



## Diet and trophic structure in assemblages of montane frugivorous phyllostomid bats



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### ABSTRACT

Neotropical frugivorous bats display a trophic structure composed of bat species with dietary preferences of core plant taxa (*Artibeus-Ficus* + *Cecropia*, *Carollia-Piper*, *Sturnira-Solanum* + *Piper*). This structure is hypothesized to be an ancestral trait, suggesting that similar diets would be observed throughout a species' range. However, most evidence comes from lowlands where data from montane habitats are scarce. In high mountain environments both diversity of bats and plants decreases with altitude; such decline in plant diversity produces less plants to feed from, which should ultimately affect the trophic structure of frugivorous bats in mountain environments. Here, we present a comprehensive review of the diet of frugivorous bats in Neotropical montane environments and evaluate their trophic structure in middle and higher elevations by combining a literature database with field data. We use the concept of modularity to test whether frugivorous montane bats have dietary preferences on core plant taxa. Our database revealed 47 species of montane bats feeding on 211 plant species. We find that the networks are modular, reflecting the trophic structure previously reported. We also found that in highlands the tribe Ectophyllini are *Cecropia* + *Cavendishia*-specialists rather than *Ficus*-specialists, and we describe new interactions reflecting 14 species of plants, including three botanical families previously not reported to be consumed by bats.

### 1. Introduction

Frugivory has been considered the essential condition for the morphological and ecological diversification of the family Phyllostomidae (Rojas et al., 2012). Compared to other families within Chiroptera, the Phyllostomidae is the most taxonomically diverse both in terms of number of genera and number of feeding strategies (Baker et al., 2003; Rojas et al., 2012). Phyllostomid species that feed on fruits, either as their main or complementary resources, represent almost half of the family. All species in the subfamilies Carollinae, Rhinophyllinae and Stenodermatinae (at least 25 genera) are considered obligate frugivores, and 25 genera in the subfamilies Macrochinae, Micronycterinae, Lonchorhininae, Phyllostominae, Glossophaginae, Lonchophyllinae, Glyphonycterinae are opportunistic frugivores (Rojas et al., 2011). These bats feed on at least 550 species of plants (62 plant families) in the Neotropics (Lobova et al., 2009).

Despite the great diversity of bats within the Phyllostomidae and the high number of fruits that they consume, assemblages of neotropical frugivorous bats display a trophic structure composed of bat species with dietary preferences of core plant taxa (*sensu* Fleming, 1986). The

three main preferences are: *Artibeus* (feed primarily on fruits of Moraceae *sensu lato* *Ficus* and *Cecropia*), *Carollia* (feed primarily on *Piper*, Piperaceae), and *Sturnira* (feed primarily on *Solanum*, Solanaceae and *Piper*). Various authors (e.g., Giannini and Kalko, 2004; da Silva et al., 2008; Sánchez et al., 2012; Andrade et al., 2013; Parolin et al., 2016) have explored the predictive power of these preferences and have also extended them beyond *Artibeus*, *Carollia* and *Sturnira* to include the clades that contain these bat genera (*Ectophyllini*, *Carollinae*, and *Sturnirini*, respectively). These dietary associations are hypothesized to be an ancestral trait, suggesting that very similar diets should be observed throughout a species' range (Sánchez et al., 2012). Despite the central role that dietary preferences have played in the study of Phyllostomidae, most of the evidence for phyllostomid bats has been collected in lowland habitats (< 1000 m a.s.l.). The evidence for dietary preference from montane habitats is quite scarce. For example, less than 15 studies have been published from highlands compared to approximately 350 papers from lowland habitats (Geiselman et al., 2015; Lobova et al., 2009).

By virtue of their lower temperatures, high mountain environments demand higher energetic expenditures for endotherms to maintain a

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constant body temperature (Soriano et al., 2002). Therefore, low temperatures of montane environments may impose important constraints on bat physiology that in turn should affect the composition of frugivorous bat assemblages in the highlands (Castaño and Corrales, 2010; Soriano, 2000). In fact, the differences between high mountain bat assemblages in terms of composition and diversity with respect to their lowland counterparts (Patterson et al., 1996) may be due to changes in physiological constraints and dietary preferences triggered by changes in temperature (i.e. elevation). Likewise, the relative importance of plant families and the structure and composition of plant communities changes with elevation (Vázquez and Givnish, 1998). There is a linear decline of plant diversity in Andean forests above 1500 m (Gentry, 1988). Such a decline produces a less diverse flora to feed from, which should ultimately affect the trophic structure of frugivorous bats in mountain environments.

The trophic structure formed by groups of animals that have dietary preferences from core plant taxa is equivalent to the concept of modularity in network theory; a network is considered modular if it is formed by cohesive subgroups of closely connected animals and plants (Dormann and Strauss, 2014; Mello et al., 2011). Traditionally, the way to find and delimit link-rich clusters of species in the assemblages of neotropical frugivorous bats (i.e. modules) has been through group species (or genera) using ordination techniques (i.e. Giannini and Kalko, 2004; da Silva et al., 2008). Despite its benefits, ordinations are not able to identify modules with enough precision, even if modules are perfectly separated into compartments, that is there are no species with interactions that reach beyond their own modules (Dormann and Strauss, 2014). Contrary to ordinations, modularity does a much better job at measuring how well links and interactions can be separated into different modules. In sum, network theory facilitates an understanding of the structure of interactions at the community level and it provides the adequate tools to study dietary preferences in frugivorous bat assemblages.

In this study we first present a comprehensive review of the diet of frugivorous bats in Neotropical montane environments (> 1000 m a.s.l.). Second, we hypothesize that the structure of the interactions between montane bats and fruits at middle elevations (1000–2000 m a.s.l.) are modular (according to the network theory) and whether the species composition of the modules reflects dietary preferences on the core plant taxa observed in the lowlands (e.g. *Artibeus* feeding primarily on fruits of *Ficus* and *Cecropia*, *Carollia* on *Piper* and *Sturnira* on *Solanum* and *Piper*; Fleming, 1986; Giannini and Kalko, 2004). Third, we hypothesize that, as a consequence of the reduction of available resources in highlands (> 2000 m a.s.l.), frugivorous bats become generalists without modularity in the network.

## 2. Material and methods

The dataset comprises a literature review and field data collected by the authors.

### 2.1. Literature review

We compiled information on the diet of montane phyllostomid bats from the literature. We built our database by using “bats,” “Phyllostomidae,” “seed dispersal,” “diet,” and “frugivory” as key words in Google Scholar (search in English and Spanish translation) and ISI Web of Knowledge databases. We also searched for studies in the Bat Eco-Interactions Database (Geiselman et al., 2015) and then complemented with additional literature cited by relevant studies. The search was not limited by year of publication or by journal and we also included the data found in the gray literature (thesis). We selected studies from the literature when 1) it reported a given bat species fed on a given fruit taxa, 2) when the bats were identified to species, 3) when the plants were identified to genus or species and this identification was supported by a reference collection of the study site, 4) when the study

site was located over 1000 m a.s.l. Data relating to bats that were unidentified at species level or plants unidentified to genus or species were omitted. Given that elevation was not reported in every study, we obtained an approximate elevation by using the geographic coordinates on GoogleEarth software (Google, Inc., version 7.0.2, Mountain View, California) when necessary. We consider a record every time a given bat species was reported as feeding on a given fruit species. Finally, we decided to include studies with sampling efforts shorter than 1 year because our goal was a comprehensive review of the interactions between frugivorous bats and plants in Neotropical montane environment, and because our analyses was conducted at genus rather than species level.

### 2.2. Field data

We conducted bat surveys in 10 localities within the municipality of Santa Rosa de Cabal, Risaralda, Colombia (elevation ranges 1600–2300 m a.s.l.) during August 2016 to August 2017. Each locality was surveyed four consecutive nights every three months. We used 5–7 mist nets (12 × 2.5 m; 30 mm mesh) per survey, opened mist nets at 18:00 p.m. and closed them at 06:00 a.m. In the event of ongoing heavy rain, nets were closed. Species were identified using the taxonomic keys in Diaz et al. (2016).

We collected fecal samples from captured frugivores. Bats were held in cloth capture bags for no longer than 2 h to allow them to defecate so we could maximize sample yield. We cleaned the bags thoroughly between captures to prevent cross-contamination of fecal samples. Bats were released after the collection of data and fecal samples. Voucher specimens were collected to represent the species diversity of bats at each sampling locality and were deposited in “Colección de Vertebrados UNISARC (CUS-M)”. Each sample from each individual was collected separately and then dried and stored in plastic bags. Seeds were identified to species based on a reference collection of the study area deposited in “Herbario UNISARC (CUS-P)”.

We built a mixed database with our field data and 28 studies from literature review (14 journal articles, 14 theses) representing 936 independent records of bat–fruit interactions in montane forests between 1000 and 2850 m a.s.l. from Central America (México, El Salvador, Costa Rica) and South America (Argentina, Bolivia, Colombia, Ecuador, Perú, Venezuela) (Table 1).

The taxonomy and nomenclature of frugivorous bats across all studies was updated according to the following authors. We followed Solari et al. (2009) for *Dermanura*; Larsen et al. (2010) for *Artibeus* (*A. intermedius* synonym of *A. lituratus*); Velazco and Patterson (2013) for *Sturnira* (*S. parvidens* for the little yellow-shouldered bat of Mexico, Central America and Colombia, *S. lilium* for South América, *S. hondurensis* for the big yellow-shouldered bat of Mexico and Central America, and *S. adrianae* for the big yellow-shouldered bat of Venezuela (Molinari et al., 2017)); and Mantilla-Meluk (2014) for *Uroderma* (*U. convexum* for Yucatan, Northern Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, and the Pacific slope of Colombia and Ecuador, *U. davisii* for El Salvador, southern Guatemala, and México, and *U. bilobatum* for cis-Andean populations of South America). Plant taxonomy and nomenclature were updated to follow Tropicos® Database.

### 2.3. Trophic structure in montane fruit bats

We use the concept of modularity from network theory to test whether frugivorous montane bats have dietary preferences on core plant taxa (*Carollia-Piper*, *Artibeus-Ficus/Cecropia*, *Sturnira-Solanum*). A network is considered modular if it is formed by cohesive subgroups of closely connected animals and plants that are linked to each other by species with interactions that reach beyond their own modules (i.e., connectors). Therefore, the concept of modules in network theory is related to the ecological concepts of guilds and functional groups, and may be used as a tool to test predictions derived from ecological theory

**Table 1**  
Localities in montane environments (> 1000 m.a.s.l.) where interactions between frugivorous bats and plants have been studied.

Country	Locality	Elevation	Source
Argentina	Las Capillas-Jujuy	1000	(Sánchez et al., 2012)
	Tucuman	600–1850	(Giannini, 1999)
Bolivia	Tunquini-Cotapata	1400–1700	(Loayza et al., 2006)
Colombia	Chinchiná-Caldas	1000	(Lozano-Ríos, 2013)
	Curití-Santander	1553	(Borray-Escalante, 2015)
	Filandia-Quindío	2000–2200	(Aguilar-Garavito et al., 2014)
	Jamundí-Valle del Cauca	990–1000	(Montoya-Bustamante et al., 2016)
	Manizales-Caldas	1900	(Ceron and Orozco, 2013)
	Pereira-Risaralda	1800–2100	(Estrada-Villegas et al., 2010, 2007)
	Santa Rosa de Cabal-Risaralda	1600–2300	This study.
	Bogotá-Cundinamarca	2750–2850	(Bolaños-Silva, 2000; Pérez-Torres, 2004)
	Yotoco-Valle	2300	(Moreno-Mosquera, 2011)
Perú	Chanchamayo-Junín	1370–1900	(Arias-Arone, 2016)
	San Pedro-Cusco	1100–1600	(Maguiña et al., 2012)
Ecuador	Zamora-Chinchi	950–2080	(Zamora-Delgado, 2008)
Venezuela	Calderas-Barinas	1400–1600	(Castaño, 2009)
	Mérida	2000–2500	(Molinari, 1984; Ruiz, 2006)
	Mérida	1400	(Muñoz-Romo and Herrera, 2010)
El Salvador	Santa Ana-Metapán	1000–2418	(Morales-Rivas, 2016)
	Santa Ana-Metapán	1000–2368	(Quijano-Vásquez, 2017)
Mexico	San Luis Potosí	0–1500	(García-Morales et al., 2012)
	Soconusco-Chiapas	1080–1550	(García-Estrada et al., 2012)
	Xalapa-Veracruz	1300–1500	(Hernández-Montero et al., 2015; Saldaña-Vázquez et al., 2010)
	Sierra Manantlán-Jalisco	1600–2180	(Schöndube Friedewold, 1994)
	Sierra Manantlán-Jalisco	1600–2100	(Hernández-Conrique et al., 1997)
Costa Rica	Monteverde	700–1850	(Dinerstein, 1986; Engriser, 1995).

(Mello et al., 2011).

We pooled all the datasets into two quantitative matrices of interactions, one for middle elevations between 1000 and 2000 m a.s.l. and the other for higher elevations > 2000 m a.s.l. Given that many studies did not report quantitative data for the interactions, each bat species reported in each study was considered as one observation. So the intensity of the interaction between a bat genus (rows) and a fruit genus (columns) was assigned by the number of localities where the same interaction (bat genus-plant genus) has been recorded.

We estimated the degree of quantitative modularity (Q) using the algorithm QuanBiMo (Dormann and Strauss, 2014). This algorithm uses the hierarchical random graph approach, which organizes interacting species into a graph so that close species are more likely to interact. Then it swaps branches at different levels randomly and reassesses the modularity of the network selecting the more modular organization. We calculated Q (varying from 0 to 1) using the bipartite package for R (Dormann et al., 2008). To test the significance of the modularity, we generated 1000 random networks fixing the probability that two species interact, based on the observed real networks. We used the Patefield null model to estimate the significance of the observed network metrics. We then calculated the modularity of the networks and evaluated whether observed modularity fell within the 95% confidence interval calculated from the randomized matrices. We finally standardized the modularity by calculating the Z-score Q (ZQ). Although there is a new algorithm for maximizing weighted modularity in bipartite networks (Beckett, 2016), we continued using QuanBiMo in our modularity analysis because we employ pairwise comparisons (between QuanBiMo and the new algorithm DIRTLPAwb+) and both algorithms

**Table 2**

Dietary diversity of frugivorous bats in neotropical mountains and number of families (Fam), Genus (Gen) and Species (spp.) of plants consumed, from Argentina (Ar), Bolivia (Bo), Colombia (Co), Costa Rica (Cr), Ecuador (Ec), El Salvador (Sv), Perú (Pe) and Venezuela (Ve). Elevation refers to where the interaction was registered, middle elevations (m) between 1000 and 2000 m a.s.l., and higher elevations (h) > 2000 m a.s.l.

Bats	Plants			Country	Elevation
	Fam	Gen	Spp		
<b>Phyllostominae</b>					
<i>Phyllostomus hastatus</i>	1	1	3	Co, Pe, Ve	m
<b>Glossophaginae</b>					
<i>Anoura caudifer</i>	1	1	1	Ve	m
<i>Anoura cultrata</i>	2	2	2	Ve	m
<i>Glossophaga commissarisi</i>	2	2	2	Me, Sv	m, h
<i>Glossophaga soricina</i>	3	4	6	Me, Ve	m
<b>Lonchophyllinae</b>					
<i>Lonchophylla robusta</i>	2	2	2	Ve	m
<b>Carollinae</b>					
<i>Carollia brevicauda</i>	15	27	91	Bo, Co, Cr, Ec, Pe, Ve	m, h
<i>Carollia castanea</i>	2	2	4	Co	m
<i>Carollia perspicillata</i>	12	13	42	Bo, Co,	m
<i>Carollia sowelli</i>	6	7	14	Sv, Me	m
<b>Stenodermatinae</b>					
Tribe Ectophyllini					
<i>Artibeus amplus</i>	4	4	4	Ve	m
<i>Artibeus jamaicensis</i>	17	23	43	Co, Sv, Me, Ve	m, h
<i>Artibeus lituratus</i>	17	21	42	Co, Sv, Me, Ve	m, h
<i>Artibeus planirostris</i>	5	5	7	Ar	m
<i>Chiroderma salvini</i>	3	4	5	Co, Ve	m, h
<i>Chiroderma trinitatum</i>	3	3	3	Bo	m
<i>Dermanura bogotensis</i>	9	10	12	Co	m, h
<i>Dermanura glauca</i>	7	10	13	Ec, Pe, Ve	m, h
<i>Dermanura phaeotis</i>	8	11	20	Co, Me	m
<i>Dermanura tolteca</i>	15	19	43	Cr, Sv, Me	m
<i>Enchisthenes hartii</i>	5	5	9	Co, Pe, Ve	m, h
<i>Mesophylla macconnelli</i>	7	7	10	Co, Pe, Ve	m
<i>Platyrrhinus albericoi</i>	2	2	7	Co, Ve	m
<i>Platyrrhinus angustirostris</i>	3	3	4	Ve	m
<i>Platyrrhinus dorsalis</i>	5	5	5	Co	m, h
<i>Platyrrhinus incarum</i>	1	1	1	Pe	m
<i>Platyrrhinus infuscus</i>	3	4	7	Ec, Pe	m, h
<i>Platyrrhinus lineatus</i>	1	1	1	Ec	h
<i>Platyrrhinus masu</i>	7	7	12	Bo, Pe	m
<i>Platyrrhinus umbratus</i>	4	4	6	Ve	m
<i>Platyrrhinus vittatus</i>	1	1	1	Co	m
<i>Uroderma bakeri</i>	2	2	3	Ve	m
<i>Uroderma bilobatum</i>	2	3	3	Pe	m
<i>Vampyressa melissa</i>	3	3	7	Pe	m
<i>Vampyressa thuyone</i>	4	4	5	Co, Ve	m
Tribe Sturnirini					
<i>Sturnira adrianae</i>	7	12	22	Ve	m, h
<i>Sturnira arathomasi</i>	1	1	1	Co	h
<i>Sturnira bidens</i>	7	10	17	Co, Ec, Ve	h
<i>Sturnira bogotensis</i>	11	12	20	Co, Ve	m, h
<i>Sturnira erythromos</i>	13	21	48	Ar, Co, Ec, Pe, Ve	m, h
<i>Sturnira hondurensis</i>	18	25	69	Cr, Sv, Me	m, h
<i>Sturnira lilium</i>	9	12	30	Ar, Co, Ve	m
<i>Sturnira ludovici</i>	10	12	26	Co, Ec	m, h
<i>Sturnira magna</i>	3	3	4	Pe	m
<i>Sturnira oporaphilum</i>	2	2	3	Ar	m
<i>Sturnira parvidens</i>	10	18	47	Co, Sv	m, h
<i>Sturnira tildae</i>	3	3	5	Bo, Pe	m

detected the same modularity score and similar community partitions. However, QuanBiMo was the appropriate null model to measure the significance of the observed network metrics.

### 3. Results

Our interaction database revealed 47 species of montane bats (subfamilies Glossophaginae, Lonchophyllinae, Phyllostominae, Carollinae and Stenodermatinae Table 2) feeding on 211 plant species

**Table 3**

Plants consumed by frugivore bats in montane forest of neotropical mountains. The bats are grouped by categories, obligate frugivorous include subfamily Carollinae and the tribes Ectophillini and Sturnirini in the subfamily Stenodermatinae, Facultative frugivorous include subfamilies Phyllostominae (Phy.), Glossophaginae (Glo.) and Lonchophyllinae (Lon.). Names of bats are represented by the first letter of the genus and first two letters of specific epithet. Asterisk (\*) indicates new records of plants consumed by bats.

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
<b>Actinidiaceae</b>						
<i>Saurauia brachybothrys</i>	Cbr					
<i>Saurauia bullosa</i>			Sbi			
<i>Saurauia excelsa</i>	Cbr		Sbi			
<i>Saurauia kegeliana</i>			Spa			
<i>Saurauia madrensis</i>		Dph, Dto	Sho, Spa			
<i>Saurauia peruviana</i>			Ser			
<i>Saurauia</i> spp.	Cbr, Cso		Sho		Gco	
<i>Saurauia tomentosa</i>	Cbr					
<i>Saurauia veraguensis</i>		Dto	Sho			
<b>Anacardiaceae</b>						
<i>Mangifera indica</i>		Ali				
<b>Annonaceae</b>						
<i>Rollinia</i> sp.	Cbr					
<b>Araceae</b>						
<i>Anthurium bernardii</i>	Cbr		Sad			
<i>Anthurium effusipathum</i>			Sbi			
<i>Anthurium humboldtianum</i>			Sad, Sbi			
<i>Anthurium longistrorsum</i>			Sbi, Ser			
<i>Anthurium myosuroides</i>	Cbr, Cpe		Sbo, Spa			
<i>Anthurium nymphaeifolium</i>	Cbr		Sad, Sbi			
<i>Anthurium</i> spp.	Cbr, Cpe	Dbo	Sad, Sbo, Sho, Slu, Sma, Spa			
<i>Anthurium triphyllum</i>	Cbr					
<i>Anthurium versicolor</i>	Cbr, Cpe					
<i>Monstera</i> sp.		Dgl				
<i>Philodendron</i> spp.	Cbr	Dph, Pma	Sad, Sbi, Ser, Slu			
<i>Xanthosoma daguense</i>			Ser			
<i>Xanthosoma microrhiza</i>			Sho			
<i>Xanthosoma</i> spp.	Cbr	Dgl				
<b>Araliaceae</b>						
* <i>Schefflera</i> sp.		Dbo				
<b>Asteraceae</b>						
<i>Aldama</i> sp.		Aja				
<i>Barnadesia spinosa</i>			Sbo, Slu			
<i>Tridax</i> sp.		Aja				
<i>Vernonia</i> sp.		Aja				
<b>Bromeliaceae</b>						
<i>Aechmea tillandsioides</i>	Cpe					
<b>Calophyllaceae</b>						
<i>Calophyllum brasiliense</i>		Aja, Ali				
<b>Campanulaceae</b>						
<i>Burmeistera cyclostigmata</i>		Dto	Sho			
<i>Centropogon</i> sp.	Cbr					
<b>Cannabaceae</b>						
<i>Celtis iguanaeus</i>		Apl	Ser, Sli			
<i>Trema micrantha</i>		Aja, Ali, Dto	Sho, Spa		Gco	
<b>Caryophyllaceae</b>						
<i>Drymaria</i> sp.		Aja				
<b>Chloranthaceae</b>						
<i>Hedyosmum mexicanum</i>	Cso		Sho, Spa			
<b>Clusiaceae</b>						
<i>Garcinia intermedia</i>		Ali	Sho			
<b>Cyclanthaceae</b>						
<i>Asplundia</i> sp.			Sma			
<i>Asplundia tetragona</i>	Cbr					
<i>Asplundia vagans</i>	Cbr	Pum	Sad, Ser, Sho			
* <i>Cyclanthus</i> sp.	Cbr, Cpe	Ali, Dbo, Dph, Mma	Sbo			
* <i>Sphaeradenia</i> sp.	Cbr		Sad			
<b>Ericaceae</b>						
* <i>Cavendishia pubescens</i>	Cbr	Dbo				
* <i>Cavendishia</i> sp.		Ali, Dbo, Eha, Pdo	Sbo, Ser, Slu			
* <i>Cavendishia zamorensis</i>			Ser			
* <i>Psammisia penduliflora</i>	Cbr, Cpe	Aam, Aja, Dgl, Mma, Pum	Ser, Sli			
* <i>Psammisia</i> sp.		Dbo				
<b>Euphorbiaceae</b>						
<i>Alchornea latifolia</i>		Aja, Dto				
<b>Fabaceae</b>						
<i>Acacia</i> sp.	Cpe					
<b>Gesneriaceae</b>						

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Table 3 (continued)

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
* <i>Columnnea</i> sp.	<i>Cbr</i>					
<i>Drymonia rubra</i>		<i>Dto</i>	<i>Sho</i>			
Gesneriaceae indet.	<i>Cbr</i>					
<b>Hypericaceae</b>						
<i>Vismia baccifera</i>	<i>Cbr, Cpe</i>	<i>Aam, Aja, Ali, Dgl, Mma, Pan, Vth</i>	<i>Sad, Sbi, Sbo, Ser, Sli</i>		<i>Acu, Gso</i>	
<i>Vismia glaziovii</i>	<i>Cpe</i>					
<i>Vismia guianensis</i>	<i>Cbr, Cpe</i>	<i>Aja, EhaPdo</i>	<i>Slu, Spa</i>			
<i>Vismia mexicana</i>	<i>Cso</i>	<i>Dto</i>	<i>Sho, Spa</i>			
<i>Vismia</i> spp.	<i>Cbr, Cpe,</i>	<i>Ctr, Pma</i>	<i>Sti</i>			
<i>Vismia tomentosa</i>			<i>Ser</i>			
<b>Lamiaceae</b>						
<i>Salvia</i> sp.		<i>Dph, Dto</i>	<i>Spa</i>			
<b>Malvaceae</b>						
<i>Guazuma ulmifolia</i>		<i>Aja, Ali</i>				
<b>Marcgraviaceae</b>						
<i>Marcgravia helverseniana</i>			<i>Ser</i>			
<i>Marcgravia</i> spp.	<i>Cbr</i>					
<b>Melastomataceae</b>						
<i>Clidemia</i> sp.					<i>Gso</i>	
<i>Conostegia icosandra</i>		<i>Dto</i>				
<i>Conostegia volcanalis</i>		<i>Dto</i>	<i>Sho</i>			
<i>Conostegia xalapensis</i>			<i>Spa</i>			
Melastomataceae indet.	<i>Cbr</i>	<i>Pma</i>	<i>Vme</i>			
<i>Miconia glaberrima</i>			<i>Sho</i>			
<i>Miconia mexicana</i>			<i>Spa</i>		<i>Gso</i>	
<i>Miconia</i> spp.	<i>Cso</i>	<i>Ali, Dbo, Pdo</i>				
<b>Moraceae</b>						
<i>Ficus americana</i>		<i>Ali, Eha, Pal, Pdo, Pma</i>	<i>Sbi, Spa, Slu</i>			
<i>Ficus aurea</i>		<i>Aja, Ali, Dph, Dto</i>	<i>Sho</i>			
<i>Ficus citrifolia</i>		<i>Dgl</i>				
<i>Ficus cotinifolia</i>		<i>Aja, Ali, Dto</i>	<i>Sho, Spa</i>			
<i>Ficus cuatrecasasiana</i>		<i>Csa, Dbo</i>				
<i>Ficus insipida</i>		<i>Aja, Ali, Csa, Dgl, DphEha, Mma, Pal, Pan, Pvi, Uba, Vth</i>				
<i>Ficus maxima</i>	<i>Cbr</i>	<i>Aam, Aja, Ali, Apl, Dgl, Mma, Pan, Pum, Uba, Vme, Vth</i>				<i>Lro</i>
<i>Ficus obtusifolia</i>		<i>Ali, Aja, Dto</i>				
<i>Ficus pertusa</i>		<i>Ali, Aja, Dph, Dto</i>	<i>Sho</i>			
<i>Ficus</i> spp.	<i>Cbr, Cpe</i>	<i>Aja, Ali, Dph, Dto, Mma, Pal, Pin, Pma, Pum, Ubi, Vme</i>	<i>Sad, Sho, Slu</i>			
<i>Ficus tonduzii</i>		<i>Aja, Ali, Pal</i>				
<i>Ficus yoponensis</i>		<i>Dto</i>	<i>Sho,</i>			
<i>Maclura tinctoria</i>	<i>Cpe</i>	<i>Ali</i>	<i>Sho, Spa</i>			
<i>Poulsenia armata</i>		<i>Csa</i>				
<i>Trophis mexicana</i>		<i>Aja, Ali</i>	<i>Spa</i>			
<b>Muntingiaceae</b>						
<i>Muntingia calabura</i>		<i>Aja, Ali</i>				
<b>Myrtaceae</b>						
<i>Eugenia acapulcensis</i>		<i>Dto</i>				
<i>Myrcia popayanensis</i>	<i>Cpe</i>					
<i>Psidium caudatum</i>	<i>Cbr</i>					
<i>Psidium guajava</i>	<i>Cca</i>	<i>Aja, Ali, Dto</i>	<i>Slu</i>			
<i>Psidium</i> sp.	<i>Cbr</i>					
<i>Syzygium jambos</i>		<i>Aja, Ali</i>				
<b>*Onagraceae</b>						
* <i>Fuchsia hartwegii</i>	<i>Cbr</i>					
* <i>Fuchsia microphylla</i>			<i>Sho</i>			
* <i>Fuchsia</i> sp.		<i>Dbo</i>				
<b>Passifloraceae</b>						
<i>Passiflora kalbreyeri</i>			<i>Ser</i>			
<i>Passiflora</i> sp.	<i>Cbr</i>					
<i>Passiflora umbilicata</i>			<i>Sli</i>			
<b>Piperaceae</b>						
<i>Peperomia</i> spp.		<i>Aja, Ali, Dph, Dto</i>	<i>Sho, Spa</i>			
<i>Piper imperiale</i>			<i>Slu</i>			
<i>Piper aduncum</i>	<i>Cbr, Cca, Cpe</i>	<i>Aja, Ali, Ctr, Dgl, DphMma, Pma</i>	<i>Sad, Sbo, Ser, Sli, Slu, Spa, Sti</i>			
<i>Piper aequale</i>			<i>Sho</i>			
<i>Piper amalago</i>		<i>Aja, Dto</i>	<i>Sho, Spa</i>			
<i>Piper augustum</i>	<i>Cpe</i>		<i>Sli, Slu</i>			
<i>Piper auritum</i>	<i>Cbr, Cso</i>	<i>Aja, Ali</i>	<i>Sho, Spa</i>			
<i>Piper barbatum</i>	<i>Cbr</i>		<i>Sad, Ser</i>			
<i>Piper bisasperatum</i>		<i>Dto</i>	<i>Sho</i>			
<i>Piper carpunya</i>	<i>Cbr</i>					
<i>Piper crassinervium</i>	<i>Cbr, Cpe</i>	<i>Ali, Dph, Vth</i>	<i>Slu, Spa</i>			
<i>Piper diffamatum</i>	<i>Cbr, Cpe</i>	<i>Ali, Dgl, Mma</i>	<i>Sad, Sbi, Sbo, Ser</i>			
<i>Piper dotanum</i>		<i>Dto</i>	<i>Sho</i>			

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Table 3 (continued)

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
<i>Piper ecuadorensis</i>			Ser, Slu			
<i>Piper epigynum</i>		Dto	Sho			
<i>Piper gibbosum</i>			Sho			
<i>Piper glabratum</i>	Cbr, Cca, Cpe		Slu			
<i>Piper glabrescens</i>			Sho			
<i>Piper hieronymi</i>			Ser			
<i>Piper hispidum</i>	Cbr, Cpe, Cso	Aja, Dph, Dto	Sho, Spa		Gso	
<i>Piper lanceifolium</i>		Dto	Sho			
<i>Piper lapathifolium</i>	Cso	Aja	Sho, Spa			
<i>Piper longispicum</i>	Cbr, Cpe		Sad			
<i>Piper marginatum</i>	Cbr, Cpe					
<i>Piper obliquum</i>			Sho			
<i>Piper peltatum</i>	Cbr, Cpe					
<i>Piper phytolaccifolium</i>	Cbr, Cpe	Csa	Sad, Sho			
<i>Piper pseudo-lindenii</i>			Sho, Spa			
<i>Piper psilophyllum</i>	Cbr, Cpe	Pma	Sti			
<i>Piper schiedeanum</i>	Cbr, Cca, Cpe	Dph				
<i>Piper septulinervium</i>	Cca, Cpe					
<i>Piper spp.</i>	Cbr, Cso	Aja, Dto	Sbi, Sbo, Ser, Sho, Slu, Spa		Gso	
<i>Piper tuberculatum</i>	Cbr, Cpe	Ali	Sli			
<i>Piper tucumanum</i>		Apl	Ser, Sli, Sop			
<i>Piper umbellatum</i>	Cbr		Sho			
<i>Piper yzabalanum</i>	Cso	Dto	Sho, Spa			
<b>Rhamnaceae</b>						
<i>Frangula hintonii</i>			Sho			
<b>Rosaceae</b>						
<i>Eriobotrya japonica</i>		Aja, Dto				
* <i>Hesperomeles</i> sp.			Sbo			
<i>Prunus integrifolia</i>		Ali				
<b>Rubiaceae</b>						
<i>Randia micracantha</i>			Sad, Sli			
<b>Rutaceae</b>						
<i>Casimiroa sapota</i>		Aja, Ali				
<i>Zanthoxylum</i> sp.			Sho			
<b>Salicaceae</b>						
<i>Neosprucea</i> sp.	Cpe					
<b>Sapotaceae</b>						
<i>Sideroxylon capiri</i>		Aja, Ali				
<b>Siparunaceae</b>						
<i>Siparuna</i> sp.			Sbo			
<b>Solanaceae</b>						
<i>Acnistus arborescens</i>	Cbr		Sho			
<i>Cestrum</i> sp.	Cbr		Sad, Sli, Uba			
<i>Cuatresia riparia</i>	Cbr		Sad, Sbi, Sbo, Ser, Slu			
<i>Juanulloa mexicana</i>		Dph	Sho, Spa			
<i>Lycianthes geminiflora</i>	Cso	Ali, Dto	Sho, Spa			
<i>Lycianthes radiata</i>			Sbi, Ser			
<i>Lycianthes</i> spp.	Cbr	Dgl	Sad, Ser, Sli, Spa			
<i>Lycianthes surotatensis</i>			Sho			
<i>Nicandra physalodes</i>	Cbr	Dgl, Ubi	Spa			
<i>Nicotiana</i> sp.	Cbr	Pin	Spa			
<i>Physalis</i> sp.		Dph	Ser, Sli			
<i>Schultesianthus venosus</i>		Dto				
Solanaceae indet.		Mma	Spa			
<i>Solanum abutiloides</i>		Apl	Ser, Sli, Sop			
<i>Solanum acerifolium</i>	Cbr	Ali,	Sho, Sli, Spa			
<i>Solanum aligerum</i>			Ser, Sli			
<i>Solanum aphyodendron</i>	Cbr, Cpe, Cca	Aja, Ali, Apl, Dbo, Dph, Dto, Eha	Sad, Sbi, Sbo, Ser, Sho, Sli, Slu, Sop, Spa			
<i>Solanum appendiculatum</i>			Sho, Sli, Spa			
<i>Solanum appressum</i>			Sti			
<i>Solanum argenteum</i>		Dto	Sho			
<i>Solanum bicolor</i>	Cbr	Ali	Sli			
<i>Solanum</i> cf. <i>abitaquense</i>	Cbr, Cpe		Spa, Ubi			
<i>Solanum</i> cf. <i>sessile</i>	Cbr, Cpe	Eha	Spa			
<i>Solanum chrysotrichum</i>		Aja, Ali, Dph, Dto	Sho, Spa			
<i>Solanum confusum</i>			Ser			
<i>Solanum diphyllum</i>		Aja, Dto	Sho, Spa			
<i>Solanum dissimile</i>	Cbr		Sbo, Ser			
<i>Solanum erianthum</i>			Sho, Spa			
<i>Solanum grandiflora</i>			Ser, Slu			
<i>Solanum gratum</i>	Cbr					
<i>Solanum hispidum</i>			Sho			
<i>Solanum mauritanium</i>	Cpe					

(continued on next page)

Table 3 (continued)

Plants	Obligate			Facultative		
	Carollinae	Ectophyllini	Sturnirini	Phy.	Glo.	Lon.
<i>Solanum meridense</i>	<i>Cbr</i>					
<i>Solanum muela</i>	<i>Cbr</i>					
<i>Solanum nigricans</i>		<i>Dto</i>	<i>Sho</i>			
<i>Solanum ovalifolium</i>			<i>Sbi, Spa</i>			
<i>Solanum pseudocapsicum</i>	<i>Cso</i>		<i>Ser, Sli, Sho, Sli</i>			
<i>Solanum rovirosanum</i>			<i>Sho</i>			
<i>Solanum schlechtendalianum</i>	<i>Cso</i>	<i>Aja</i>	<i>Sho, Spa</i>			
<i>Solanum scuticum</i>			<i>Slu</i>			
<i>Solanum</i> spp.	<i>Cbr, Cpe</i>	<i>Dbo, Dgl, Pin</i>	<i>Sad, Sbi, Sbo, Ser, Sho, Sli, Slu, Spa</i>			
<i>Solanum sycophanta</i>			<i>Sar</i>			
<i>Solanum tanysepalum</i>	<i>Cpe</i>		<i>Sbo, Ser</i>			
<i>Solanum tenuispinum</i>			<i>Ser, Sli</i>			
<i>Solanum ternatum</i>			<i>Sbo, Ser</i>			
<i>Solanum trichoneuron</i>			<i>Ser, Sli</i>			
<i>Solanum umbellatum</i>	<i>Cbr</i>	<i>Apl, Ctr, Dto, Pma</i>	<i>Ser, Sho, Sli, Sti</i>			
<i>Solanum undulatum</i>		<i>Aja, Ali</i>	<i>Slu, Spa</i>			
<i>Trianaea</i> sp.			<i>Ser</i>			
<i>Vassobia lorentzii</i>			<i>Ser</i>			
<b>Urticaceae</b>						
<i>Cecropia angustifolia</i>	<i>Cbr</i>	<i>Ali, Pal</i>				
<i>Cecropia gabrielis</i>		<i>Pin, Pli</i>	<i>Slu</i>			
<i>Cecropia latiloba</i>			<i>Ser</i>			
<i>Cecropia membranacea</i>	<i>Cbr</i>	<i>Pinc, Pma, Vme</i>		<i>Pha</i>		
<i>Cecropia obtusifolia</i>		<i>Aja, Ali</i>	<i>Sho, Spa</i>			
<i>Cecropia peltata</i>		<i>Aja, Ali, Dto</i>	<i>Sho</i>			
<i>Cecropia polyplebia</i>			<i>Sho</i>			
<i>Cecropia reticulata</i>				<i>Pha</i>		
<i>Cecropia sararensis</i>	<i>Cbr, Cpe</i>	<i>Aam, Ali, Dgl, Eha, Mma, Pal, Pan, Pum</i>	<i>Sas, Sli, Vth</i>	<i>Pha</i>	<i>Aca, Acu</i>	<i>Lro</i>
<i>Cecropia</i> spp.	<i>Cbr</i>	<i>Aja, Pma, Sma</i>	<i>Sho</i>			
<i>Cecropia telealba</i>	<i>Cbr, Cpe</i>	<i>Aja, Ali, Csa, Dbo, Eha, Pal, Pdo, Pum</i>	<i>Sbo, Ser, Slu, Spa</i>			
<i>Coussapoa villosa</i>		<i>Dto</i>				
<i>Urera caracasana</i>		<i>Apl</i>	<i>Ser, Sli</i>			
<i>Urera</i> sp.			<i>Sho</i>			
<b>*Winteraceae</b>						
<i>*Drimys</i> sp.			<i>Sbo, Slu</i>			

from 79 genera and 39 families (Table 3).

### 3.1. Bats

Of the 47 frugivorous bat species, 19 were present in both the middle and higher elevations, 28 only in middle elevations and only 3 in the higher elevations (Table 2).

The most important frugivore montane bat was *C. brevicauda*, which ate 91 species of fruit from 27 genera in 15 families of plants across the elevation gradient from both Central and South América. The second most important species was *S. hondurensis*, which ate 69 species of fruit from 25 genera in 18 families of plants across the elevation gradient from Central América only. Finally, the most important order of frugivorous bat genera in terms of richness of plants consumed were *Sturnira* (46 genera), followed by *Carollia* (34 genera), *Artibeus* (32 genera), *Dermanura* (32 genera), and *Platyrrhinus* (12 genera).

### 3.2. Plants

The genera of plants most commonly consumed by montane bats at middle elevations (1000–2000 m a.s.l.) were *Piper* (23%), *Solanum* (19%), *Ficus* (12%), *Cecropia* (9%) and *Vismia* (5%). At higher elevations (> 2000 m a.s.l.) the five most commonly consumed plant genera were *Solanum* (22%), *Piper* (17%), *Anthurium* (8%), *Cecropia* (7%), *Cavendishia* (6%), and *Vismia* (6%).

### 3.3. Trophic structure in montane fruit bats

Both middle and high elevation networks were modular. The network for middle elevations was composed of four modules (Q = 0.27,

ZQ = 15.6, p-value < 0.001 Fig. 1 right) the first was composed by *Sturnira* interacting with 20 genera of plants, especially with *Solanum*. The second module was composed by *Carollia* and *Glossophaga* interacting with 18 genera of plants especially with *Piper*, *Vismia* and *Anthurium*. The third module was composed by *Chiroderma* interacting with *Poulsenia*, and the last module was composed of 9 genera, (6 from the tribe Ectophyllini plus the 3 facultative frugivorous *Phyllostomus*, *Anoura* and *Lonchophylla*) interacting with 31 plant genera, especially with *Cecropia* and *Ficus* (Fig. 1 right).

The network from higher elevations was composed of three modules (Q = 0.26, ZQ = 4.2, p-value < 0.001; Fig. 1 left). The first was composed by *Sturnira* interacting with 13 genera of plants, especially with *Solanum* and *Anthurium*. The second module was composed by *Carollia* and *Glossophaga*, which interacted with 8 genera of plants, especially with *Piper* and *Saurauia*. The last module made up of 4 genera from the tribe Ectophyllini, which interacted with 7 genera of plants, especially *Cecropia*, *Vismia*, and *Cavendishia* (Fig. 1 left).

## 4. Discussion

Based on our extensive literature review and our field observations we add important information to our knowledge of the diet and trophic structure of montane frugivorous phyllostomid bats by describing that the networks are modular, where each module reflects the trophic structure previously reported for frugivorous bat assemblages. We also found that at high altitudes, species of the tribe Ectophyllini are *Cecropia* + *Cavendishia*-specialists rather than *Ficus*-specialists as reported for the lowlands, and finally we describe new interactions reflecting 14 species of plants, including three botanical families, previously not reported to be consumed by bats.



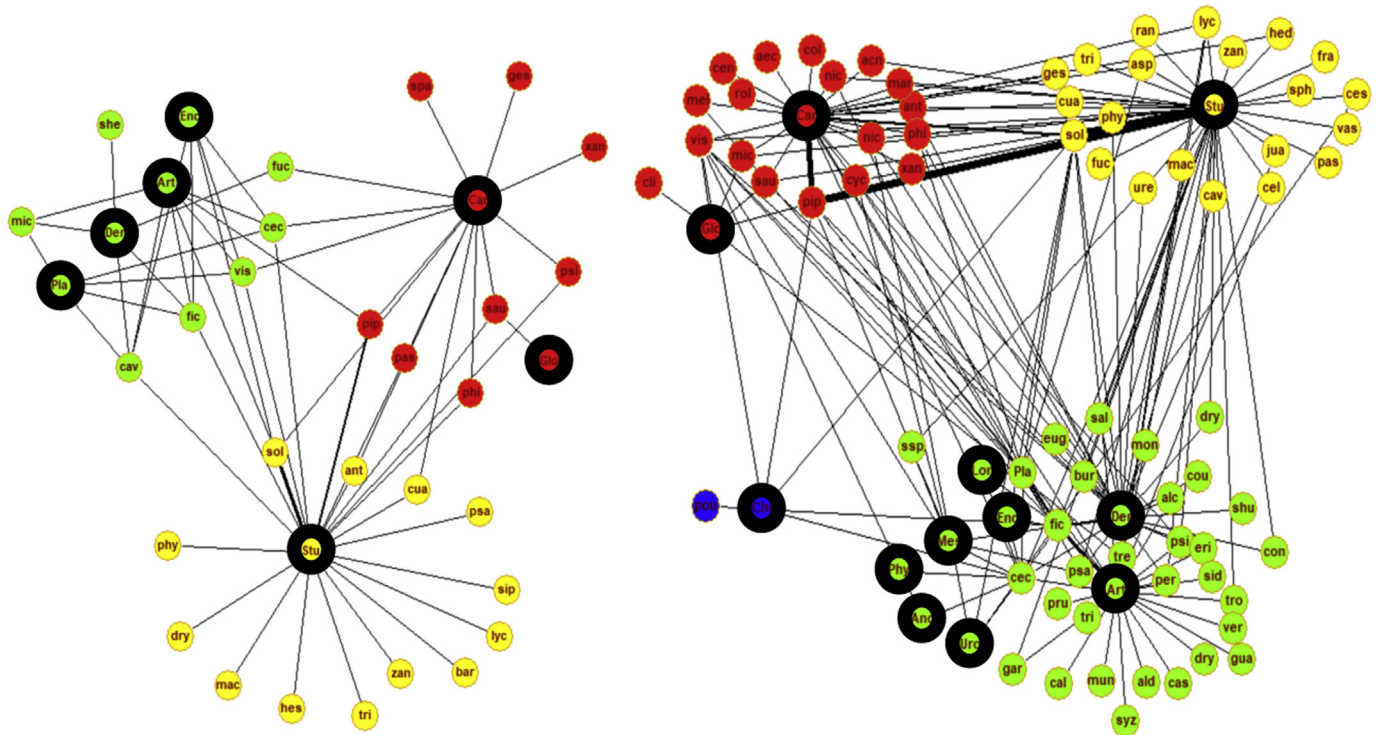


Fig. 1. The modular structure (representing dietary preferences in the interactions between genera of Neotropical frugivorous bats (broad border circles) and fruits (slender border circles) in montane environments. Species in the same module (same color) are more densely connected to each other than to other species in the same network. Right: middle elevations network (between 1000 and 2000 m a.s.l.)  $Q = 0.27$ , four modules. Left: higher elevations network ( $> 2000$  m. a.s.l.)  $Q = 0.26$ , three modules. Line width (edge) represents a frugivory interaction. Genus names are represented by the first three letters.

The modularity analysis was able to separate the three most important clades of frugivores, Ectophyllini, Carrollinae, and Sturnirini, into different modules. Even though the structure we found is similar to the tropic structure previously reported employing ordination analysis (i.e. Giannini and Kalko, 2004; da Silva et al., 2008), the network analysis is far more intuitive to understand, easier to visualize, and more amenable to analyze than ordination analysis. Moreover, our modularity analysis showed the modules are not perfectly separated into compartments. Bats consume not only their preferred food items but share resources between modules. This is evidence that the whole assemblage is interconnected.

At middle elevations (1000–2000 m a.s.l.) the trophic structure of the frugivorous montane bat assemblage reflected the dietary preferences of core plant taxa with *Artibeus* feeding primarily on *Ficus* and *Cecropia*, *Carollia* feeding primarily on *Piper*, and *Sturnira* feeding primarily on *Solanum* and *Piper* (da Silva et al., 2008; Fleming, 1986; Giannini and Kalko, 2004). However, the most important difference at higher elevations ( $> 2000$ m) is the lack of association between *Artibeus* and *Ficus*. *Ficus* was a rare dietary item for *Artibeus* and was also rare in the diet of other bat genera in the Ectophyllini (*Platyrrhinus*, *Enchisthenes*, *Dermanura*). *Artibeus* were initially hypothesized to be *Ficus*-specialists (Fleming, 1986) and this hypothesis was later extended to the whole Ectophyllini tribe (Giannini and Kalko, 2004). However, our findings support what Saldaña-Vázquez et al. (2013) reported that *Artibeus* reduces the intake of *Ficus* and *Cecropia* as elevation increases (between 0 and 2000 m a.s.l.) probably because *Ficus* is less diverse at higher elevations (Franco-Rosselli and Berg, 1997; Gentry, 1995; Shanee and Peck, 2008). *Ficus*-specialists at higher elevations were found to be *Cecropia* + *Cavendishia*-specialists and we found no *Ficus* specialists at high altitudes ( $> 2000$ ). In fact, *Cecropia* and *Cavendishia* were commonly consumed not only by Ectophyllini but by the majority of the mountain frugivorous bat assemblages.

This result supports previous observations that *Cecropia* is an

important dietary item for many frugivores (Charles-Dominique, 1986; da Silva et al., 2008; Horsley et al., 2015), but this is the first report of the consumption of *Cavendishia* and *Psamissia*, both from the family Ericaceae family. Ericaceae was previously unknown to be consumed by bats (Geiselman et al., 2015; Lobova et al., 2009) but it seems to be a common food at higher elevations ( $> 2000$ m) in the Andes in Colombia (Bolaños-Silva, 2000; Ceron and Orozco, 2013; Pérez-Torres, 2004), Venezuela (Castaño, 2009) and Ecuador (Zamora-Delgado, 2008). At higher elevations near the timberline Ericaceae is one of the most diverse woody families of woody flora in the Andes (Gentry, 1995). This could explain the importance of *Cavendishia* in the diets observed in the montane bats of the Ectophyllini tribe (*Artibeus*, *Platyrrhinus*, *Enchisthenes*, and *Dermanura*).

Compared to the lowlands there are very few data on diet from the frugivorous bats of the high mountains, especially above the higher level ( $> 2500$  m a.s.l.). There is just one locality studied in the western part of the savanna of Bogotá, Colombia (Bolaños Silva, 2000; Pérez-Torres, 2004). This information gap in the diet of montane bats is reflected by our findings of 14 species (10 genera) previously unknown that are consumed by bats. This includes three botanical families (Ericaceae, Onagraceae, Winteraceae) not previously reported to be consumed by bats (Table 2).

There is a reduction in the number of frugivorous bats found at higher elevations compared to middle elevations. The decline in species numbers from different fauna groups associated with an altitudinal gradient is a phenomenon widely referred to in the literature (Carvajal-Quintero et al., 2015; Lomolino and Brown, 2009; Soriano, 2000). For bats this has been interpreted as a consequence of the reduction of available resources or physiological limitation in order to face decreases in the ambient temperature (Ruiz, 2006; Soriano, 2000; Soriano et al., 2002). We cannot separate the concomitant effects of the two possible causal factors of this phenomenon (decrease in temperature, and the reduction in abundance of resources). On the one hand, the reduction in



the number of species in the genus *Chiroderma*, *Artibeus*, *Dermanura* and *Platyrrhinus*, could be due to a reduction in the abundance of their preferred plant genus *Ficus* at higher elevations (Gentry, 1995). On the other hand, the reduction in number of species in the genus *Carollia* could be due to physiological limitations; the preferred plant genus for *Carollia* (*Piper*) seems to be abundant at higher elevations (Saldaña-Vázquez et al., 2013) and there is only one species from the Carollinae subfamily at higher elevations. The wide elevational distribution of *C. brevicauda* over 2000 m a.s.l. could be due to adaptations such as very dense fur, reduction of uropatagium, small ears, and densely haired feet and toes allowing them to face lower temperatures. Similarly some species are exclusively associated with the higher elevations (e.g. *S. bidens*, *S. aratathomasi*), which seems to be an indicator that some bat species at higher elevations must possess certain adaptive features to those environments, which at the same time makes their presence incompatible with the prevalent conditions at the lower elevations (Soriano et al., 2002). It is probable that at least for *Carollia* spp. and *Sturmira* spp. the determining factor that limits their altitudinal distribution are of a physiological nature and linked to their thermoregulatory capacity, since the types of food consumed along their altitudinal range are the same.

## 5. Conclusions

Our modularity analysis partially confirms that montane frugivorous phyllostomid bats are faithful to core plant taxa, as originally suggested by Fleming (1986), with *Carollia* feeding primarily on fruits of *Piper*, *Sturmira* on *Solanum* and *Artibeus Ficus* and *Cecropia*. However, our study showed that in montane environments especially above 2000 m, species of the tribe Ectophillini switch to resources different from those they prefer in the lowlands. This new result is particularly important because it shows that a loss in the abundance and diversity of *Ficus* at higher elevation might force species in the Ectophillini to change their dietary preferences. Moreover, this finding supports and extends the idea that *Artibeus* (as proposed by Saldaña-Vázquez et al., 2013), as well as the other genera in the Ectophillini (*Platyrrhinus*, *Enchisthenes*, and *Dermanura*), have the ability to use other plant species as they exploit a wide diversity of habitats from the lowlands to mountain ecosystems.

## Author's contributions

JHC and JPT formulated the idea, JHC and JAC conducted the fieldwork, JHC performed network analyses, JHC, JAC, and JPT wrote the manuscript.

## Declarations of interest

None.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2018.06.005>.

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