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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 Carolliinae, Rhinophyllinae and Stenodermatinae (at least 25 genera) are considered obligate frugivores, and 25 genera in the subfamilies Macrotinae, Micronycterinae, Lonchorininae, Phyllostominae, Glossphaginae, 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. davisi* 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