg & Rayner, 1987). To reduce drag and enhance aerodynamic performance, bats have small ears that enable fast flights over open habitats (Norberg & Rayner, 1987; Gardiner *et al.,* 2011a; Håkansson *et al.,* 2017). In forest edges, the wings are wide and somewhat short to avoid obstacles and dodges like trunks, branches, shrubs and foliage (Kalko *et al.,* 2008). Prior studies have shown that tolerance of insectivorous bats to urbanization is more likely to occur in species that forage in open and edge spaces as well as in bats with flexible roosting strategies (Jung & Threlfall, 2018).

Vertical stratification: related to habitat specialization (Pereira *et al.,* 2010; Farneda *et al.,* 2015; Gregorin *et al.,* 2017) and wing ecomorphology (Olaya-Rodríguez *et al.,* 2019). In frugivorous bats, vertical stratification can occur depending on fruit-sized differences among forest strata, considering that fruit size is related to bat size (Kalko *et al.,* 1996; Muscarella & Fleming, 2007; Lacher *et al.,* 2019). Thus, small species feed mainly on small fruits in the understory, whereas large species tend to consume large fruits in the canopy (Kalko *et al.,* 1996; Rex *et al.,* 2011). However, this is a flexible trait (Meyer *et al.,* 2008;

García-García, *et al.,* 2014) that may not reflect the foraging height (Rex *et al.,* 2011), but depending the functional group and ecological context, stratification can be a good predictor of vulnerability of species (Duchamp & Swihart, 2008; Farneda *et al.,* 2015).

Home range: related to connectivity of species between habitat patches (Bernard & Fenton, 2003; Loayza & Loiselle, 2008). The ability to flight long distances over open areas affects the processes of seed dispersal, pollination, and arthropod control, respectively (Galindo-González, 1998; Bernard & Fenton, 2003; Kalka & Kalko, 2006; Mello *et al.,* 2008). In frugivorous bats, seed dispersal over long distances reduces intraspecific competition and seed predation (Janzen, 1970; Muscarella & Fleming, 2007), and promote seed deposition in suitable microsites enhancing germination (Heithaus & Fleming, 1978; Galindo-González, 1998; Mello *et al.,* 2008). In the case of nectarivores, pollen movement over short and long distances, and trap-lining foraging resulting in outcrossing pollination, thus increasing gene flow in plants (Muchhala, 2006; Fleming *et al.,* 2009), especially in fragmented landscapes (Quesada *et al.,* 2003). For insectivorous bats, some gleaners display high efficiency in exploitation of preys even on small forest patches where habitat suitability is very low (Kalko *et al.,* 2008). To some extent, home range appear to be directly related to body size in fig-eating stenodermatines (Kalko *et al.,* 1996).

Type of roost: related to skull morphology, body size, pelage patterns, social organization and group size (Kunz, 1982; Santana *et al.,* 2011b; Garbino & Tavares, 2018). Diurnal roosts are a fundamental resource for bats because, on one hand, they spend at least half of their lives in these sites (Kunz, 1982) and, on the other hand, roost environments allow species coexistence and are linked to morphological or behavioral adaptations of bats (Voss *et al.,* 2016). The remarkable variety of diurnal refugia used by bats include caves, rock outcrops, termite nests, foliage, crevices and shallow grottoes, fallen trees, tree barks and vine tangles (Kalko *et al.,* 1999; Sampedro *et al.,* 2008; Voss *et al.,* 2016). This is important because bats play a key role in nutrient cycling by fertilizing sites that are used as roosts (Castillo-Figueroa, 2020b), thus increasing, for instance, nitrogen content in the trees and soils (Voigt *et al.,* 2015). The potential effect of bats in the increase of nutrients by defecating within and nearby the roost tree (nutrient hot spot hypothesis), remains to be explored in Neotropical bats (Pierson, 1998; Duchamp *et al.,* 2010; Castillo-Figueroa, 2020b). Roosting ecology is also phylogenetically informative, and along with other traits, roost selection may explain morphological variation in bats; for example, species that use leaf tents are smaller than bats that use other type of roosts, and pelage markings such as white stripes of stenodermatines are related to foliage roosting (Garbino & Tavares, 2018). In terms of *community ecology,* the availability and the type of roosts may play a major role in environmental filtering of bat species at a local or regional scale (Voss *et al.,* 2016). For instance, tolerance to urbanization is more likely to occur in insectivorous bats with flexible roosting strategies and this could influence species composition in urban environments (Jung & Threlfall, 2018).

Echolocation dimension

Echolocation is, probably, one of the most important traits of bats to perceive their environment. Bats can produce calls of extraordinary high frequencies ranging from 20 kHz to 212 kHz (Thiagavel *et al.,* 2017). These tonal signals, emitted mainly in the larynx, can return in echoes that enable the detection, localization, and characterization of reflecting targets, including preys and obstacles in the habitat (Schnitzler *et al.,* 2003). This allows bats to orient themselves spatially, recognize biotopes, and find their food (Neuweiler, 2000; Denzinger & Schnitzer, 2013). Therefore, identifying echolocation signals is useful to study the interactions between bats and their environments (Neuweiler, 2000), especially for insectivores' guilds, which usually escape from traditional techniques such as mist-nets (Estrada-Villegas *et al.,* 2010). Indeed, resource partitioning by echolocation is, arguably, a key factor to understand the structuring of bat communities (Houston *et al.,* 2004).

Duration: related to the efficiency of prey-acquisition according to the habitats (Saldaña-Vázquez, 2014b). Short-duration signals may enable the detection of different prey sizes but is limited to short ranges by atmospheric attenuation, whereas long-duration signals reach distant preys but may limit availability of small preys (Houston *et al.,* 2004). Accordingly, in uncluttered spaces bats can emit calls of longer duration, increasing the probability to record distant objects or preys, whereas in cluttered habitats the duration of the calls is shorter, enhancing the spatial orientation and prey detection in dense foliage (Jones & Holderied, 2007; Barboza-Marquez *et al.,* 2013; Denzinger & Schnitzer, 2013). Pulse duration is related to body mass (Jones, 1999) and wing morphology (Norberg & Rayner, 1987); that is, larger bats have high wing loading and high aspect ratio reflected in faster flights, thus allowing to search for distant preys (Norberg & Rayner, 1987). In such circumstances, bats can increase pulse duration because echoes will return late from distant targets (Jones, 1999). Conversely, small and maneuverable bats with low wing loading and low aspect ratio are capable to detect a wide range of target sizes over nearby distances by emitting shorter pulses to avoid pulse-echo overlap (Jones, 1999; Houston *et al.,* 2004).

Interval: similar to the duration, the interval of the call can be reduced while the bat is approaching the prey since its echolocation system does not allow to discern the overlap between the emitted signal and the echo that returns, either during or soon after call emission (Kalko, 1995; Jones & Holderied, 2007; Saldaña-Vázquez, 2014b). In open habitats, where no objects can mask the echoes of the prey, bats can generate calls of longer intervals, improving the chances of detecting preys that are from far distances (Barclay, 1985). In dense habitats, intervals are short to improve aerial navigation and insect-acquisition in complex habitats (Barboza-Marquez *et al.*, 2013; Denzinger & Schnitzer, 2013).

Frequency: in echolocation, this is probably the most variable trait (Saldaña-Vázquez, 2014b). Broadly, low frequencies and long signals reduce the probability for detect small preys, whereas high frequencies in conjunction with short signals increase the capacity to detect large preys, but only in short distances (Barclay, 1985; Kalko, 1995; Houston *et al.*, 2004; Jones & Holderied, 2007). This because at high-frequency calls there is a high atmospheric attenuation, making these signals only operational over short ranges (Jones, 1999; Houston *et al.*, 2004). Bats with larger ears can detect low frequency calls and improve directionality (Obrist *et al.*, 1993; Huihua *et al.*, 2003). Frequency is also related to size (Jones, 1999) and wing morphology (Norberg & Rayner, 1987); smaller bats with low wing loading, low aspect ratio and rounded wingtips produce higher frequency signals to move in cluttered habitats, conversely, larger bats with high wing loading, high aspect ratio and pointed wingtips use lower frequency sounds to forage on uncluttered spaces (Jones, 1999; Thiagavel *et al.*, 2017; Núñez *et al.*, 2019; López-Cuamatzi *et al.*, 2020).

Intensity: the variation of this trait is minute in comparison to the other call parameters (Saldaña-Vázquez, 2014b). Bats tend to emit intense tonal signals when hunting and can also adjust the sound level of search calls according to the distance of closest obstacles in their natural habitats (Surlykke & Kalko, 2008). High intensity is found in bats that forage on uncluttered spaces due to the attenuation of the sound through space (Jones & Holderied, 2007). However, low intensity calls, typical of sit- and wait foragers, can increase the efficiency in tracking preys since their tonal signs are not overlapping with the glints in insects' echoes (Holderied *et al.*, 2010). Intensity is unrelated to body size, being that smaller species can emit both high and low intensity sounds (Saldaña-Vázquez, 2014b).

Harmonics: the use of harmonics enhance the resolution of preys and objects without modulation of the frequency (Holderied *et al.*, 2010; Bates *et al.*, 2011), allowing to exploit insect preys of different size (Jones & Holderied, 2007). Bats that forage close to objects usually modulate the frequency of the calls by adding harmonics (Denzinger & Schnitzer, 2013). Harmonics allow to discriminate clutter echoes from target echoes by sacrificing delay acuity to avoid masking effect (Bates *et al.*, 2011).

Application of the framework

Historically, body size and wing morphology, *e.g.*, body mass, wing loading and aspect ratio, have been employed to assess species performance and ecological correlations with several environmental characteristics (Cisneros *et al.*, 2014; Farneda *et al.*, 2015; Cisneros *et al.*, 2015; Cisneros *et al.*, 2016). In our review, we found 19 study cases using trait-based approach in Neotropical bats, and most of them have focused on response traits across human-dominated landscapes (Presley *et al.*, 2017; Farneda *et al.*, 2019; Ramírez-Mejía *et al.*, 2020) and elevational gradients (Rodrigues Coelho *et al.*, 2018; Mancini *et al.*, 2019) as is shown in Table 2 and Fig. 2. It is clear enough that this framework is particularly useful for studying biodiversity patterns and species response across human-made landscapes in the Neotropics, as specific combinations of traits may predict the ecological structure of communities in urban or rural contexts (Jung & Threlfall, 2018; Ramírez-Mejía *et al.*, 2020).

However, effect traits have been largely neglected. To our knowledge, only one paper directly related traits to seed dispersal process through ecological network approach (Laurindo *et al.*, 2020). Nonetheless, some physiological and behavioral studies related to foraging ecology have started to shed light on trait relations to ecological processes (Baldwin & Whitehead, 2015; Ortega-García *et al.*, 2020; Saldaña-Vázquez *et al.*, 2020) as we mentioned above. We consider that these studies may be a point of reference for further investigations on effect traits in bats.

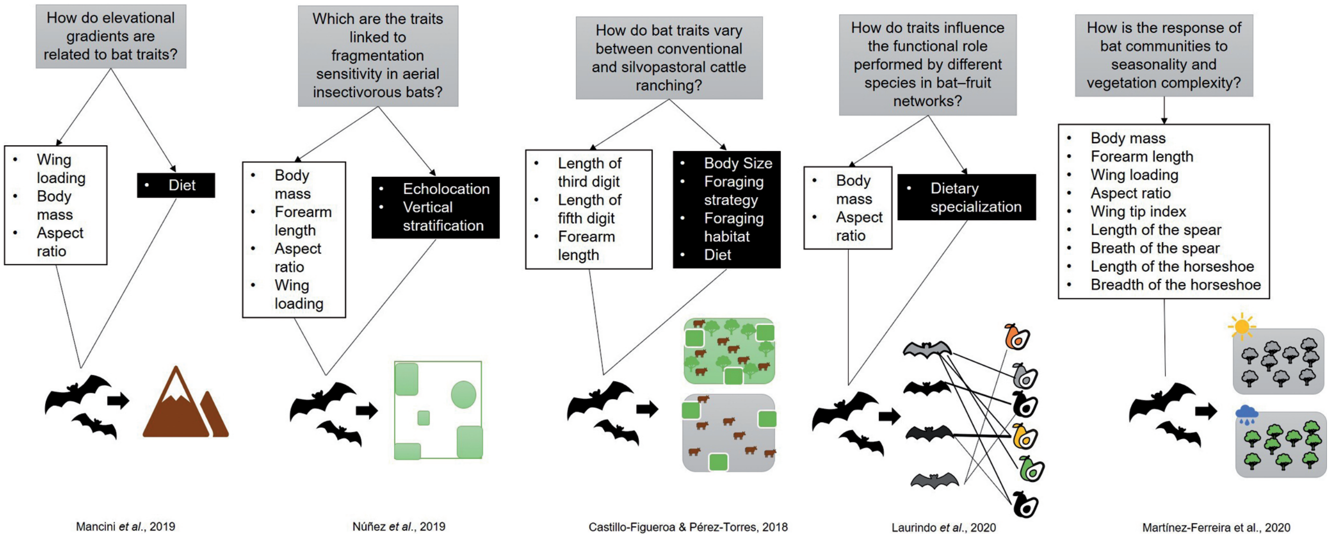

Figure 2. Study cases using trait-based approach in Neotropical bats. Life history traits in black boxes whereas morphological traits are depicted in white boxes.

Table 2. Functional ecology studies of Neotropical bats using traits.

Morphological Trait	Life history trait	Location	Application	Reference
Body size, forearm length, greatest length of skull, condylobasal length, length of maxillary toothrow, breadth across upper molars, width across post-orbital constriction, breadth of braincase, wing loading, aspect ratio	Diet, foraging location, foraging strategy	Manu Biosphere Reserve, Perú	Response to elevational gradient	Cisneros *et al.,* 2014
Body size, forearm length, greatest length of skull, condylobasal length, length of maxillary toothrow, breadth across upper molars, width across post-orbital constriction, Breadth of braincase, Wing loading, aspect ratio	Diet, foraging location, foraging strategy, roost type	Caribbean lowlands in northeastern Costa Rica	Response to human-modified landscapes	Cisneros *et al.,* 2016
Body size, forearm length, greatest length of skull, condylobasal length, length of maxillary toothrow, breadth across upper molars, width across post-orbital constriction, breadth of braincase, wing loading, aspect ratio	Diet, foraging location, foraging strategy, roost type	Caribbean lowlands of northeastern Costa Rica	Response to human-modified landscapes	Cisneros *et al.,* 2015
Body mass, wing aspect ratio, wing loading	Trophic level, dietary specialization, vertical stratification, mobility	Manaus, Central Amazon, Brazil	Response to habitat fragmentation	Farneda *et al.,* 2015
Body mass, forearm length, wing morphology	Echolocation, Vertical stratification	Manaus, Central Amazon, Brazil	Response to habitat fragmentation	Núñez *et al.,* 2019
Body mass	Trophic level, diet, habitat breath	Colombia, México, Bolivia, Brazil, Costa Rica, Guatemala, Nicaragua, Perú	Human-modified landscapes	Farneda *et al.,* 2019
Body mass, wing loading	Trophic level, dietary specialization, vertical stratification	Manaus, Central Amazon, Brazil	Response to habitat fragmentation	Farneda *et al.,* 2018
Forearm length, aspect ratio, wing load and body mass	foraging guild, main feeding habits, main trophic level	Tocantins State, Central Brazil	Response to human-modified landscapes	Pereira *et al.,* 2018
Body mass, wing aspect ratio, relative wing loading	Trophic level, vertical foraging area	Los Chimalapas, México	Habitat fragmentation	García-García *et al.,* 2014
Body weight, forearm, wing loading, aspect ratio	Diet	Hidalgo, México	Response to human-modified landscapes	García-Morales *et al.,* 2016
Body mass, aspect ratio, wing load	Type of food	the Serra da Mantiqueira massif, Minas Gerais and São Paulo, Brazil	Response to elevational gradient	Mancini *et al.,* 2019
Weight (body mass), size (forearm), wing morphology (aspect ratio and wing loading)	Dietary specialization	North of the state of Paraná, Brazil	Response to human-modified landscapes	Pereira *et al.,* 2019
Weight, aspect ratio	Feeding guild, type of shelter used	Minas Gerais and Bahia, Brazil	Response to elevational gradient	Rodrigues Coelho *et al.,* 2018
Length of third digit, length of fifth digit, forearm length	Size, foraging strategy, foraging habitat, diet	Córdoba, Colombia	Response to human-modified landscapes	Castillo-Figueroa & Pérez-Torres, 2018
Body mass, wingspan, aspect ratio, wing loading	Trophic guild	Villavicencio, Colombia	Response to human-modified landscapes	Ramírez-Mejía *et al.,* 2020
Body mass, aspect ratio, greatest length, braincase and zygomatic breadth	Degree of frugivory	México, Perú, Brazil, Guatemala	Relation to seed dispersal networks	Laurindo *et al.,* 2020
Aspect ratio, wing loading, forearm length, body mass, breadth across molars, breadth of braincase, condylobasal length, greatest length of skull, maxillary toothrow, postorbital constriction	Diet, foraging location, foraging strategy	Sarapiquí, Costa Rica	Response to human-modified landscapes	Presley *et al.,* 2017
Weight, forearm lenght, wing loading, aspect ratio, wing tip index, length of the spear, breadth of the spear, length of the horseshoe, breadth of the horseshoe	Trophic guild	Chamela-Cuixmala Biosphere Reserve (CCBR), México	Response to regenerating forests and seasonality	Martínez-Ferreira *et al.,* 2020
Body mass, wing loading, relative wing loading, aspecto ratio	Diet, peak frequency, bandwidth, call duration, roost duration	Las Cruces Biological Station, Costa Rica	Response to human-modified landscapes	Frank *et al.,* 2017

DISCUSSION

Intraspecific variation: as Neotropical bats have marked differences at the intraspecific level, including secondary sexual dimorphism (Camargo & Oliveira, 2012; Stevens *et al.,* 2013; Hurtado *et al.,* 2015; Castillo-Figueroa, 2018b), morphological variations among individuals (Magalhães de Oliveira *et al.,* 2020), and between populations (Louzada & Pessoa, 2013), the use of traits would allow to assess the effect of demography on ecological functions as has been done for other taxa (Violle *et al.,* 2012; Siefert *et al.,* 2015). It is important to evaluate whether intraspecific variations found in frugivorous bat diet between males and females (Alviz & Pérez-Torres, 2020) and between reproductive stages of the females (Bohlender *et al.,* 2018) affect processes such as seed rain and seed germination. Also, in the case of insectivorous bats, inter-individual variation on habitat exploitation and dietary preferences (Magalhães de Oliveira *et al.,* 2020) may have differential impacts on insect control. An obstacle to conduct these studies has been the lack of complete and bat-adjusted list of traits. Therefore, we believe that this proposal is a benchmarking to establish a bat functional traits protocol and will help in addressing ecological and functional questions. We recommend providing separately intraspecific stats (mean, ranks, standard deviation) for each trait analyzed.

Correlation between traits: many traits presented here can be correlated with each other as we pointed out in the description of the traits. Among all the 50 traits, many of them are expected to vary allometrically, but testing the relations between them may provide a better basis for functional description of Neotropical bats instead of using only those more-common traits from the literature. Moreover, empirical evidence gathered in our revision (Table 2 and Fig. 2) indicates that the analysis of a large set of different and informative traits improves the understanding of species response to human-dominated landscapes, rather than the analysis of a single or few attributes (Martínez-Ferreira *et al.,* 2020). Frequently, traits from wing morphology and body size are used (Pereira *et al.,* 2019; Farneda *et al.,* 2019; Ramírez-Mejía *et al.,* 2020), but many others from complexes such as the tail, hindlimbs, and natural history are neglected oftentimes and can provide other type of information to an in-depth understanding of bat ecology under different environmental contexts. It should be noted that we are not suggesting using simultaneously all the 50 traits. Researchers should first decide the set of suitable traits to use according to the objectives and hypothesis of their own investigations by following the theoretical framework proposed in this paper. Collinearity between traits should be evaluated posteriorly in data analysis and then they can take their own decisions about the utility of each trait. Our objective with this proposal is to conceptualize an extensive set of traits that can be useful in ecological studies of Neotropical bats and show their applicability, but researchers should test the utility of each one of them.

Response-Effect framework: as aforementioned, in animal taxa the study of the link between traits and ecological processes is still in its infancy (Hortal *et al.,* 2015). To better understand the nature of these relationships, empirical and experimental studies should be conducted. Given the multiple interactions in which Neotropical bats participate (*e.g.,* frugivorous, nectarivory, insectivorous, and animalivory), their impact on ecological processes becomes more important in conditions where communities have low redundancy. Measuring simultaneously traits and ecosystem processes would contribute to disentangling the mechanisms of these interactions. It is important to document those traits that are potentially related to ecological processes (*i.e.,* gut size, bite force, lingual papillae).

In contrast, response traits have been largely studied in environmental gradients as predictors of bat assemblages (Table 2), according to the trait-based environmental filtering (Keddy, 1992). Nevertheless, few studies have parsed out variations of response traits between land-use management types across agricultural areas. This can assess the sustainability of agricultural systems for bats, providing key information in conservation planning and decision-making (Castillo-Figueroa & Pérez-Torres, 2018). Identifying also the traits that make species more vulnerable to habitat modification is fundamental to design of effective conservation strategies that reduce local extinctions of Neotropical bats (Jung & Threlfall, 2018; Núñez *et al.,* 2019).

Global datasets: this paper is the first step toward a functional trait-based approach in New World bats. However, conducting investigations by using the traits presented here, a plethora of ecological information can be gathered from many species in several study sites across the Neotropics. Some websites like Bat Eco-Interactions platform (Geiselman *et al.,* 2015) have successfully facilitated datasets on bat diets and interactions, promoting scientific research on bat ecology and conservation (Castaño *et al.,* 2018; Saldaña-Vázquez *et al.,* 2019). Additionally, remarkable trait databases such as Atlantic Mammal Traits (Gonçalves *et al.,* 2018), Elton Traits (Wilman *et al.,* 2014) and PanTheria (Jones *et al.,* 2009b) are key tools in functional investigations and are successful models of global databases from which new ones can be inspired to accomplish big and detailed bat trait databases in the Neotropics. In the same way, we want to encourage the accessibility of trait information based on this list to take advantage of big data for Neotropical studies. This trait list can also be extended to other geographical regions and bat faunas.

Outstanding functional questions: the use of bat traits can be useful in several trending topics in ecology and conservation. The most obvious but also crucial is the quantification of ecosystem processes and ecosystem services. Removal experiments have shown key findings related to biodiversity-function relationships in several groups, including the assessment of traits and their effects on ecosystem function (Díaz *et al.,* 2003). It is well-known the prominent role of phyllostomid bats in numerous ecological processes, nevertheless, as far as we are aware of the literature, there are very few studies that relate directly bat traits to ecosystem processes. In addition, is important to know:

- How are bat traits related to ecological processes and how this can vary across environmental gradients and human-modified landscapes?
- How do bat traits match with the traits of plants or animals they interact with?
- There is any difference between intraspecific categories (*e.g.,* males, females) in terms of their functional contribution? And if so, is this reflected in their traits?
- How can traits explain the efficiency of bats in ecological processes different from those they are primarily involved? (*e.g.,* carnivorous and insectivorous as seed dispersers)
- What are the trade-offs between bat traits when analyzing a specific ecological process?

On the other hand, as secondary forests are nowadays quite common in the Neotropics, understanding how this forest type affect animal species becomes critical (Chua & Potts, 2018). It is important to generate indicators that effectively assess ecological resilience as well as ecological resistance, in a way that complement taxonomic studies with functional trait-based dimension using a multi-scale and multi-coverage approach (Martínez-Ferreira *et al.,* 2020). In line with this argument, long-term studies at the Biological Dynamic of Forest Fragment Project (BDFFP) have shown the applicability of functional approach to ecological succession (Farneda *et al.,* 2018). Thus, including the functional approach can contribute to practices of restoration ecology. The impact of agricultural systems on biodiversity and ecosystem functioning is one of the most important conservation concerns in the Neotropics (González-Maya *et al.,* 2017). Due to this, considering the type of management is urgent to better select agriculture practices that minimize environmental impacts and improve sustainability of productive systems. Some questions rise about this regard:

— Can traits be a useful tool in rapid assessment of human impacts? Can they become bioindicators?
— Which bat traits are good predictors of sustainable ecological and conservation practices?
— To what extent a trait can vary in the same species across environmental gradients? What are the biotic and abiotic drivers?

CONCLUSIONS

In this paper, we provided an extensive guide of biological traits for studying Neotropical bats with their respective description of measurement, definitions, attributes, trait obtention and ecological information. Experimental studies are needed to test if a trait is effectively functional or not, considering that all functional traits are biological traits but not all biological traits are functional (Mlambo, 2014). This is the first contribution to achieve a bat functional traits protocol that supports the legitimate ecological reasons of each trait by using solid evidence and not just by theoretical deductions or surmises. It is essential to identify an adequate set of traits to assess bat ecological roles in ecosystems, for which is necessary to expand the base knowledge in open access databases. Also, it is important to test for correlations between traits. Finally, we encourage to use response traits in human-made landscapes, agricultural managements, and environmental gradients. Accounting this source of information, a better understanding of ecosystem functions and anthropogenic disruptions in the Neotropics can be achieved through a trait-based approach of bats.

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AUTHORS' CONTRUBUTIONS

D.C.-F.: conceived the idea, contributed to the theoretical and conceptual framework, wrote the paper, prepared figures and tables, reviewed drafts of the paper. J.P.-T.: wrote the paper, contributed to the theoretical and conceptual framework, reviewed drafts of the paper. The authors declare no conflict of interests.

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