Temporal variation in bat-fruit interactions: Foraging strategies influence network structure over time

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A B S T R A C T

Mutualistic interactions, such as seed dispersal, are important for the maintenance of structure and stability of tropical communities. However, there is a lack of information about spatial and temporal variation in plant-animal interaction networks. Thus, our goal was to assess the effect of bat's foraging strategies on temporal variation in the structure and robustness of bat-fruit networks in both a dry and a rain tropical forest. We evaluated monthly variation in bat-fruit networks by using seven structure metrics: network size, average path length, nestedness, modularity, complementary specialization, normalized degree and betweenness centrality. Seed dispersal networks showed variations in size, species composition and modularity; did not present nested structures and their complementary specialization was high compared to other studies. Both networks presented short path lengths, and a constantly high robustness, despite their monthly variations. Sedentary bat species were recorded during all the study periods and occupied more central positions than nomadic species. We conclude that foraging strategies are important structuring factors that affect the dynamic of networks by determining the functional roles of frugivorous bats over time; thus sedentary bats are more important than nomadic species for the maintenance of the network structure, and their conservation is a must.

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1. Introduction

Mutualisms are interactions among species in which both species derive benefits from the interaction, and are recognized as critical components of ecological and evolutionary processes occurring in ecosystems (Boucher et al., 1982; Bronstein, 2001; Stachowicz, 2001). In addition, mutualistic interactions such as seed dispersal and pollination are important for the maintenance of the structure and stability of communities since they affect the population dynamics of the interacting species (Bascompte and Jordano, 2014). Among these mutualistic interactions, the interactions between plants and frugivorous animals are vital for tropical ecosystems, since between 50 and 90% of the woody plants are dispersed by animals (Fleming et al., 1987). However, these interactions are highly variable over time due to phenological changes of the interacting species (Bascompte and Jordano, 2014).

Bat-dispersed plants are characterized by an opportunistic strategy, with fast growing and dissemination of a great number of seeds that develop under direct exposure to sunlight (Charles-Dominique, 1986; Lobova et al., 2009). Therefore, these plants participate in early stages of secondary succession of forests; an important process for conservation since it initiates the regeneration of anthropogenic-affected areas such as pasturelands or abandoned crops (Castaño, 2009). Seed dispersers, such as bats, are highly important to maintain plant diversity in tropical forests (Muscarella and Fleming, 2007). Since the abundance of frugivorous bats overpasses that of the other frugivorous (mammals and birds), they are considered as the most valuable seed dispersers in tropical forests (Molinari, 1993). In addition, seed shadows generated by bats are temporal and spatially more homogeneous than those generated by others dispersers, increasing the likelihood of finding optimal growing sites for seeds (Murray, 1986; Wilson and Traveset, 2000). Thus, the decline in abundance of frugivorous bats would potentially have catastrophic consequences, including the disappearance of plenty of terrestrial biodiversity (Thompson, 2006). Consequently, species conservation cannot be achieved without considering species interactions; thus, the study of bat-fruit mutualistic networks is highly relevant for the conservation of tropical forests (Muscarella and Fleming, 2007; Bascompte and

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Jordano, 2006).

Among all the seed-dispersal mutualistic interactions in the Neotropics, there are highly prevalent relations between bat (Phyllostomidae) and plant genera: *Artibeus* with *Ficus* (Moraceae) and *Cecropia* (Urticaceae) (Heithaus et al., 1975; Saldaña-Vázquez et al., 2013; Montoya-Bustamante et al., 2016); *Carollia* with *Piper* (Piperaceae) (Marinho-Filho, 1991; Thies and Kalko, 2004; Mello et al., 2004; Saldaña-Vázquez et al., 2013; Montoya-Bustamante et al., 2016), and *Sturnira* with *Solanum* (Solanaceae) (Marinho-Filho, 1991; Mello et al., 2008; Saldaña-Vázquez et al., 2013). However, these bat-fruit interactions vary temporal and spatially more than what was previously known (Montoya-Bustamante et al., 2016; Laurindo et al., 2017), and the consequences of this variation are poorly known (Laurindo et al., 2017).

Traditionally, studies of plant-animal mutualisms have been focused on highly specific interactions between pairs of species, which are frequently constrained and coevolved (Doebeli and Knowlton, 1998; Holland et al., 2002). However, there is a general tendency to diffuse relations in nature (those that happen among groups of species), so this approach does not allow to understand the importance of mutualistic interactions on community structure (Jordano et al., 2009). Mutualistic interactions form complex networks with structures characterized by: (1) asymmetric relations in which many species have few interactions (specialist) and few species present most of the interactions (generalists), property also known as heterogeneity (Bascompte and Jordano, 2014); (2) a tendency to form a core of generalist species interacting mainly among themselves, whereas specialist species interact mainly with that network core, a property known as nestedness (Bascompte et al., 2003; Bascompte and Jordano, 2014); and (3) subgroups of species that frequently interact among them rather than with species outside their group (module), a property called modularity (Bascompte and Jordano, 2014).

This structure of mutualistic networks (heterogeneous, nested and modular) confers robustness against species extinction and interaction loss (Bascompte et al., 2003; Bascompte and Jordano, 2006, 2014). Therefore, an approach that considers mutualistic interactions as a network of interactions is vital to fully understand plant-animal interactions and its importance for ecosystem stability and biodiversity maintenance. However, the understanding of mutualistic interactions has been impeded by a lack of information about spatial and temporal variation in the structure of plant-animal interaction networks (Winemiller, 1990).

Our goal was to assess the temporal variation in the structure and robustness of bat-fruit seed dispersal mutualistic networks in two contrasting localities. We hypothesize that networks vary in time (i.e., size, species, Olesen et al., 2008; Laurindo et al., 2017), present a nested and modular structure (Bascompte and Jordano, 2014; Laurindo et al., 2017), and have a low complementary specialization (Mello et al., 2011a). Also, despite of the temporal variation, we hypothesize their robustness not to change due to interaction "rewiring" (the absence of a partner species causes a switch to an alternative partner, making a resilient response to loss of mutualist in time, Bascompte and Jordano, 2014). Finally, we hypothesize bat species to play different functional roles in time according to their foraging strategy (Soriano, 2000). To our knowledge, only few studies have been published about the structure of bat-fruit mutualistic networks (Mello et al., 2011a, 2015, 2011b; Sarmento et al., 2014; Hernández-Moreno et al., 2015), and there is only one work published about temporal variation of bat-fruit networks, with no further information about the influence of bat behavior in network structure (Laurindo et al., 2017).

2. Materials and methods

2.1. Datasets and study areas

We used two datasets on the interaction of Neotropical frugivorous bats and plants, each one with information of six-month sampling in two different ecosystems; a tropical dry forest (from Montoya-Bustamante et al., 2016) and a tropical rain forest (new information provided by this study). In both cases, bat-fruit interactions were recorded, by capturing bats using mist nets, and their feces were collected in paper bags. Observations on fruit carried by bats, when captured in the mist nets, were registered as well. Mist nets were opened from 1900 to 2400 h, decreasing the probability of capturing bats that had not fed yet.

The tropical rain forest study area corresponds to the Pericos Basin Conservation Area, located at the locality of Triana (Buenaventura, department of Valle del Cauca, Colombia), in the Pacific slope of the Western Andes range. Its steep topography covers an altitudinal gradient from 200 to 400 m a.s.l. This study area is part of the Colombian Biogeographic Chocó, which is one of the most biodiverse regions with a high endemism of fauna and flora (Gentry, 1993). The study area, in particular, is a secondary forest and it was sampled seven nights per month from July to December 2015, using 10 mist nets (three 6 × 3 m nets and seven 12 × 3 m nets) set up at the understory level. Netting effort in this case was 1785 net-hours.

The second study area is located in the locality of Robles (Jamundí, department of Valle del Cauca, Colombia) in the Cauca river valley at an average altitude of 990 m a.s.l. The landscape includes farms and tropical dry forest. A detailed description of this study area can be found in Montoya-Bustamante et al. (2016). This area was sampled 19 nights per month from June to November 2014, using six mist nets (three 6 × 3 m nets and three 12 × 3 m nets) set up at the understory level. Netting effort in this case was 2565 net-hours.

2.2. Reference plants and fruit availability

A reference seed collection was collected in order to identify the plant species consumed by bats, and collected plants were compared against specimens deposited at the Universidad del Valle herbarium (CUVC) for identification. We also used seed guides (Ríos et al. (2004); Linares and Moreno-Mosquera (2010); Lobova et al. (2009)) to identify seeds to the species level. Fruit availability was estimated by monitoring plant species usually eaten by bats (e.g., *Cecropia, Solanum, Ficus, Piper, Vismia*) (Mello et al., 2011a; Saldaña-Vázquez et al., 2013) through *ad libitum* searches. Plants were marked and inspected every month for ripe fruits.

2.3. Data analysis

In both cases, sampling effort was assessed using species accumulation curves for captured bats, consumed plants (found in feces), and interactions (which records the number of distinct pairwise interactions as a function of the sampling time). However, it might be impossible to record all the potential interactions, due to forbidden interactions (non-biologically possible interactions because of constrains made by the natural history of the species), and highly dynamic interactions over time (Bascompte and Jordano, 2014; Falcão et al., 2016). We used the non-parametric richness estimator Chao 1 to estimate completeness of the sampling for species and interactions (Villareal et al., 2004).

To analyze network structure and robustness, the observed