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**ANÁLISIS DE LA HIPÓTESIS DE ESTRATIFICACIÓN VERTICAL PARA LA
COEXISTENCIA DE MURCIÉLAGOS FRUGÍVOROS DEL BOSQUE TROPICAL
SECO**

TESIS

Que presenta

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*"Mira profundamente en la naturaleza y entonces
comprenderás todo mejor.*

"Albert Einstein"

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RESUMEN

Se analizó si la coexistencia de murciélagos frugívoros se explica siguiendo la hipótesis de estratificación vertical (HEV) considerando las propiedades intrínsecas tanto de murciélagos como de plantas frutales en un bosque tropical seco. Se evaluó simultáneamente la disponibilidad temporal y vertical de recursos frutales, la tasa de captura y dieta de murciélagos frugívoros. Se capturaron un total de 382 murciélagos frugívoros correspondientes a 7 especies, tres de estas especies son forrajeadores de dosel y tres de sotobosque. Aunque se observó un recambio en la fructificación de especies de plantas que sugiere una disponibilidad continua de los recursos alimentarios durante todo el año, en realidad, la fructificación fluctuó estacionalmente entre estratos. El número de capturas por estrato mostró la misma tendencia estacional que el patrón de fructificación, pero la influencia no fue significativa. A pesar de esto, la estructura de la dieta y el análisis de modularidad en la red indicaron que la dieta de las especies de murciélagos del dosel *Dermanura phaeotis*, *Artibeus jamaicensis* y *Artibeus lituratus*, se compone casi exclusivamente de frutos presentes en dosel caracterizado por especies de *Ficus insipida*, *Ficus obtusifolia* y *Cecropia obtusifolia*. Mientras que las especies de murciélagos del sotobosque *Centurio senex*, *Sturnira hondurensis* y *Sturnira parvidens*, consumieron exclusivamente especies como *Solanum rudepannum*, *Solanum erianthum* y *Piper aduncum*. Las especies de murciélagos forrajeadoras de dosel *A. lituratus* y *D. phaeotis* se determinaron como especies conectoras de módulos, ya que consumieron frutos de sotobosque pertenecientes a las especies *Solanum rudepannum* y *Piper aduncum*. Los resultados concuerdan con la hipótesis de estratificación vertical y sugiere que la estratificación de los murciélagos frugívoros en un bosque tropical seco podría ser una estrategia evolutiva, determinada por la estratificación vertical de las plantas consumidas, que actúa separando las especies de murciélagos, reduciendo la superposición de nichos ecológicos y permitiendo la coexistencia.

Palabra clave: comportamiento, forrajeo, México, recurso, segregación de nicho.

ABSTRACT

We tested the Vertical Stratification Hypothesis for segregation of frugivorous bats considering intrinsic properties of both bats and their diet plants in a tropical dry forest. We simultaneously evaluated the vertical and temporal availability of fruit resources, our capture rate of frugivorous bats, and the diet of these bats. We captured 382 frugivorous bats comprising three canopy and three understory bat species. There was a high plant species turnover throughout the year, which created an apparent continuous availability of food resources. However, there was significant seasonal fluctuation in fruiting between strata. The number of captures per stratum showed the same seasonal trend as the fruiting pattern, but the influence was not significant. Despite this, diet structure and network modularity analyses indicated that the diet of canopy bat species, *Dermanura phaeotis* and *Artibeus* spp., almost exclusively comprised of canopy plant species, such as members of the Moraceae family and *Cecropia* sp, while core plant species in the diet of the understory bat species *Centurio senex* and *Sturnira* spp., were exclusively plant species from the understory, such as *Solanum* spp., and *Piper* spp. Our results support the Vertical Stratification Hypothesis for frugivorous bats in a tropical dry forest, which may be mediated by the vertical stratification of core diet plants, resulting in an evolutionary strategy that acts to segregate bat species, reduce niche overlap and enable coexistence.

Key word: behavior, foraging, Mexico, niche segregation, resource.

INTRODUCCIÓN GENERAL

Los bosques tropicales secos se caracterizan por presentar una marcada estacionalidad, que impacta la disponibilidad de recursos para los organismos que ahí coexisten (Lieberman 1982, Van Schaik *et al.* 1993). En particular, la producción de los recursos frutales de las diferentes especies de plantas están altamente influenciadas por la estacionalidad, lluvia y radiación solar (Gautier-Hion *et al.* 1989, White 1994, Haugaasen *et al.* 2005). Por lo tanto, la disponibilidad temporal de frutos se ve modificada de una estación a otra, ocasionando periodos con diferente abundancia de frutos (Fleming *et al.* 1986, Pereira *et al.* 2010). Esta disponibilidad fluctuante de los recursos frutales puede influir en la reproducción, comportamiento, dieta, abundancia, migración, competencia o repartición de recursos de los animales frugívoros (Fleming *et al.* 1986, Loayza *et al.* 2006, Saldaña 2014, Jara-Servín *et al.* 2017, Lee *et al.* 2017).

Además de las variaciones en la disponibilidad temporal de los frutos, la disponibilidad espacial juega un papel importante en la repartición y uso de recursos entre animales frugívoros (Bonaccorso 1979, Rieger *et al.* 1988). También, las características del fruto como el color, olor, dureza, tamaño, forma y calidad nutricional, pueden ser factores clave que permitan la especialización de ciertas especies de frugívoros (Dumont 1999, Duan 2014, Saldaña 2014, Suárez *et al.* 2015). De esta manera, los animales frugívoros pueden disponer de una gran variedad de frutos que aprovechar como recurso principal a lo largo del año. En consecuencia, dividirse los recursos puede ser una estrategia evolutiva que les permite reducir la competencia, especializándose en ciertos recursos y así las especies simpátricas puedan coexistir dentro de la comunidad (Marinho-Filho 1991, Delaval *et al.* 2005). Dado lo anterior, la repartición de recursos juega un papel importante en la estructura de comunidades ecológicas (Schoener 1974).

Las comunidades de animales frugívoros están compuestas por diferentes grupos, principalmente aves y mamíferos (murciélagos y primates), los cuales suelen especializarse en el consumo de ciertas especies (Molinari 1993). En estos grupos de animales la repartición de recursos es determinante para la coexistencia de las

especies simpátricas; por ejemplo, en murciélagos frugívoros se ha descrito que la estratificación vertical de los frutos en bosques tropicales lluviosos se refleja en una segregación espacial de las especies simpátricas y es un factor fundamental para la coexistencia (Bonaccorso 1979, Fleming *et al.* 1982, Marinho-Filho 1991, Molinari 1993, Delaval *et al.* 2005, Suárez *et al.* 2015). Por ejemplo, los murciélagos de los géneros *Carollia* y *Sturnira* son considerados frugívoros de sotobosque, que tienden a consumir fruta de arbustos menores a tres metros de altura, principalmente de los géneros *Piper* y *Solanum*. Mientras que los murciélagos de los géneros *Artibeus* y *Dermanura* son considerados frugívoros del dosel, porque prefieren consumir fruta de árboles mayores a tres metros de altura, principalmente del género *Ficus* y *Cecropia* (Bonaccorso 1979, Molinari 1993, Suárez *et al.* 2015).

La estratificación vertical como estrategia de repartición de recursos se ha descrito en murciélagos frugívoros, artrópodos (Ulyshen 2011), aves (Derlindati *et al.* 2005, Anderson 2009), murciélagos insectívoros (Marques 2015) y zorros voladores Pteropodidae (Hodgkison 2004). Los factores que los limitan a determinados estratos pueden ser; 1) disponibilidad vertical de recursos, 2) capacidad de vuelo, 3) gradientes climáticos e 4) interacciones intra e interespecíficas (Ulyshen 2011, Hodgkison 2004, Derlindati *et al.* 2005, Anderson 2009, Marques 2015). De tal manera, la estratificación vertical en bosques tropicales juega un papel fundamental en la repartición de nichos ecológicos.

En este estudio, evaluamos la hipótesis de estratificación vertical en murciélagos frugívoros. Hasta donde tenemos conocimiento este es el primer estudio que evalúa esta hipótesis en bosques tropicales secos.

CAPÍTULO 1

A test of the vertical stratification hypothesis for the coexistence of frugivorous bats in
a dry tropical forest

REVISTA: OECOLOGIA

PRESENTACIÓN DEL ARTÍCULO

A test of the vertical stratification hypothesis for the coexistence of frugivorous bats in a dry tropical forest

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ABSTRACT

We tested the Vertical Stratification Hypothesis for segregation of frugivorous bats considering intrinsic properties of both bats and their diet plants in a tropical dry forest. We simultaneously evaluated the vertical and temporal availability of fruit resources, our capture rate of frugivorous bats, and the diet of these bats. We captured 382 frugivorous bats comprising three canopy and three understory bat species. There was a high plant species turnover throughout the year, which created an apparent continuous availability of food resources. However, there was significant seasonal fluctuation in fruiting between strata. The number of captures per stratum showed the same seasonal trend as the fruiting pattern, but the influence was not significant. Despite this, diet structure and network modularity analyses indicated that the diet of canopy bat species, *Dermanura phaeotis* and *Artibeus* spp., almost exclusively comprised of canopy plant species, such as members of the Moraceae family and *Cecropia* sp, while core plant species in the diet of the understory bat species *Centurio senex* and *Sturnira* spp., were exclusively plant species from the understory, such as *Solanum* spp., and *Piper* spp. Our results support the Vertical Stratification Hypothesis for frugivorous bats in a tropical dry forest, which may be mediated by the vertical stratification of core diet plants, resulting in an evolutionary strategy that acts to segregate bat species, reduce niche overlap and enable coexistence.

Key word: feeding behavior, foraging, niche segregation, resource availability.

INTRODUCTION

Temporal and spatial heterogeneity in food resource availability (Van Schaik et al. 1993; Hanya and Bernard 2013) is a strong driving force for competition that has long intrigued researchers (Creel 2001), and the manner in which animals coexist is therefore a key topic in ecology. Niche partitioning plays an important role in structuring ecological communities since it reduces competition (Schoener 1974; Delaval et al. 2005). Partitioning in niche axes, such as diet, acts to facilitate coexistence in animals where food resources are a limiting factor (Schoener 1974). Competition may occur not only among conspecifics but also among individuals from different species. This leads to a mechanism that partitions niches and facilitates coexistence in a hierarchical fashion.

One strategy enabling interspecific coexistence is the vertical stratification of interacting species. This is a strategy present in a number of animal groups such as arthropods (Ulyshen 2011) and birds (Derlindati and Caziani 2005; Anderson 2009). The mechanisms mediating this stratification and constraining species to a given stratum are diverse. For instance vertical stratification in these animal groups can be mediated through 1) vertical availability of food resources, 2) presence of refuges, 3) limited dispersal capabilities among strata, 4) vertical local environmental conditions fostering a climatic gradient, 5) differential susceptibility to predation at certain strata, and 6) forest successional stages fostering the presence of strata to segregate (Hodgkison et al. 2004; Derlindati and Caziani 2005; Anderson 2009; Ulyshen 2011; Marques et al. 2015). Hence, the vertical stratification of potential competing species is a key strategy in ecological niche segregation.

Bats constitute a good model for studying how species segregate, not only temporally but also spatially (Van Schaik et al. 1993; Muscarella and Fleming 2007), as there is a large diversity of coexisting bat species competing for resources (Estrada-Villegas et al. 2010). Furthermore, vertical stratification has been reported as a strategy segregating insectivorous bat communities in America (Marques et al. 2015), where the vertical stratification of prey drive enable this segregation. Alternatively, the relationship between wing morphology and forest structure drives vertical stratification

in flying fox bats (Hodgkison et al. 2004). The vertical stratification has also been determined for new world frugivorous bats from tropical rain forests , where the main strategy driving the stratification and segregation of frugivorous bat species is the vertical stratification of core fruits in their diet (Bonaccorso 1979; Fleming 1982; Marinho-Filho 1991; Molinari 1993; Delaval et al. 2005; Loayza et al. 2006; Suárez and Montenegro 2015; Castaño et al. 2018; Gregorin et al. 2017). Nevertheless, vertical stratification of bat species has been posited only in the context of an alignment with the vertical distribution of core plant species in their diet, and lacks a framework for the mechanism that facilitates dietary segregation and coexistence of frugivorous bat species.

Individuals of *Dermanura* spp. and *Artibeus* spp. provide an example of this stratification since they have been found to forage mainly on canopy plant species from the Moracea family and *Cecropia* spp. These plant species are characterized by fruiting asynchronously and producing a heavy crop, which creates a large but unpredictable availability of food resources (Korine et al. 2000; David et al. 2012). Conversely, bat species of *Sturnira* spp. and *Carollia* spp. forage on understory plant species, such as *Piper* spp. and *Solanum* spp. (Bonaccorso 1979; Pereira et al. 2010; Suárez and Montenegro 2015). These plant species are characterized by low crop yield and by fruiting synchronously over a longer period of time (Bizerril and Raw 1997; Fleming 1982; Fleming and Heithaus 1986; Pereira et al. 2010), which creates feeding constraints due to the low availability of food resources that occur in a more predictable way than is the case for the core plant species consumed by canopy bat species (Bizerril and Raw 1997; Fleming 1982; Pereira et al. 2010). This association would align with the Vertical Stratification Hypothesis (VSH), where bat species will segregate vertically based on core diet preferences following the vertical distribution of food resources. These diet preferences would then lead exclusive canopy or understory bat segregation.

However, application of the VSH to frugivorous bats relies on a combination of mechanisms associated with the intrinsic properties of both bats and diet plant species that aid niche segregation and act to constrain the bat species to each particular stratum. One such intrinsic property is variation in plant nutritional quality, since

understory plant species have been found to exhibit a higher nutritional quality than canopy species (Wendeln and Runcle 2000; Castaman 2006). This could be a strong constraint for the exploitation of food resources given the differences in digestive capacities that exist among bat species. Understory bat species have a low digestive capacity, which could preclude them from foraging for the low quality food resources located in the canopy (Saldaña-Vázquez and Schondube 2013).

Another intrinsic property of plants facilitating vertical stratification relies on fruit hardness; it has been found that understory fruits are softer than those of the canopy plant species (Santana and Dumont 2009). This could drive the selection of food resources mediated through bite force and bat species size (Dumont 1999; Santana and Dumont 2009). Smaller bat species would have smaller bite force, constraining them to avoid the canopy where the fruits are harder than those in the understory. These features mean that understory bat species would be obliged to forage exclusively among the plant species from this stratum, while canopy bat species are not so constrained in this manner and can exploit a larger amount of resources (Morrison 1980; Fleming and Heithaus 1981; Molinari 1993; Ayala-Berdon et al. 2008).

The tropical dry forest is characterized by a strong seasonality and the presence of a smaller inter-stratum space than is the case in the tropical rain forest. Tropical rain forest are characterized by having a well-defined canopy stratum at 25 - 40 m in height, while the understory stratum is also well defined but features plant species that do not exceed 4 m in height (Bonaccorso 1979; Loayza et al. 2006). Canopy plant species of the tropical dry forest has are 10 m in height, while understory species are normally no higher than 5 m (Segura et al. 2003). However, this reduced inter-stratum space could mean that bats from the tropical dry forest would exhibit reduced vertical stratification, and their diet would not be constrained to the core-plant species of each stratum. In the present study, we aimed to evaluate the Vertical Stratification Hypothesis for frugivorous bats in a seasonal dry forest of western Mexico. We predict that the frugivorous bat diet will be closely associated with a segregation of bat species between strata, which corresponds with the stratal segregation of plant species based on intrinsic plant and bat species properties

METHODS

Study area

This study was conducted in the tropical dry forest of the 900 ha La Bonetera property in Lázaro Cárdenas municipality, Michoacán, Mexico (18° 05' N; 102° 25' W). The landscape is undulating, ranging from 100 to 430 m a.s.l. Two main vegetation types are found; deciduous forest on slopes and hills, which is characterized by plant species such as *Piper aduncum*, *Jacaratia mexicana*, *Stemmadenia grandiflora* and *Cupania sp.* Semi-deciduous forest occurs along valleys and watercourses, and features plant species such as *Cecropia obtusifolia*, *Solanum erianthum*, *Solanum rudepannum*, *Ficus insipida*, *Ficus obtusifolia* and *Brosimum alicastrum*. The tropical dry forest has a marked seasonality in rainfall with a rainy season from June to October and a dry season from November to May (Murphy and Lugo 1986).

Bat trapping

We conducted monthly six-day long field-trips to the study area from April 2016 to March 2017. Adverse weather conditions prevented sampling in June. We established six 40 meters wide by 1-km long transects each, three in each vegetation type. Eight 6 x 2.5 m mist-nets were set-up in each transect to capture bats, with a different transect sampled each night. Mist netting was suspended on nights of a full moon as bat activity is reduced on these nights (Pech-Canché et al. 2018). Mist nets were opened from 9:00 pm to 2:00 am and checked every 30 minutes. Captured bats were weighed, measured, sexed and their breeding status determined according to Jones et al. (1996). Species were identified using field keys for Mexican bats (Medellín et al. 2007).

Fruiting phenology

Monthly availability of fruits was evaluated along the same transects where the mist nets were located to capture bats. We registered all fruiting plants along the transects, but collected data only for those plant species recorded as potential diet items for frugivorous bats. Potential diet plant species were identified to species level, and classified as understory (≤ 3 m total height) or canopy (≥ 3.1 m total height) species. For plant species included in the diet of frugivorous bats, we recorded their diameter at

breast height (DBH), total height, and fruit crop abundance. For understory plant species fruit crop abundance was determined directly by counting all fruits, while for canopy plant species used binoculars. A unique identification mark was assigned to each individual plant evaluated in order to keep track of the number of fruits throughout the study period.

Diet structure

Captured bats were kept individually in a canvas bag for a maximum of two hours so that they defecated in the bag and the feces could be sampled. Each fecal sample was stored in an Eppendorf tube with 70% alcohol. Fecal samples were subsequently analyzed in the laboratory under a stereoscopic microscope. Different fecal items were separated into categories of seed, pulp, and fiber. Insects were found in two samples, but were not included in analysis. We simultaneously developed a reference collection of seeds of plant species potentially ingested by bats, as indicated in the literature (García-Estrada et al. 2012; García-Morales et al. 2012; Bolívar-Cime et al. 2014). This reference collection helped identify seeds found in the fecal samples to species level. Fruit pulps and fiber could only be determined to morpho level as their identification to species level is unreliable given the limited knowledge of how these materials change color with passage through the digestive tract.

Statistical analysis

We assigned items consumed in diet of frugivorous bats to one of two seasons, dry or rainy season (Murphy and Lugo 1986), as well as to one of two stratum, canopy or understory. Stratum membership of bat species was assigned according to literature (Bonaccorso 1979; Pereira et al. 2010; Suárez and Montenegro 2015). To segregate bat species by stratum, we constructed a weighted bipartite interaction network using the number of fecal samples in which seeds of each of the diet plants were found. We obtained the modularity Q value using the QuanBiMo algorithm with $1E6$ steps (Dormann and Strauss 2014). A network is modular if sub-groups or modules are found. A Q value closer to one is considered to indicate that the network is more modular (Dormann and Strauss 2014), while higher Q values are expected as network size increases, since more interactions occur with greater network size. We then used the

Patefield (1981) null model with 1000 simulated networks, employing the r2d method to identify whether the Q value was the result of a random process. Significant differences were evaluated by obtaining Z-scores using the observed Q value, as well as those from the randomizations. Modularity is considered significant when the Z score is > 2 (Dormann and Strauss 2014). Modularity of frugivorous bats with core plant species per stratum in our network would indicate the presence of vertical segregation in the bat community.

We also determined the functional role of bat and plant species by identifying module types in the network (Olesen et al. 2007). We calculated the contribution to modularity within (z) and among modules (C) for each bat and plant species and then plotted these estimates. The cut-off points were considered to include 80% of the data for each variable. We then determined the roles of module hub, network hub, peripheral and connector bat and plant species (Olesen et al. 2007). Peripheral species would present few links, and module hub species would present many links, with species within their own module of canopy or understory. Connector species would have links with other modules, which would indicate that there are species interacting between the canopy and the understory. Network analyses were performed with the 'bipartite' package (Dormann et al. 2009) in R (R Core Team 2018).

We obtained the Hurlbert niche breadth and overlap indices for diets of frugivorous bat species in the dry and the rainy season. The Hurlbert indices takes into account the availability of food resources (Hurlbert 1978). The niche breadth analysis allows determination of whether a species is generalist or specialist. The values of the index range from zero to one, where values close to zero indicate that a species is specialist. Hurlbert's overlap index provides a value of 0 when two species do not share resources, and values >1.0 when both species use certain resources more intensively than others and resource preferences of the two species tend to coincide (Hurlbert 1978). We then constructed an alluvial graph to graphically represent the diet segregation in the tropical dry forest.

We used GLM models with Poisson distribution and a log link function to evaluate spatial-temporal variation in both the availability of food resources and bat

captures. The dependent variable for food resources was the total number of fruits available per month per plant species. The independent variables were stratum, with two levels: canopy and understory, and season, with two levels: the rainy and dry seasons. The rainy season was considered as the period from July to October, and the dry season from November to May. The model to evaluate bat captures included the total number of bats captured as an independent variable, while the dependent variables were stratum and season. Our models also evaluated the interactions between stratum and seasonality in terms of food availability and bat captures.

RESULTS

Fruiting phenology

We registered a total of 70 individual plants that provide fruit consumed by bats, comprising 15 plant species. Nine species were trees in the canopy stratum, while the six remaining species were categorized in the understory stratum. The plant species with the largest number of individuals recorded were *Spondias purpurea* (n = 18 trees) and *Jacaratia mexicana* (n = 11 trees). Fruit availability was constant throughout the year; however, we observed interspecific differences in fruiting over the sampling period, which indicates the occurrence of temporal species turnover (Fig. 1). The tree species of *Brosimum alicastrum* and *Ficus obtusifolia* contributed the most in terms of number of fruits in the canopy stratum compared to other plant species, while the shrub *Solanum rudepannum* and small tree *Solanum erianthum* contributed the most fruit in the understory stratum. Species in the canopy stratum fruited preferentially in the dry season, while understory species fruited mainly in the rainy season (Fig. 1).

The GLM analysis indicated that both factors of seasonality ($X^2_1 = 543$, $P = 0.001$) and stratum ($X^2_1 = 478$, $P < 0.001$) significantly explained variation in the availability of food resources for frugivorous bats. We recorded more fruits during the dry season compared to the rainy season, and a greater number of fruits in the canopy than the understory stratum. There was also a significant interaction between seasonality and stratum ($X^2_1 = 1573$, $P < 0.001$), where fruit abundance in the canopy stratum increased greatly during the dry season, while in the understory more fruits were recorded during the rainy season with a slight decline during the dry season (Fig. 2a).

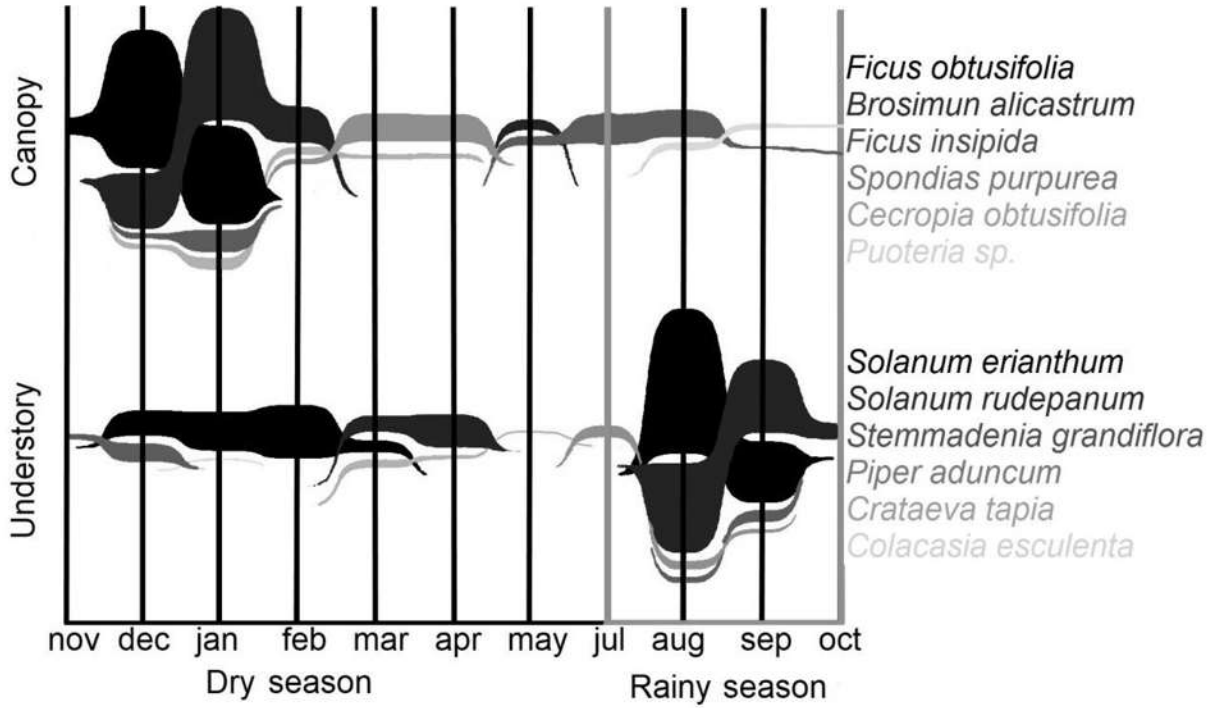


Fig 1. Alluvial plots showing the per stratum monthly fruit availability based on the number of fruits per month per species. Only those species with the largest contribution to the availability of food resources throughout the year in the canopy are shown; all understory species are included.

Bat captures

We recorded a sampling effort of 2640 net-hours, during which time we captured 708 bat individuals. Of these, 382 were frugivorous bats belonging to seven species. *Artibeus jamaicensis* was the most abundant species, while *Carollia subrufa* was captured only once. Of the seven frugivorous bat species captured, *Artibeus lituratus*, *A. jamaicensis* and *Dermanura phaeotis* were considered as canopy-foraging bat species, while *C. subrufa*, *Sturnira parvidens*, *Sturnira hondurensis* and *Centurio senex* were classified as understory-foraging species (Bonaccorso 1979). The three canopy-foraging bat species presented constant abundance values through the year. However, understory-foraging bat species showed a mixed pattern where *Sturnira hondurensis* recorded constant abundance values through the year but with a lower number of captures than was the case for the canopy-foraging bats, while *Sturnira parvidens* was captured from February to July and *Centurio senex* in February, April and May, both species in low numbers.

The GLM analysis indicated that although we captured more bats during the dry season, seasonality did not significantly explain variation in the number of frugivorous bats captured ($X^2_1 = 0.70$, $p = 0.40$). On the other hand, stratum significantly explained variation in captures of frugivorous bats ($X^2_1 = 63.4$, $P < 0.001$), with more frugivorous bats captured from the canopy than the understory (Fig. 2b). Finally, although there was an increase in the number of canopy bats captured during the dry season, the number of understory bats captured was similar between seasons (Fig. 2b), the GLM analysis found no significant interaction between stratum and seasonality ($X^2_1 = 3.41$, $P = 0.06$).

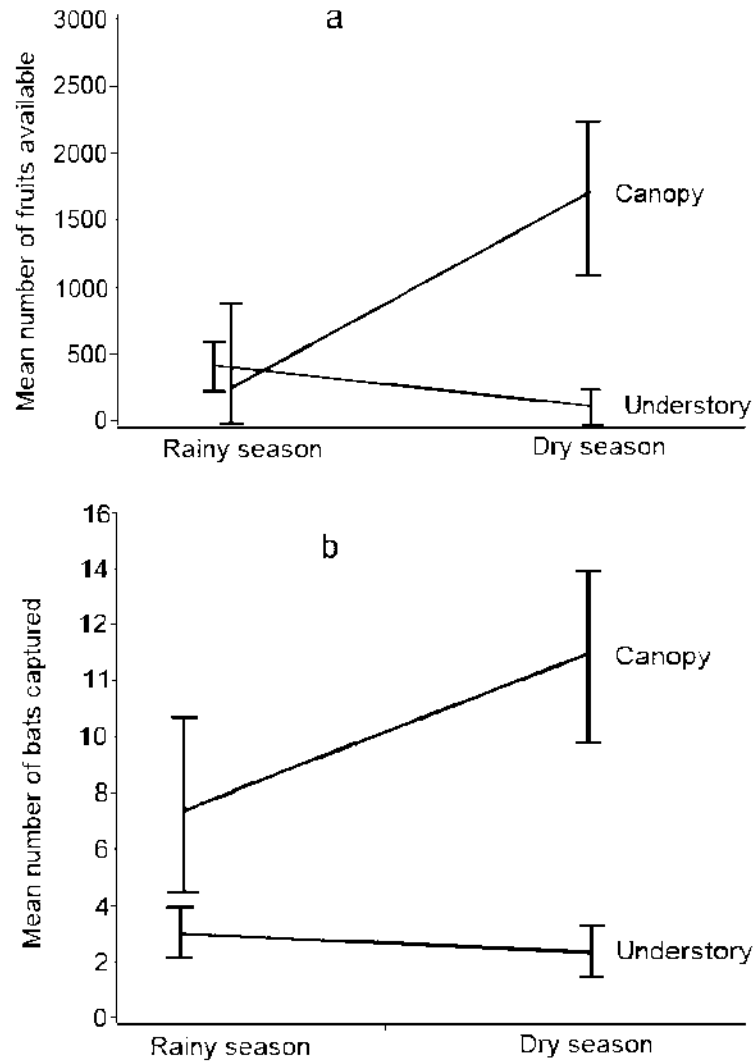


Fig 2. Interaction plots of season and stratum for a) food resource availability as indicated by mean number of fruits per month ($X^2_1 = 1572.65$, $p < 0.001$), and b) mean number of frugivorous bats captured per month ($X^2_1 = 3.41$, $p = 0.06$). Error bars indicate standard error.

Diet structure

We obtained 132 fecal samples from captured bats. These samples were composed of 51% seeds, 21% pulp and 28% fiber. The species *C. subrufa* was excluded from further diet analysis, and *C. senex* was only included in the overlap analysis due to the small number of captures of these bat species. We identified the seeds of six plant species in fecal samples: *C. obtusifolia*, *F. insipida*, *F. obtusifolia*, *P. aduncum*, *Solanum eriathum* and *S. rudepannum*. Although the diet overlap for both strata was higher in the rainy season (Fig. 3; Table 1a), no overlap was observed between the canopy and understory bat species in the dry season (Table 1b). Canopy bat species such as *A. lituratus* and *D. phaeotis* overlapped with the understory bat species of *S. hondurensis*, but only during the rainy season (Fig. 3; Table 1a). Furthermore, the canopy bat species of *Artibeus* spp. and *D. phaeotis* recorded a large niche overlap with each other. While understory bat species of *S. parvidens*, *S. hondurensis* and *C. senex* also overlapped with each other, the overlap was low with species from different strata or modules. (Fig. 3; Table 1b). The niche breadth analysis indicated that canopy bat species may expand or contract their dietary niche depending on the season (Table 2). For understory bat species, dietary niche in both the dry and rainy season could only be determined for *S. hondurensis*, which demonstrated a similar dietary niche between seasons (Table 2).

Table 1a. Hurlbert's niche overlap index for diet of frugivorous bat species determined from fecal samples during the rainy season. Bat species *S. parvidens* and *C. senex* were not collected during this season.

Bat species	Canopy frugivorous			Understory frugivorous
	<i>A. lituratus</i>	<i>A. jamaicensis</i>	<i>D. phaeotis</i>	<i>S. hondurensis</i>
<i>A. lituratus</i>	-	1.825	5.786	7.714
<i>A. jamaicensis</i>		-	0	0
<i>D. phaeotis</i>			-	7.714
<i>S. hondurensis</i>				-

Table 1b. Hurlbert's niche overlap index for diet of frugivorous bat species determined from fecal samples during the dry season.

Bat species	Canopy frugivorous			Understory frugivorous		
	<i>A. lituratus</i>	<i>A. jamaicensis</i>	<i>D. phaeotis</i>	<i>S. parvidens</i>	<i>S. hondurensis</i>	<i>C. senex</i>
<i>A. lituratus</i>	-	0.944	1.392	0	0	0
<i>A. jamaicensis</i>		-	2.474	0	0	0
<i>D. phaeotis</i>			-	0	0	0
<i>S. parvidens</i>				-	6.074	3.788
<i>S. hondurensis</i>					-	1.263
<i>C. senex</i>						-

Table 2. Hurlbert's niche breadth index for frugivorous bat species in the dry and rainy season, as determined from fecal samples. ND indicates no data available. ID indicates insufficient capture data for analysis.

	<u>Rainy season</u>	Confidence limits	<u>Dry season</u>	Confidence limits
<u>Canopy</u>				
<i>A. lituratus</i>	0.387	0.200-0.574	0.600	0.367-0.833
<i>A. jamaicensis</i>	0	0	0.703	0.504-0.902
<i>D. phaeotis</i>	0.211	0.094-0.327	0.691	0.455-0.927
<u>Understory</u>				
<i>S. parvidens</i>	ND	ND	0.888	0.704-1.073
<i>S. hondurensis</i>	0.365	0.185-0.545	0.236	0.087-0.385
<i>C. senex</i>	ND	ND	ID	ID

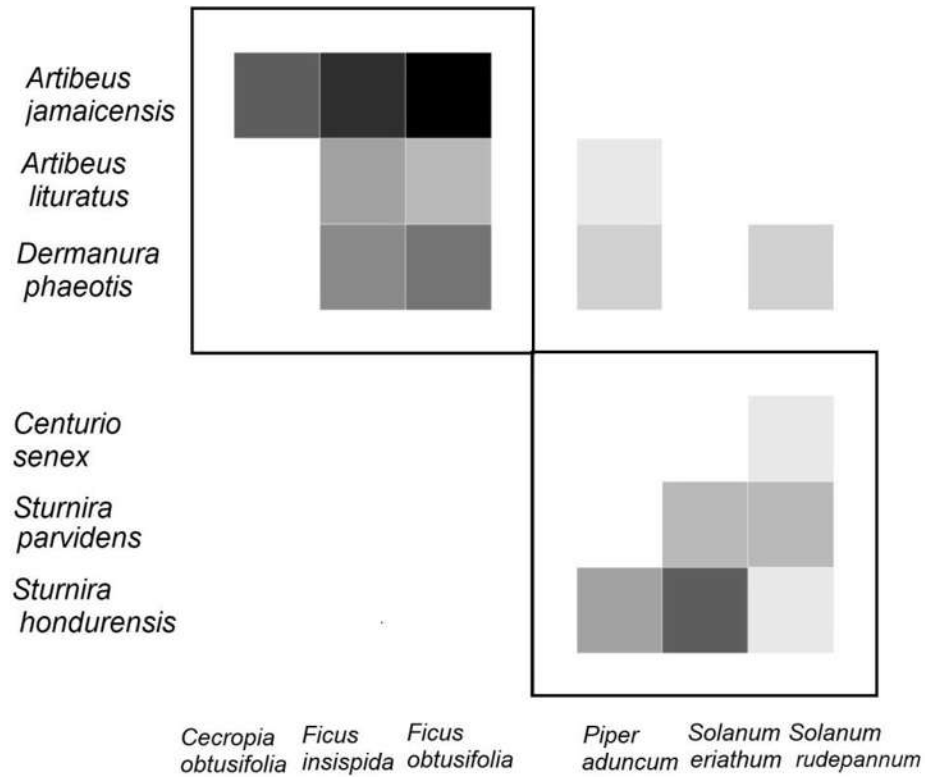


Fig 3. Modularity plot using the QuanBiMo algorithm with the number of fecal simples of frugivorous bats. Larger squares indicate bat and plant modules, smaller squares indicate interaction inside modules. Darker shading indicates higher proportion of interactions.

The observed values indicated a moderate modularity in our network ($Q= 0.359$). Two modules were identified, with the canopy bat species *Artibeus* spp., and *D. phaeotis* in one module, along with the plant species *C. obtusifolia*, *F. insipida* and *F. obtusifolia*. The second module included understory bat species of *C. senex*, *S. parvidens* and *S. hondurensis* along with the plant species *P. aduncum*, *S. eriathum* and *S. rudepannum*. This indicates the occurrence of vertical segregation. This indicated modularity by stratum; one module for canopy frugivorous bat species and another for understory frugivorous bat species. Our modularity analysis indicated that the canopy bat species *D. phaeotis* and *A. lituratus* played the functional role of connectors in our network since they were recorded feeding on the connector understory plant species *P. aduncum* (Fig. 4). The observed modularity module was found to be significantly larger than that expected from a random process ($Z = 6.09$, $p < 0.05$).

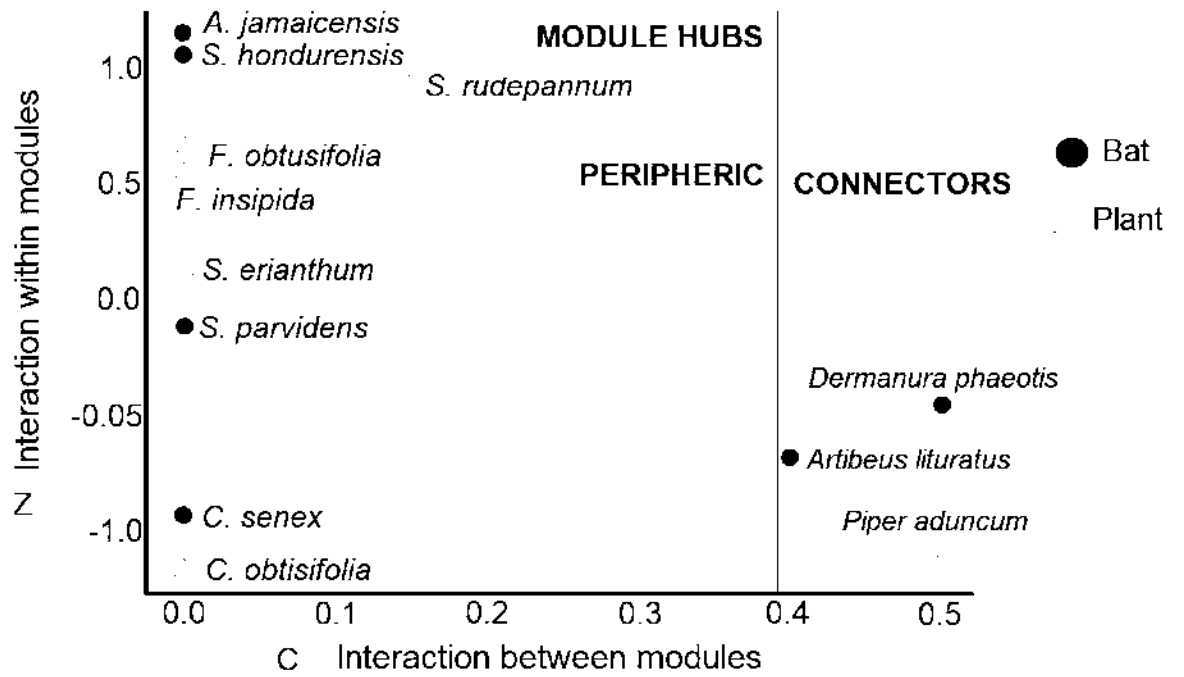


Fig 4. Plot indicating the functional role of both bat species and plants in a modular network

DISCUSSION

We found that both canopy and understory bat species form separate modules with their corresponding stratal core plant species. Bat species from the understory were found to feed exclusively from understory plant species, while canopy bats fed mostly from canopy plants, but occasionally consumed understory plant species, pointing to a vertical stratification. This stratification is supported by the higher niche overlap of canopy bat species of *A. lituratus*, *A. Jamaicensis* and *D. phaeotis* among themselves and the higher overlap of understory bat species of *S. hondurensis*, *S. parvidens* and *C. senex* among themselves. This per stratum segregation suggested by the two modules and the dietary overlap has been suggested previously in the tropical rain forest (Bonaccorso 1979; Fleming 1982; Marinho-Filho 1991; Molinari 1993; Delaval et al. 2005; Marques et al. 2012; Suárez and Montenegro 2015), that would enable species segregation and coexistence mediated through constraints imposed by both bat and plant species intrinsic properties. The tropical rain forest is characterized by a more marked differentiation between the canopy and the understory (Bonaccorso 1979; Loayza et al. 2006) than is the case in the tropical dry forest, and we therefore did not expect the vertical stratification found in our tropical dry study site. This could suggest that the lack of well-defined strata and reduced inter-stratum separation in this forest type are not factors that influence frugivorous bat species segregation.

Our analysis of fecal samples also found that the canopy bat species *A. lituratus* and *D. phaeotis* included understory plant species in their diet during the rainy season when few resources are available in the canopy. In addition, this is the time of the year when fruiting in *P. aduncum* and *S. rudepanum* occurs and then crop size increases compared to the dry season. One plausible explanation is that the consumption of these food items could potentially be the result of chance due to their availability when the canopy bats visit the understory to forage from those species that are available in greater number. However, it remains unclear why understory bat species do not take advantage of canopy plant species during the dry season when these have abundant fruit, although this may be due to intrinsic properties of the bat species themselves, such as digestive capacity (Herrera 1999; Saldaña-Vázquez and Schondube 2013) and bite strength (Santana and Dumont 2009), as well as the fruit hardness and food

nutritional quality (Wendeln and Runcle 2000; Castaman 2006). Taken together, this suggests that intrinsic bat and fruit properties influence the visits of canopy bat species to the understory, while understory bat species do not feed on canopy plant species.

We found not only that core food resources are available throughout the year in both strata, but also that there is a vertical-temporal fluctuation in the availability of fruiting resources. Both the temporal consistency of food resources and the plant species turnover have been observed in other tropical forests for frugivorous animals in general (Gautier-Hion and Michaloud 1989; David et al. 2012) and bats in particular (Bonaccorso 1979). Overall, this suggests that, food resources do not represent a limiting factor for the frugivorous bats in our study. However, the intrinsic properties of the plant and bat species of each stratum, such as the relationship between fruit nutritional quality and bat digestive capacity, or fruit hardness and size, would reduce the availability of these fruits to the bat species present in each stratum, thus reducing the true availability of resources per stratum. It is therefore important to perform evaluations of intrinsic properties of food resources in each stratum in order to identify the extent to which these resources are actually available to those bat species preferentially foraging in each stratum.

We also observed an interaction between food availability per stratum and season, with a larger number of fruits in the canopy stratum during the dry season, while fruit abundance in the understory is greater during the rainy season and declines in the dry season. This interaction resulted from fluctuation in fruit crop size in the canopy plant species, since the understory plant species did not vary in fruit crop size from one season to another. This pattern could be explained by the occurrence of two non-exclusive fruiting patterns. First, fluctuations in the canopy stratum are to be expected since most species in this stratum are characterized by asynchronous mast fruiting, which can increase the availability of food resources within a short period of time. For instance, several species of the canopy asynchronous mast fruiting *Ficus* genus produce an average of 500 – 40,000 fruits per individual (Korine et al. 2000). This fruiting strategy provides a large, but unpredictable, availability of fruiting resources in the canopy stratum (Fleming et al. 1977; David et al. 2012). A second

explanation is that understory species show a contrasting pattern, where they have the tendency to fruit synchronously and with a small fruit crop size per individual. One example of this fruiting strategy is provided by *Piper arboreum*, in which many individuals can produce 40 fruits at a time on average per individual (Bizerril and Raw 1997). This strategy may provide resources in a predictable way, but with a smaller crop size.

We also found that captures of frugivorous bats corresponded with this fruiting pattern between strata, although season was not a significant factor influencing bat captures. This contrasts with the significant influence of seasonal on food resource abundance, and may be due to the fact that fruiting patterns are strongly influenced by rainfall (Haugaasen and Peres 2005, David et al. 2012). On the other hand, bats present a broad range of strategies that can give them the plasticity to cope with fluctuations in food resources, and to avoid having to rely uniquely on the availability of local food resources. For instance, bats move to other areas where food resources are more available (Cornejo-Latorre et al. 2011). Two examples of this in our study are provided by the species *C. senex*, *S. parvidens* and *C. subrufa*, which are present in the study site from February to July but then absent for the rest of the year. This suggests that these species could be performing local movements in order to track fruiting plant species located outside our study site. Tracking food resources is a widespread strategy adopted in birds (Johnson and Sherry 2001) and could also be employed by the frugivorous bats.

Our study supports the Vertical Stratification Hypothesis for frugivorous bats. We found that specific stratum frugivorous bat species were associated with plant species of that stratum. To the best of our knowledge, this is the first study to evaluate and offer supporting evidence for this hypothesis in a tropical dry forest. Our study also provides evidence for vertical stratification in tropical dry forest where the inter-stratum distance is reduced, compared to the marked stratification in tropical rain forests.

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Ethical statement

We followed all national and institutional recommendations for the handling of animals in this study.

Conflict of interest

The authors declare no conflict of interest

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DISCUSIÓN GENERAL

Se encontró que las especies de murciélagos *S. hondurensis*, *S. parvidens* y *Centurio senex* consumen especies de plantas a nivel de sotobosque, mientras que *A. lituratus*, *A. jamaicensis* y *D. phaeotis* consumen frutos a nivel de dosel. Esto indica una estratificación vertical de murciélagos frugívoros apoyada en el índice de traslape de nichos alimentarios y el análisis de modularidad. Esta estratificación vertical se ha sugerido previamente en bosques tropicales lluviosos, (Bonaccorso 1979, Fleming 1982, Marinho-Filho 1991, Molinari 1993, Marques *et al.* 2012, Suárez *et al.* 2015) la cual podría estar mediada por las propiedades intrínsecas (dureza y contenido energético del fruto, fuerza de mordida y capacidad digestiva) de las especies de murciélagos y plantas (Herrera 1999, Wendeln *et al.* 2000, Castaman 2006, Santana *et al.* 2009, Saldaña-Vázquez *et al.* 2013).

Sin embargo, aunque se identificaron dos módulos la estratificación vertical no fue completa, ya que las especies de murciélagos de dosel *A. lituratus* y *D. phaeotis* conectaron los módulos al consumir plantas del sotobosque en la temporada lluviosa. Esto puede ser explicado debido a que en esta temporada la disponibilidad de alimento en el dosel disminuye, y a nivel de sotobosque las especies de plantas como *S. rudepannum* y *P. aduncum* incrementan su fructificación.

Se observó un recambio en la fructificación de las diferentes especies de plantas a lo largo del periodo de muestreo. Este recambio, provoca a una disponibilidad continua de frutos durante todo el año para murciélagos frugívoros. Este patrón en la fenología de fructificación en especies de plantas tropicales ya se ha registrado anteriormente. Por ejemplo, Gautier-Hion *et al.* (1989) y David *et al.* (2012) identifican un recambio temporal en la fructificación de diferentes especies de higos. Sin embargo las relaciones entre las propiedades intrínsecas de murciélago y frutos pueden estar reduciendo la disponibilidad real de alimento en el bosque tropical seco.

Se determinó una interacción significativa entre la estacionalidad y el número de frutos disponibles por estrato. Con un mayor número de frutos en el estrato del dosel durante la estación seca, mientras que la abundancia de frutos en el sotobosque es mayor durante la temporada de lluvias. Esta interacción resultó de una fructificación

masiva en especies de dosel durante la temporada seca, pero esta fructificación no se presentó en las especies de sotobosque. Este patrón puede explicarse por las diferencias en la fenología de fructificación entre especies de dosel y sotobosque. Primero, se esperan fluctuaciones en el dosel, ya que la mayoría de las especies se caracterizan por fructificar de manera asíncrona aumentando masivamente el tamaño de fructificación en un periodo corto de tiempo. Por ejemplo, varias especies de árboles del dosel del género *Ficus* sp. producen un promedio de 500 - 40,000 frutas por individuo (Korine *et al.* 2000). Esta manera de fructificar de las plantas de dosel proporciona una gran disponibilidad de frutos, pero impredecible (Fleming *et al.* 1977; David *et al.* 2012). En cuanto a las especies del sotobosque, muestran un patrón contrastante, ya que tienden a fructificar de forma sincrónica manteniendo un tamaño pequeño de fructificación en un periodo considerable de tiempo. Un ejemplo de esta fructificación es *Piper arboreum*, en el que muchos individuos sincronizados producen 40 frutas en promedio (Bizerril y Raw 1997). Esta estrategia puede proporcionar recursos de manera predecible, pero con un tamaño de fructificación más pequeño.

Los resultados de este estudio apoyan la hipótesis de estratificación vertical en murciélago frugívoros en bosques tropicales secos. Posiblemente esta estratificación este permitiendo la segregación y coexistencia de especies mediada por la relación entre propiedades intrínsecas de las especies de murciélagos y plantas.

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