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## Original Investigation

## Bat frugivory in two subtropical rain forests of Northern Argentina: Testing hypotheses of fruit selection in the Neotropics

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## ABSTRACT

Phyllostomid bats are prominent components of mammalian assemblages in the Neotropics. With many species specialized in frugivory, phyllostomids represent major partners of fleshy-fruited plants in the mutualism of seed dispersal. Here we present dietary data from two subtropical rainforests of Argentina, where fruit diversity is low and thus offer unique opportunities to test hypotheses of diet selection originally proposed for species-rich tropical assemblages. Particularly, we tested whether frugivorous phyllostomids exhibit pronounced dietary specialization in core plant taxa where fruit offer is greatly reduced as compared to tropical rainforests. We analyzed dietary overlap and niche breadth of subtropical frugivorous bats on the basis of >1000 dietary records plus >500 samples from a previous study in the region. We show that in the subtropics, frugivores from different genera remain faithful to their respective core plant taxa with few exceptions, rather than shifting toward alternative fruit resources available in the study sites. This supports predictions of specialization, which is confirmed to have a deep historical origin. The response of phyllostomid ensembles to restricted fruit diversity is at the level of species composition: absence of species for which preferred fruits do not occur in the sites. Taken together, these data lend strong support to hypotheses that explain coexistence of frugivorous phyllostomids on the basis of dietary specialization on core plant taxa with chiropterophilous fruits.

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## Introduction

Neotropical rainforest bat assemblages are dominated by leaf-nosed bats (Phyllostomidae). These bats make up to 90% of mist-net captures at the majority of study sites reported, and account for at least 50% of total bat species richness at sampled communities (Bonaccorso, 1979; Kalko et al., 1996a; Simmons and Voss, 1998; Giannini, 1999; Bernard, 2001; Kalko and Handley, 2001; Aguirre, 2002; Sampaio et al., 2003; Klingbeil and Willig, 2009). Phyllostomids display the greatest diversity of feeding habits among mammalian families (Freeman, 2000), playing a crucial functional role in community structure as predators of arthropods and small vertebrates (Humphrey et al., 1983; Giannini and Kalko, 2005; Kalko et al., 2008), and as dispersers of pollen and seeds (e.g., van

der Pijl, 1972; Fleming and Heithaus, 1981; Fleming, 1988; Lobova et al., 2009).

A number of workers have investigated trophic structure of phyllostomid ensembles and the mechanisms of coexistence among syntopic species in Neotropical rainforests (Fleming, 1986; Palmeirim et al., 1989; Fleming, 1991; Marinho-Filho, 1991; Gorchoy et al., 1995; Hernández-Conrique et al., 1997; Giannini, 1999; Giannini and Kalko, 2004, 2005; Fleming, 2005; Lopez and Vaughan, 2007). Most of these studies focused on frugivores, particularly members of the dominant genera *Artibeus*, *Carollia* and *Sturnira*, and their mutualistic interactions with fleshy-fruited plants. Many species in these genera are syntopic; coexistence of these species has been explained primarily in terms of dietary specialization in different core-plant taxa with extended phenology, with *Artibeus* feeding primarily on fruits of Moraceae *sensu lato* (*Ficus* and *Cecropia*), *Carollia* on *Piper* (Piperaceae) and *Sturnira* on *Solanum* (Solanaceae) and *Piper* (Fleming, 1986). Bat species in these genera have also shown consumption of other bat-dispersed fruits as they become seasonally available, therefore leaving room for some degree of behavioral flexibility in diet choice (Fleming, 1986). Results from different study sites (e.g., Fleming, 1988, 1991; Marinho-Filho, 1991; Hernández-Conrique et al., 1997; Kalko et al.,

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1996b; Giannini, 1999) have generally supported these hypotheses, emphasizing co-adaptations between attributes of bats in association with fruit traits that compose the seed-dispersal syndrome of chiropterochory (e.g., Kalko and Condon, 1998). Fruits corresponding with this syndrome are characterized by drab colors (e.g., green, yellow), musty scent, medium-to-large size with possession of relatively large seeds, extended phenology, and attachment to the stem with exposure outside the foliage (van der Pijl, 1972; Lobova et al., 2009). Although the syndrome hypothesis has been called into question (e.g., Herrera, 1987; Fischer and Chapman, 1993; Jordano, 1995), fruit traits generally match sensory, morphofunctional, and behavioral traits of bats (e.g., Lomáscolo et al., 2008; Lomáscolo and Schaefer, 2010).

Giannini and Kalko (2004) explored the predictive power of these hypotheses using data from a speciose community of phyllostomids inhabiting Barro Colorado Island, Panama. As a result, Fleming's (1986) hypotheses of fruit selection were largely confirmed and extended from *Artibeus*, *Carollia* and *Sturnira* to the more inclusive clades containing these bat genera (Stenodermatini, Carollinae, and Sturnirini, respectively), thereby demonstrating a strong historical component to the contemporary trophic structure of syntopic phyllostomids in the tropics (Giannini and Kalko, 2004).

Here we investigated diet and niche relationships of South American subtropical populations of frugivorous phyllostomid species on the basis of a large dataset of >1000 new dietary records from the field plus >500 samples from a previous study in the region (Giannini, 1999). With this information basis, we set out to dissect the quantitative trophic structure of these subtropical bat ensembles. The subtropics are particularly interesting because they provide the opportunity to examine dietary specialization of tropical frugivorous bats (Fleming, 1986; Giannini and Kalko, 2004) in a context of comparatively reduced fruiting plant diversity. The only subtropical wet forests of South America are the lowland Paranean forest in SE South America in the Parana River Basin, and the montane Yungas forest of the Andes (Hueck, 1978; Burkart et al., 1999). These forests harbor between one-sixth and one-third of reported tropical fruit-plant richness per site at the community level (cf. Giannini, 1999; Giannini and Kalko, 2004). The diversity difference is even more marked regarding fruits that are key resources for these bats; for instance, 2–4 species of *Piper* are present in our study sites, and 0–2 species of *Ficus*, whereas richness in each of these genera is around 20 species in a landmark tropical

site, Barro Colorado Island (Panama; Croat, 1978). Still, phyllostomids are abundant in subtropical rainforests (e.g., Giannini, 1999). With significantly less plant species to choose from, these bats from clades of tropical affiliation may depart from predictions based on diet selection in tropical sites, perhaps revealing important aspects of diet selection by phytophagous bats. The observed low-diversity of resources generates specific predictions about diet choice by frugivorous bats in the subtropics that we put to test with our data: 1. subtropical phyllostomids remain faithful to the high, historically deep specialization in chiropterochorous core plant taxa observed in the tropics (e.g., *Sturnira* specialized in *Piper* + *Solanum*; Fleming, 1986; Giannini and Kalko, 2004); or alternatively, 2. coping with reduced fruit richness, subtropical phyllostomids become generalists able to exploit most fruit (or other) resources available.

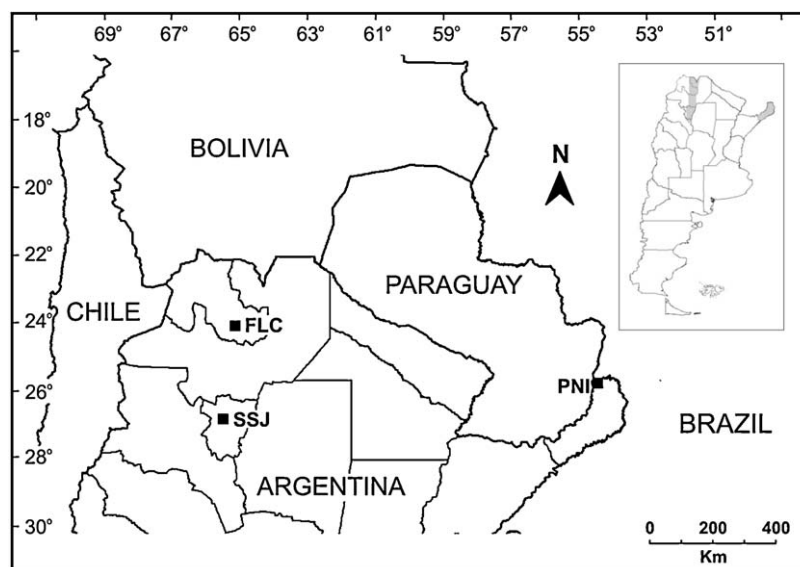
## Material and methods

### Study sites

Our study sites, located in NW Argentina (Fig. 1), are 1. Parque Nacional Iguazú (hereafter "Iguazú"), Misiones Province, NE Argentina (hereafter "NEA", 25° 40'S, 54° 27'W, 200 m.a.s.l.) in the Paranean rainforest; and 2. Finca Las Capillas (hereafter "Las Capillas"), Jujuy Province, NW Argentina (hereafter "NWA", 24° 02'S, 65° 07'W, 1000 m.a.s.l.), in the Yungas rainforest of the Eastern slopes of the Andes. For comparison in niche overlap analyses (see below), we also included previously published dietary data from another subtropical site in the NWA, Sierra de San Javier, Tucumán Province, Argentina (26° 47'S, 65° 21'W, 600–1850 m.a.s.l.), hereafter "San Javier" (see below; Fig. 1).

### Iguazú

This National Park comprises 67,000 ha of subtropical lowland rainforest and is next to the Provincial Park Urugua-í and the Brazilian Iguazú National Park. Floristic associations are strongly dependent on soil composition (Surr et al., 2007). Climate is hot and wet, with mean maximum temperature at 22 °C, and only mildly seasonal as the annual rainfall (2000 mm) is distributed rather uniformly throughout the year (Cabrera, 1976; Cabrera and Willink, 1980; Brown et al., 2001). The study site was located in lauraceous and rutaceous forest formations (Cabrera and Willink, 1980), with dense understory and abundant vascular epiphytes and vines.



**Fig. 1.** Map of Northern Argentina showing the location of sampling sites of this study. Subtropical rainforests in Argentina are shaded in the inset map. Abbreviations: FLC, Finca Las Capillas; SSJ, Sierras de San Javier; PNI, Parque Nacional Iguazú.

### Las Capillas

This study site is located in well-preserved montane rainforest (Cabrera, 1976; Brown, 1995). Climate is bi-seasonal, with a wet and hot austral “summer” (wet season, November–April) and a dry and mild austral “winter” (dry season, May–October). Annual rainfall (2000 mm) is concentrated in the wet season (Cabrera, 1976); mean annual temperature is 19 °C (Minetti et al., 2005). The canopy presents a combination of lauraceous and mirtaceous trees, with the understory dominated by Piperaceae and Solanaceae. Vascular epiphytes are extremely abundant, as well as vines and climbers.

### San Javier

This is a protected site belonging to the Universidad Nacional de Tucumán (14,000 ha) and is located in a relatively impoverished rainforest of the Southern Yungas (further details in Giannini, 1999). In this site, c. 900 bats from three species of *Sturnira* (the only frugivorous bats) were captured in a monthly sampling schedule over two years in three sites along an altitudinal transect. Giannini (1999) reported a strong selection of Piperaceae and Solanaceae (97–99% of 552 dietary records) for the three species of *Sturnira* captured.

### Bat netting and dietary samples

We visited Iguazú twice in dry seasons and twice in wet seasons from October 2006 to February 2008, and Las Capillas twice in dry seasons and three times in rainy seasons from January 2006 to April 2007. At each study site we sampled bats by setting ten mist nets (12, 9 and 6 m by 2.5 m) 40–50 m apart from each other, half at ground level and half at the subcanopy level in suitable locations (e.g., flight passageways). We operated all mist nets for approximately 6 h from sunset. Nets were checked every 30 min. In each visit we sampled bats during five consecutive nights, changing net location frequently. Sampling coincided with periods of dark moon to avoid the effect of lunar phobia (Lang et al., 2006). Each bat was removed from nets and placed in cloth bags for about 1 h. We recorded forearm length to the nearest 0.1 mm using a digital caliper, body mass to the nearest 0.5 g using a spring scale, sex and age (juvenile and adult) of each specimen. Bats were released near the capture site. We preserved dietary samples as individually labeled dry pellets.

We identified vegetable dietary items to the level of species whenever possible, primarily using a local reference collection of seeds. Each plant species present in a fecal sample was considered a dietary record (i.e., a separate event of feeding; Gorchoff et al., 1995; Giannini, 1999; Aguiar and Marinho-Filho, 2007). This technique may be biased toward small seeds given that ingestion of larger seeds may be avoided by bats, thus under-representing some plant species (e.g., Mello et al., 2008). However, color, odor and structures of botanical relevance (e.g., fruit epidermis, calices) found in the bat pellets made possible the identification of ingested fruits from most medium-to-large-seeded species, including *Celtis iguanaeus* (Celtidaceae), *Chrysophyllum gonocarpum* (Sapotaceae) and *Psidium guajava* (Myrtaceae), thereby reducing considerably this source of bias in the estimation of dietary composition.

### Niche analysis

We calculated Levins normalized index *BA* as a descriptive statistic of niche breadth in bat species in each forest. In this application, *BA* is based on proportions in the diet (Krebs, 1999):

$$BA = \frac{B - 1}{n - 1}$$

where *n* is the number of dietary items available, and  $B = 1 / \sum p_i^2$  where  $p_i$  is the proportion of resource *i* in the diet. *BA* ranges

between 0 (only one resource used) and 1 (all available resources used evenly).

We calculated feeding niche overlap in each study site using two formulae. First, Pianka's index *O* (Pianka, 1973; Krebs, 1999) approaches 0 for species that share no resources and approaches 1 for species that have identical patterns of resource utilization and is calculate as:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^n P_{2i} \times P_{1i}}{(\sum_{i=1}^n P_{2i}^2 \times P_{1i}^2)^{0.5}}$$

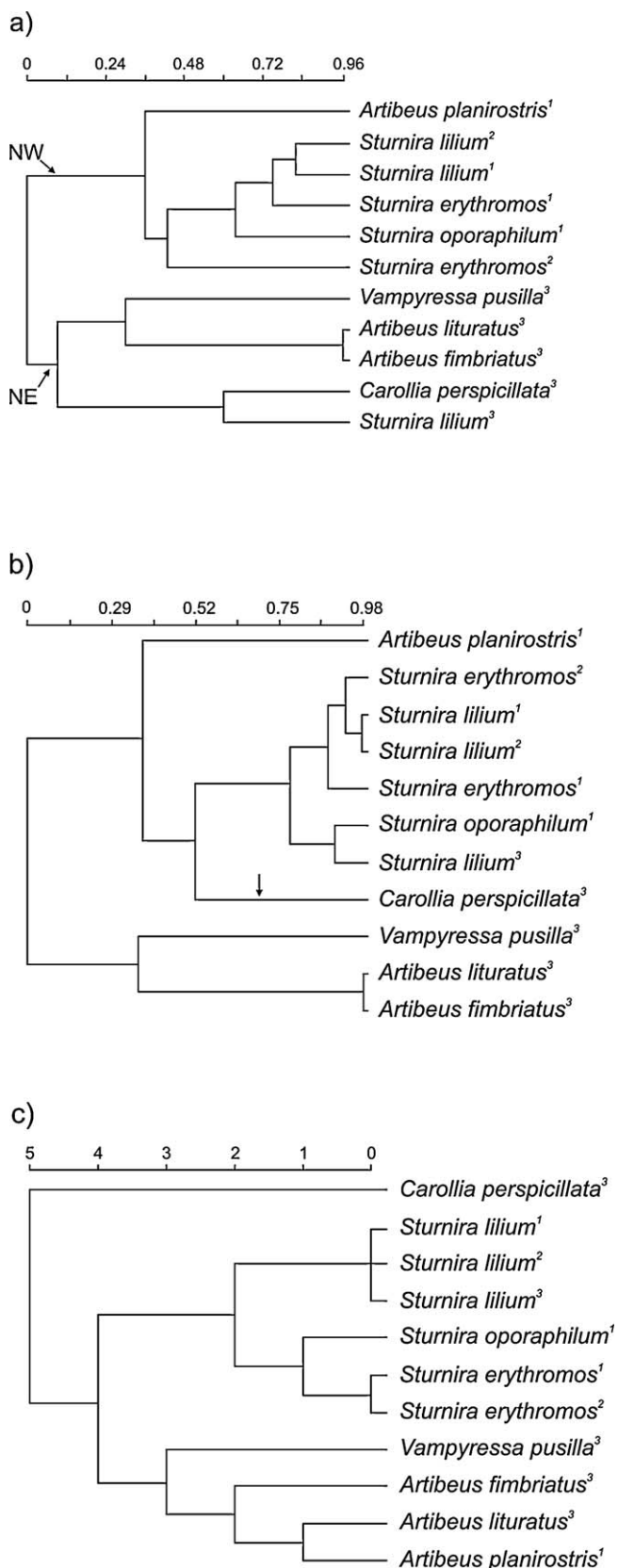
where  $P_{1i}$  and  $P_{2i}$  are the proportion of resource *i* from the total of *n* resource items used by species 1 and 2, respectively. Statistical significance of overlap patterns was calculated by generating 1000 randomized samples of observed resource use by species keeping their niche breadth (see Lawlor, 1980; Gotelli and Entsminger, 2006) using EcoSim ver. 7.72 software (Gotelli and Entsminger, 2006). Observed overlap was then compared to the distribution of simulated niche overlap values, with the null expectation (for lack of overlap) that the observed value be smaller than the majority (e.g., 95%) of overlap values generated by chance. We used algorithm R3 in Ecosim, which preserves niche breadth and degree of specialization during randomization for each of the species compared.

Second, we used Horn's modifications of Morisita's index of similarity *C* as an alternative measure of resource overlap (Horn, 1966; Gorchoff et al., 1995) with the aim of applying *C* to cluster analysis at two plant taxonomic levels. *C* ranges between 0 (no overlap) and 1 (complete overlap) and is calculated as:

$$C = \frac{2 \sum x_{ij} x_{ik}}{(\sum x_{ij}^2 / N_j^2 + \sum x_{ik}^2 / N_k^2) N_j N_k}$$

where  $x_{ij}$  is the proportion of resource *i* in the total resources used by species *j*;  $x_{ik}$  is the proportion of resource *i* in the total used by species *k*; and  $N_j$  and  $N_k$  is sample size of each species. *C* was applied at the level of 1. plant species and 2. families, and used as input matrix in cluster analysis in order to depict the possibly hierarchical structure of trophic relationships among bats. To construct the dendrogram, we used *C* (niche overlap) as a similarity measure and applied the UPGMA method to construct the dendrogram (see Gorchoff et al., 1995; Giannini and Kalko, 2004). We tested the fit of the dendrogram to matrix *C* (degree of distortion) using a Mantel test with 999 unrestricted permutations of the *Z* statistic (an analogue of the correlation coefficient *r*; see Manly, 1997). We also considered overall topological congruence (i.e., tree similarity) between the dietary dendrograms and phylogenetic structure. The topology used (Fig. 2c) is a composite of trees from Baker et al. (2000) and Wetterer et al. (2000; for backbone structure), Villalobos and Valerio (2002; for resolution within *Sturnira*), and Lim et al. (2004; for resolution within *Artibeus*). We used a randomized test of the correlation coefficient *r* (equivalent to the Mantel test; Mantel, 1967; Manly, 1997) to compare dietary structure versus phylogenetic structure estimated as the patristic distance *PA* between taxa, as applied by Giannini and Kalko (2004) to a similar problem. The patristic distances were calculated on the ultrametric topology of Fig. 2c. The observed correlation between interspecific, pair-wise *C* and *PA* (expected negative because *C* is a similarity value whereas *PA* is a distance measure) was tested against the null distribution of 999 *r*-values resulting from random rearrangement and re-pairing of the data. Two such tests were performed, one on each of the *C*-matrices (species and families). This statistical analysis was run in R (R Development Core Team, 2004). The script is available on request.





**Fig. 2.** Diagrams grouping bat frugivore species on the basis of consumption of fruiting plant taxa at the species (a) and genus (b) level using Horn's modification of Morisita's index C (see text), and (c) phylogenetic relationships (see text for source trees). Superscripts indicate samples from Las Capillas (1), San Javier (2) and Iguazú (3). In topology b, the arrow indicates the rooting point that recovers the majority of phylogenetic relationships among these phyllostomids as in topology c (see also text). Level of distortion in the two cluster analyses (a and b) was low (matrix correlation  $0.94 < r < 0.95$ ;  $P \ll 0.01$ ).

### Fruit ecomorphology

We recorded seed, fruit and plant characteristics from plant species found in the diet of bats in all three study sites. This is key for testing hypotheses of dietary specialization because these hypotheses are formulated on the basis of selection of chiropterochorous fruits (e.g., *Piper*; Fleming, 1986; Giannini and Kalko, 2004). We use 'fruit' as a general term for fleshy diaspore, i.e., the units of dispersal irrespective of their anatomy (van der Pijl, 1972; Howe and Smallwood, 1982). Such diaspores include both simple (e.g., berries and drupes) and compound fruits (e.g., the spadix of *Piper* and syconium of *Ficus*), as well as additional structures (e.g., the fleshy perianth surrounding achenes of *Urera* [Urticaceae]). We recorded size of individual seeds (defined as mass in mg, or seed + achene in the case of compound fruits), fruit color, shape (measured as polar-to-equatorial diameter ratio), and size (mass in g), number of seeds per fruit and fresh-weight pulp-to-seed ratio, and habitat of occurrence (primary versus secondary forest and riparian habitats). Linear fruit attributes were measured with a digital caliper to the nearest 0.01 mm. Mass was measured using laboratory scales to the nearest 0.001 g in fruit mass and to the nearest 0.0001 g in the case of individual-seed mass.

### Results

#### Captures

In Iguazú we captured 1861 bats of ten species; 99.6% of these individual bats were frugivorous phyllostomids, with the remainder of the sample comprising animalivorous, insectivorous and sanguivorous bats. *Sturnira lilium* was the dominant species (1258 individuals), followed by *Artibeus lituratus* (418), *A. fimbriatus* (141), *Carollia perspicillata* (17), *Pygoderma bilabiatum* (15), *Vampyressa pusilla* (4), *Vampyressa* sp. (1).

In Las Capillas we captured 671 bats of twenty species. Again, frugivorous phyllostomids were dominant (88.2% of captures). Bats of the genus *Sturnira* comprised 67.2% of the sample (*S. lilium*: 271 individuals, *S. erythromos*: 170, and *S. oporaphilum*: 10). The other phytophagous phyllostomids included *Artibeus planirostris* (140 individuals), *Anoura caudifer* (2), and *Pygoderma bilabiatum* (1). Seasonal and other trends in captures and diet, as well as specific differences between localities, are treated in detail elsewhere.

#### Dietary data

We obtained 1089 dietary records in total, 771 from Iguazú and 318 from Las Capillas (Table 1). Bats in the genus *Sturnira* contributed the largest share of the total data comprising 77.7% of samples, followed by *Artibeus* (20.2%), and *Carollia* (2.1%). Fruits of Piperaceae (32.9%) and Solanaceae (23.4%) were the most commonly represented in dietary records, followed by Moraceae (17.5%) and Cecropiaceae (15.4%).

In Iguazú, *S. lilium* used all the 17 species of fleshy fruit consumed by bats as a group; nevertheless, Solanaceae + Piperaceae comprised as much as 70.3% of total diet (Table 1). *Artibeus lituratus* and *A. fimbriatus* preferred fruits of Moraceae *sensu lato* (Cecropiaceae + Moraceae), which together comprised 96% and 90% of dietary records, respectively. The other Stenodermatini captured, *Vampyressa pusilla* yielded 4 samples, all containing seeds of Moraceae (*Ficus*). *Carollia perspicillata* specialized in *Piper* (94.7%). For each fruit bat only a few species of plants dominated the diets and these largely corresponded to proposed core plant taxa for each bat genus (Table 1).

In Las Capillas, *Sturnira* consumed fruits from 17 species in six families. Solanaceae and Piperaceae families made up to 68.7%

**Table 1**

Dietary records of bat species in the two subtropical rainforests studied (Iguazú in NE and Las Capillas in NW Argentina). Data given as percentage of dietary items recorded for each bat species (with *n* = sample size per bat species). As this table compares two forests with different vegetation, a dash indicates an inapplicable comparison (the plant species does not occur in the site) whereas the blank cell represents absence in the diet of a potentially available plant species. Botanical names follow Zuloaga and Morrone (1999) with synonyms used in Giannini (1999) provided in parenthesis.

Plant species	Iguazú					Las Capillas				
	<i>Artibeus fimbriatus</i> <i>n</i> = 43	<i>Artibeus lituratus</i> <i>n</i> = 124	<i>Vampyressa pusilla</i> <i>n</i> = 4	<i>Carollia perspicillata</i> <i>n</i> = 19	<i>Sturmira litium</i> <i>n</i> = 581	<i>Artibeus planirostris</i> <i>n</i> = 53	<i>Sturmira litium</i> <i>n</i> = 170	<i>Sturmira erythromos</i> <i>n</i> = 89	<i>Sturmira oporaphilum</i> <i>n</i> = 6	
<i>Ficus luschathiana</i>	25.6	14.5	75.0		7.6	–	–	–	–	
<i>Ficus citrifolia</i>	2.3	2.4	25.0		0.2	–	–	–	–	
<i>Ficus</i> sp.	4.7	6.5			1.2	–	–	–	–	
<i>Maclura tinctoria</i>	2.3	4.8			10.4	–	–	–	–	
<i>Cecropia pachystachya</i>	55.8	67.7			3.8	–	–	–	–	
<i>Piper aduncum</i>				36.8	21.4	–	–	–	–	
<i>Piper amalago</i>	4.7	2.4		10.5	10.2	–	–	–	–	
<i>Piper gaudiichaudianum</i>				5.3	3.8	–	–	–	–	
<i>Piper hispidum</i>				36.8	6.7	–	–	–	–	
<i>Piper</i> sp.	–	–	–	5.3	0.7	11.2	21.4	–	66.7	
<i>Solanum abutiloides</i>	–	–	–	–	–	3.8	4.5	–	16.7	
<i>Solanum confusum</i> (= <i>adelphum</i> )	–	–	–	–	–	–	2.3	–	–	
<i>Solanum tenuispinum</i> (= <i>chaetophorum</i> )	–	–	–	–	–	0.6	2.3	–	–	
<i>Solanum granulosum-leprosum</i>	2.3	1.6	–	5.3	27.1	–	–	–	–	
<i>Solanum aligerum</i> (= <i>grossum</i> )	–	–	–	–	–	–	1.1	–	–	
<i>Solanum riparium</i>	–	–	–	–	–	11.3	12.4	–	–	
<i>Solanum trichoneuron</i>	–	–	–	–	–	–	3.4	–	–	
<i>Solanum pseudocapsicum</i> (= <i>tucumanense</i> )	–	–	–	–	–	–	6.7	–	–	
<i>Solanum symmetricum</i> (= <i>versabile</i> )	–	–	–	–	–	1.9	12.4	–	16.7	
<i>Solanum</i> sp. 1	–	–	–	–	0.2	–	–	–	–	
<i>Solanum</i> sp. 2	–	–	–	–	0.2	–	–	–	–	
<i>Solanum</i> sp. 3	–	–	–	–	–	0.6	–	–	–	
<i>Solanum</i> sp. 4	–	–	–	–	–	0.6	1.1	–	–	
<i>Celtis iguanaeus</i>	–	–	–	–	–	58.5	26.9	–	–	
<i>Chrysophyllum gonocarpum</i>	–	–	–	–	5.9	–	–	–	–	
<i>Passiflora amethystina</i>	–	–	–	–	0.2	–	–	–	–	
<i>Passiflora umbilicata</i>	–	–	–	–	–	–	–	–	–	
<i>Psidium guajava</i>	2.3	–	–	–	0.4	–	–	–	–	
<i>Randia micrantha</i> (= <i>armata</i> )	–	–	–	–	–	–	2.3	–	–	
<i>Urera caracasana</i>	–	–	–	–	–	13.2	1.1	–	–	
Unknown sp.	–	–	–	–	–	–	1.1	–	–	
Unknown sp. 1	–	–	–	–	0.2	–	–	–	–	
Moraceae	34.9	28.2	100.0		19.3	–	–	–	–	
Piperaceae	4.7	2.4		94.7	42.8	11.2	21.4	–	66.7	
Solanaceae	2.3	1.6		5.3	27.5	17.0	47.3	–	33.4	
Moraceae + Cecropiaceae	90.7	96.0		100.0	23.1	–	–	–	–	
Piperaceae + Solanaceae	7.0	4.0			70.3	28.2	68.7	–	100.0	
Other	2.3				6.6	71.7	31.4	–	–	

**Table 2**

Trophic niche breadth calculated using the Levin's index for the frugivorous bat species present in each of the two subtropical sites studied (see text). A dash indicates an inapplicable comparison for a bat species in a site (the species being absent from the site).

	Iguazú	Las Capillas
<i>Carollia perspicillata</i>	0.15	–
<i>Sturnira lilium</i>	0.33	0.24
<i>Sturnira erythromos</i>	–	0.33
<i>Sturnira oporaphilum</i>	–	0.06
<i>Artibeus planirostris</i>	–	0.10
<i>Artibeus fimbriatus</i>	0.10	–
<i>Artibeus lituratus</i>	0.06	–
<i>Vampyressa pusilla</i>	0.04	–

and 85.9% of total diet in *S. erythromos* and *S. lilium*, respectively (Table 1). *Artibeus planirostris* consumed fruits from four families; Celtidaceae was dominant with 58.5% of records from *Celtis iguanaeus*, followed by Solanaceae and Piperaceae that together comprised 28.2% of dietary records, and Urticaceae with 13.2%. As in Iguazú, few species of plants dominated the bat diets and in some instances these were the same for all frugivores; namely, *Piper tucumanum*, *Solanum riparium* and *Celtis iguanaeus*, which together contributed 60–80% of total diets in all four Andean frugivores (Table 1). However here *Artibeus* used plants that were chiropterophilous but were atypical for the genus as compared with Iguazú and the majority of tropical sites reported.

#### Trophic structure and niche analysis

In Iguazú, the widest trophic niche corresponded to *Sturnira lilium* ( $BA = 0.33$ ), followed by *C. perspicillata* ( $BA = 0.15$ ) and *A. fimbriatus* ( $BA = 0.10$ ; Table 2). In Las Capillas another species of *Sturnira* (*S. erythromos*) exhibited the widest trophic niche ( $BA = 0.33$ ) followed closely by *S. lilium* (0.24; Table 2).

In Iguazú, overall niche overlap was significantly higher than expected by chance (observed  $O = 0.34$ , expected  $O = 0.20$ ,  $P = 0.049$ ). However, species pairs greatly differed in degree of overlap (lower off-diagonal cells in Table 3). Niche overlap was highest between species of *Artibeus* ( $O = 0.97$ ), and lowest between any species of *Artibeus* and *Carollia perspicillata* ( $O < 0.02$ ). Overlap values involving species of *Sturnira* were close to the value expected by chance (with respect to *Artibeus*) or clearly larger than expected with respect to *Carollia* ( $O = 0.61$ ). The bat ensemble in Las Capillas also showed significant overall niche overlap (observed  $O = 0.71$ , expected  $O = 0.25$ ,  $P \ll 0.01$ ) but in this site all pairwise values were high (for instance between *S. erythromos* and *S. lilium* [ $O = 0.82$ ] and *A. planirostris* and *S. erythromos* [ $O = 0.81$ ]; upper off-diagonal cells).

Clustering of bats on the basis of fruiting species showed that, at this taxonomic level, bat species and populations split between sites (Fig. 2a), as expected due to few shared species of plants. However, within each side of this NE–NW dichotomy bat groups preserved approximate taxonomic affinities (e.g., reproducing tribe

affiliation), so still a significant correlation ( $r = -0.39$ ,  $P = 0.003$ , 999 random replications) is detected between the dietary similarity and patristic distances. By contrast, clustering based on plant families (Fig. 2b) described two main dichotomies: 1. *Solanum* and *Piper*-eating bats (*Sturnira* and *Carollia*), plus *A. planirostris*; and 2. Stenodermatini bats or primary consumers of *Ficus* and *Cecropia* (two species of *Artibeus* and *Vampyressa pusilla*). Here the patristic correlation ( $r = -0.59$ ,  $P < 0.001$ , 999 random replications) is stronger than in the previous case at the species-level analysis.

#### Fruit ecomorphology

Anatomically, fleshy diaspores eaten by bats at the two Yungas sites and Iguazú (see Table 4) were represented principally by true fruits such as berries (e.g., *Solanum*) and drupes (e.g., *Celtis*), syconia (*Ficus*), spadices (*Piper* and *Cecropia*), and achenes embedded in fleshy perianth and pedicels (*Urera*). These diaspores were green, yellow or orange when uncolored, but some also showed bicolored patterns such as green with white spots in *F. luschnathiana*, or varying from green to purplish-blue as in *Passiflora amethystina* (Table 4). One species of *Solanum* (*S. aligerum* = *S. grossum*) displayed an unusual color for bat fruits (dark violet; Giannini, 1999). In all these fruits we perceived a species-specific scent when fruits were ripe. Most fruits were relatively small (mean 4.31 g; Table 4), but on average larger than fruits present in the study sites (mean = 2.11 g; N.P. Giannini, unpub. data) and included very large fruits such as *Cecropia pachystachya* and *Psidium guajava* of 43 and 16 g, respectively (intraspecific mean values), which likely were eaten piecemeal. Seed number ranged from one in *Celtis* drupes to c. 4200 in *Cecropia*, and it was generally high (interspecific median value was 459 seeds per fruit). Individual seeds were small (mean 23 mg) compared with the community average (121 mg; N.P. Giannini, unpub. data), with the exception of very large seeds of *Celtis iguanaeus* and *Chrysophyllum gonocarpum* (mean of the single seed per fruit 340 mg and 162 mg, respectively). Pulp-to-seed ratio was commonly greater than 4, except for *Cecropia pachystachya* (2.2). *Maclura tinctoria* and *Urera caracasana* displayed an unusually high value of pulp-to-seed ratio (53 and 37). Fruits tended to be exposed away from leaves; i.e., in long-pedicled, erect or pendular (flagelliferous) infructescences, sometimes also terminal. Plant growth forms included vines (*Celtis iguanaeus*, *Passiflora amethystina* and *P. umbilicata*) and trees (species in *Ficus*, *Chrysophyllum* and *Maclura*), but the majority of plants were shrubs or small trees (<5 m in height).

#### Discussion

##### Diversity patterns

Bats in the genera *Artibeus*, *Carollia* and *Sturnira* dominate the ensembles of frugivorous bats in the tropics of the America (e.g., Brosset and Charles-Dominique, 1990; dos Reis and Muller, 1995;

**Table 3**

Food niche overlap calculated using Pianka's index between pairs of frugivorous bat species in each of our two study sites. Numbers in the lower off-diagonal cells correspond to Iguazú; numbers in the upper off-diagonal cells correspond to Las Capillas. A dash indicates an inapplicable comparison (the bat species does not occur in the site).

	<i>Carollia perspicillata</i>	<i>Sturnira lilium</i>	<i>Sturnira erythromos</i>	<i>Sturnira oporaphilum</i>	<i>Artibeus planirostris</i>	<i>Artibeus lituratus</i>	<i>Artibeus fimbriatus</i>
<i>C. perspicillata</i>	–	–	–	–	–	–	–
<i>S. lilium</i>	0.61	–	0.82	0.78	0.51	–	–
<i>S. erythromos</i>	–	–	–	0.60	0.81	–	–
<i>S. oporaphilum</i>	–	–	–	–	0.19	–	–
<i>A. planirostris</i>	–	–	–	–	–	–	–
<i>A. lituratus</i>	0.01	0.18	–	–	–	–	–
<i>A. fimbriatus</i>	0.02	0.23	–	–	–	0.97	–
<i>V. pusilla</i>	0.00	0.18	–	–	–	0.21	0.40

Table 4

Characters of fruits consumed by bats in Iguazú and Las Capillas (this study) and San Javier (Giannini, 1999). Values of meristic variables are given as average (rounded to whole numbers) or range (standard deviation in brackets when available). Shape is fruit polar/eqatorial diameter ratio. Botanical names follow Zuloaga and Morrone (1999) with synonyms used in Giannini (1999) provided in parenthesis. Abbreviations: N, sample size; NE, Northeastern forest (Iguazú); NW, Northwestern forest (Las Capillas); PF, primary forest; PSF, primary and secondary forest; SF, secondary forest; R, riparian habitats.

Species	Mass of fruit (g)	Shape of fruit	Number of seeds per fruit	Mass of individual seeds (mg)	Pulp-to-seed ratio (wet weight)	N	Diaspore type	Color of ripe fruits	Habitat	Forest	Source
<i>Ficus lusciniathiana</i>	2.45 (0.38)	0.89 (0.1)	186 (55.6)	1.2 (0.1)	10.3 (2.4)	13	Syconium	Green whit white spots	PF	NE	a
<i>Ficus citrifolia</i>	1.10 (0.50)	0.97 (0.09)	99 (48.8)	0.7 (0.2)	15.9 (6.1)	13	Syconium	Green or brown	PF	NE	a
<i>Maclura tinctoria</i>	3.20 (0.80)	0.70 (0.1)	40 (6.4)	1.8 (0.4)	53.9 (25.0)	5	Berry	Green	PF	NE	a
<i>Cecropia pachystachya</i>	16.60 (1.9)	9.90 (1.1)	4277 (297.4)	1.2 (0.2)	2.2 (0.07)	4	Spadix	Grayish-green whit brown spots	PSF	NE	a
<i>Piper aduncum</i>	3.88 (0.68)	20.98 (2.5)	1255 (488.2)	0.8 (0.1)	5.2 (1.8)	8	Spadix	Green	PSF	NE	a
<i>Piper amalago</i>	1.94 (0.89)	9.01 (1.97)	104 (58.8)	1.8 (0.4)	8.8 (3.4)	10	Spadix	Green	PSF	NE	a
<i>Piper gaudichaudianum</i>	4.19 (0.64)	21.96 (2.5)	1597 (137.2)	0.5 (0.1)	3.9 (0.8)	5	Spadix	Green	PSF	NE	a
<i>Piper hispidum</i>	3.38 (1.24)	13.58 (0.13)	2030	0.2 (0.02)	8.48	2	Spadix	Green	PSF	NE	a
<i>Solanum granulatum-leprosum</i>	1.96 (0.58)	0.96 (0.04)	139 (35.6)	1.6 (0.4)	8.3 (2.6)	15	Berry	Yellowish	SF	NE	a
<i>Chrysophyllum gonocarpum</i>	4.30 (1.66)	1.33 (0.19)	3 (2.3)	162.2 (55.9)	15.5 (14.3)	4	Berry	Yellow	PF	NE	a
<i>Passiflora amethystina</i>	–	1.6 <sup>c</sup>	60–80 <sup>c</sup>	6.5 (1.7)	–	–	Berry	Green or purple-blue	SF	NE	a
<i>Psidium guajava</i>	43.50 (18.90)	1.1 (0.1)	207 (120.9)	12.9 (2.5)	17.8 (5.3)	9	Berry	Yellow	SF	NE	a
<i>Urera caracasana</i>	0.26 (0.07)	1.47 (0.18)	24 (7.3)	0.3 (0.2)	37.4 (12.7)	19	Fleshy perianth	Yellowish green	PSF	NW	a
<i>Passiflora umbilicata</i>	–	1.08	–	–	–	–	Berry	Yellowish green	SF	NW	c
<i>Solanum abutiloides</i>	1.53 (0.2)	1.1 (0.02)	457 (93.4)	0.6 (0.1)	5.08 (0.7)	5	Berry	Yellow	R	NW	a
<i>Piper tucumanum</i>	3.8 (0.7)	15.5	257 (46.0)	2.8	4.2 (0.5)	4	Spadix	Green	PSF	NW	b
<i>Piper hieronymi</i>	2.50	11.45	590	0.5	8.80	1	Spadix	Green	PSF	NW	a
<i>Solanum algerum</i> (=egrossum)	1.0 (0.3)	0.97	42 (16)	1.9	12.0 (4.4)	17	Berry	Dark violet	PF	NW	b
<i>Solanum trichoneuron</i>	1.3 (0.3)	0.99	91 (28)	2.4	5.5 (2.3)	9	Berry	Green	PSF	NW	b
<i>Solanum symmetricum</i> (=versatile)	1.4 (0.3)	0.93	59 (20)	4.3	5.1 (3.4)	17	Berry	Green	SF	NW	b
<i>Solanum riparium</i>	0.9 (0.2)	0.99 (0.01)	113 (37)	0.9	8.3 (2.8)	10	Berry	Yellowish	PSF-R	NW	b
<i>Solanum tenuispinum</i> (=chaetophorum)	1.2 (0.2)	1.16	63 (10)	3.9	4.2 (1.0)	64	Berry	Green whit white stripes	PSF	NW	b
<i>Solanum confusum</i> (=adelphum)	1.3 (0.7)	0.94	17 (4)	6.5	10.3 (5.3)	34	Berry	Orange	PF	NW	b
<i>Solanum pseudocapsicum</i> (=tucumanense)	1.3 (0.1)	0.92	63 (11)	3.3	5.1 (0.5)	20	Berry	Orange	PSF	NW	b
<i>Eriolarynx lorentzii</i> (=Vassobia, Dunalia)	2.1 (0.5)	0.88	155 (71)	1.2	10.4 (2.5)	6	Berry	Yellowish	SF	NW	b
<i>Celtis iguanaeus</i>	1.42 (0.11)	1 (0.03)	1	340 (30)	3.24 (0.36)	8	Drupe	Orange	PSF	NW	a
<i>Randia micracantha</i> (=armata)	1.4 (0.3)	1.31	12 (2.8)	21.4	4.3 (0.5)	19	Berry	Green	PSF	NW	b

<sup>a</sup> This study.

<sup>b</sup> Giannini (1999).

<sup>c</sup> Deghani (2001).



Ascorra et al., 1996; Kalko et al., 1996a; Kalko, 1997; Simmons and Voss, 1998; Bernard, 2001; Kalko and Handley, 2001; Aguirre, 2002; Bernard and Fenton, 2002; Giannini and Kalko, 2004). Captures in our subtropical study sites reflected the dominance of those genera and none of the bat species sampled is restricted to the subtropics; rather, these are tropical species marginally extending their geographic distribution into subtropical areas of Southern South America (see Barquez, 2005; Gardner, 2007). However, expression of phyllostomid diversity at the species level was contracted as compared with tropical sites. Only a few species of *Artibeus*, *Carollia* and *Sturnira* were abundant and this was mirrored in the frequency of dietary records obtained (Table 1). Species in these genera differed in their representation across sites. Only *Sturnira* was present in the Southernmost subtropical site (San Javier, with three species), whereas *Artibeus* occurred with one or two abundant species in Iguazú and Las Capillas, and *Carollia* occurred with one species (*C. perspicillata*) in Iguazú. By comparison, tropical sites commonly harbor two or more species of *Sturnira* and *Carollia*, and at least four but usually more species of *Artibeus* including *Dermanura*, together with a host of common species of related genera of frugivorous phyllostomids like *Platyrrhinus*, *Chiroderma*, *Uroderma*, and *Rhinophylla* (Kalko, 1997; Estrada and Coates-Estrada, 2002; Sampaio et al., 2003; Giannini and Kalko, 2004). Thus, the South American subtropics exhibit a gradient of species composition from sites such as San Javier with a single genus of frugivores (*Sturnira*) to sites with representatives from each of the main frugivore clades (Carollinae, Sturnirini and Stenodermatini), such as Iguazú. This has important consequences for the interpretation of diet choice (see below).

#### Fruits and trophic structure

Fruits consumed by our sampled bats were of varying sizes but relatively large on average, frequently many-seeded, green or yellow in color, scented, with high pulp-to-seed ratio, and exposed away from leaves in long-pediced infructescences (Table 4). Altogether, these features fit the seed dispersal syndrome associated with bats, chiropterochory (van der Pijl, 1972; Lobova et al., 2009). Thus, while the concept of seed dispersal syndrome has been repeatedly challenged in the literature (e.g., Herrera, 1987; Fischer and Chapman, 1993; Jordano, 1995), our bats were committed to consume fruits with the expected combinations of characters, with few exceptions relegated to isolated fruit traits (e.g., *Solanum aligerum* bears fruits violet in color).

In our samples, *Carollia* specialized on *Piper* (94% of dietary items), *Sturnira* consumed mainly *Piper* and *Solanum* (which together comprised between 70% and 98% of diet across samples), and *Artibeus* preferred Moraceae *sensu lato* (Moraceae + Cecropiaceae) when available (see Table 1 and Giannini, 1999), as predicted by Fleming (1986) and Giannini and Kalko (2004) for tropical sites. In Iguazú where Moraceae fruits are abundant, they comprised >90% of the diet of *Artibeus* and *Vampyressa*. In the NW, where Moraceae are rare or missing altogether, the single species of *Artibeus* present (*A. planirostris*) consumed other chiropterochorous fruits shared with *Sturnira*.

Clustering of bats based on shared proportion of fruit plant species as grouping variable largely reflected the differences in floristic composition across sites (NE versus NW sites), although some systematic structuring was present; e.g., all *Sturnira* grouped together in the NW sites, as did all Stenodermatini in the NE sites (Fig. 2a). When analyzed at the genus level, floristic differences disappeared in favor of a systematic pattern. Rerooting this topology on the *Carollia* branch (arrow in Fig. 2b) recovered much of

the phylogenetic structure of frugivorous phyllostomids as currently understood (i.e., *Carollia* sister to *Sturnira* + Stenodermatini; Baker et al., 2003). This represents evidence of long-term historical effects on diet choice by contemporary species overcoming regional (e.g., tropical versus subtropical) differences, and is in line with the findings of Giannini and Kalko (2004) who reported strong historical structuring in an ensemble of tropical phyllostomids.

#### Testing hypotheses: implications of patterns of subtropical bat frugivory

The exact relationship of local fruit diversity with regional factors such as latitude is unknown, but in the subtropics, phyllostomid bat species of tropical affiliation encounter a greatly reduced diversity of fruiting plants. In spite of this, phyllostomid species occurring in our study sites remained faithful to their preferred fruits, as predicted by hypotheses of fruit selection from species-rich tropical sites (Fleming, 1986; Giannini and Kalko, 2004). This result clearly favors our prediction 1, that subtropical phyllostomids would predominantly use their core plant taxa whenever present, instead of switching to other resources in response to a scenario of reduced diversity (prediction 2). This supports specialization in chiropterochorous core-plant taxa as a major driver of the evolution of feeding habits in phyllostomids (Fleming, 1986; Giannini and Kalko, 2004).

Interestingly, the number of species per bat genus in a given site responded to number of their respective core plant taxa with a relationship very close to 1:3 (slope = 0.28, d.f. = 7,  $P < 0.01$ ,  $r^2 = 0.96$ ), a bat-to-plant species ratio predicted from tropical sites of the Neotropics (Fleming, 2005). This further supports the idea that frugivorous phyllostomid ensembles strongly depend on their core plant taxa and implies that the effect of resource diversity gradients on these ensembles is observable primarily on bat species composition rather than on the diet of the component species. So the mechanism for adjusting to varying fruit availability is predicted to be dropping or adding bat species along gradients of plant diversity rather than resource switching to adjust for the loss or rarity of their preferred plants.

To conclude, our data from subtropical sites lend strong support to hypotheses of dietary specialization in core plant taxa (Fleming, 1986; Giannini and Kalko, 2004), expected ratios of interacting animal versus plant species among Neotropical mutualists (Fleming, 2005), and fidelity to dispersal syndromes (Lomáscolo et al., 2008; Lomáscolo and Schaefer, 2010; *contra* Herrera, 1987; Fischer and Chapman, 1993; Jordano, 1995). Therefore niche specialization in specific core-plant taxa, traceable to ancestors of major clades (Giannini and Kalko, 2004), represent major drivers of the evolution of feeding habits in frugivorous phyllostomids and likely are key mechanisms favoring coexistence of syntopic frugivores in the Neotropics.

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## References

- Aguilar, L.M.S., Marinho-Filho, J., 2007. Bat frugivory in a remnant of southeastern Brazilian Atlantic forest. *Acta Chiropterologica* 9, 251–260.
- Aguirre, L.F., 2002. Structure of a neotropical savanna bat community. *Journal of Mammalogy* 83, 775–784.
- Ascorra, C., Solari, S., Wilson, D.E., 1996. Diversidad y ecología de los quirópteros en Pakitza. In: Wilson, D.E., Sandoval, A. (Eds.), *Manu. The Biodiversity of South-eastern Peru*. Editorial Horizonte, Lima, Perú, pp. 593–612.
- Baker, R.J., Hooper, S.R., Porter, C.A., Van Den Bussche, R.A., 2003. Diversifications among new world leaf-nosed bats: an evolutionary hypothesis and classifications inferred from digenomic congruence of DNA sequence. *Occasional Papers*, vol. 230. Museum of Texas Tech University, pp. 1–32.
- Baker, R.J., Porter, C.A., Patton, J.C., Van Den Bussche, R.A., 2000. Systematics of bats of the family Phyllostomidae based on RAG2 DNA sequences. *Occasional Papers*, vol. 202. Museum of Texas Tech University, pp. 1–16.
- Barquez, R.M., 2005. Orden Chiroptera Blumenbach, 1779. In: Barquez, R.M., Díaz, M.M., Ojeda, R.A. (Eds.), *Mamíferos de Argentina, sistemática y distribución*. Sociedad Argentina para el Estudio de los Mamíferos, pp. 56–86.
- Bernard, E., 2001. Vertical stratification of bat communities in primary forests of central Amazon, Brazil. *Journal of Tropical Ecology* 17, 115–126.
- Bernard, E., Fenton, M.B., 2002. Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in Central Amazonia, Brazil. *Canadian Journal of Zoology* 80, 1124–1140.
- Bonaccorso, F.J., 1979. Foraging and reproductive ecology in a Panamanian bats community. *Bulletin of the Florida State Museum Biological Sciences* 24, 359–408.
- Brosset, A., Charles-Dominique, P., 1990. The bats from French Guiana: a taxonomic, faunistic and ecological approach. *Mammalia* 54, 509–560.
- Brown, A.D., 1995. Fenología y caída de hojarasca en las selvas montañas del Parque Nacional El Rey, Argentina. In: Brown, A.D., Grau, H.R. (Eds.), *Investigación, conservación y desarrollo en selvas subtropicales de montaña*. Laboratorio de Investigaciones Ecológicas de Las Yungas, Universidad Nacional de Tucumán, Argentina, pp. 93–102.
- Brown, A.D., Grau, H.R., Malizia, L.R., Grau, A., 2001. Argentina. In: Kappelle, M., Brown, A.D. (Eds.), *Bosques nublados del Neotrópico*. Instituto Nacional de Biodiversidad, San José de Costa Rica, pp. 623–659.
- Burkart, R., Bárbaro, N.O., Sánchez, R.O., Gomez, D.A., 1999. Ecorregiones de la Argentina. Administración de Parques Nacionales, Buenos Aires, Argentina.
- Cabrera, A., 1976. Regiones fitogeográficas de Argentinas. *Enciclopedia Argentina de Agricultura, Jardinería y Flora*. Editorial ACME, Buenos Aires, Argentina.
- Cabrera, A.L., Willink, A., 1980. *Biogeografía de América Latina*. Secretaría General de la OEA. Monogr. Cient. Serie Biología n° 13, Washington, DC.
- Croat, T.B., 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California.
- Deginani, N.B., 2001. Las especies argentinas del género *Passiflora* (Passifloraceae). *Darwiniana* 39, 43–129.
- dos Reis, N.R., Muller, M.F., 1995. Bat diversity of forests and open areas in a subtropical region of south Brazil. *Ecología Austral* 5, 31–36.
- Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlá, Mexico. *Biological Conservation* 103, 237–245.
- Fischer, K.E., Chapman, C.A., 1993. Frugivores and fruit syndromes: differences in patterns at the genus and species level. *Oikos* 66, 472–482.
- Fleming, T.H., 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. In: Estrada, A., Fleming, T.H. (Eds.), *Frugivores and Seed Dispersal*. Dr. W. Junk Publ., pp. 105–118.
- Fleming, T.H., 1988. The short-tailed fruit bat: a study in plant–animal interactions. *Wildlife Behav. Ecol. Ser.* Chicago Univ. Press.
- Fleming, T.H., 1991. The relationship between body size, diet, and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). *Journal of Mammalogy* 72, 493–501.
- Fleming, T.H., 2005. The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos* 111, 556–562.
- Fleming, T.H., Heithaus, E.R., 1981. Frugivorous bats, seed shadows and the structure of tropical forest. *Biotropica, Reproductive Botany* 13, 45–53.
- Freeman, P.W., 2000. Macroevolution in microchiroptera: recoupling morphology and ecology with phylogeny. *Evolutionary Ecology Research* 2, 317–335.
- Gardner, A.L., 2007. Family Phyllostomidae Gray, 1825. In: Gardner, A.L. (Ed.), *Mammals of South America, Volume 1, Marsupials, Xenarthrans, Shrew, and Bats*. The University of Chicago Press, Chicago and London, pp. 207–363.
- Giannini, N.P., 1999. Selection of diets and elevation by sympatric species of *Sturnira* in an Andean rainforest. *Journal of Mammalogy* 80, 1186–1195.
- Giannini, N.P., Kalko, E.K.V., 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos* 105, 209–220.
- Giannini, N.P., Kalko, E.K.V., 2005. The guild structure of animalivorous leaf-nosed bats of Barro Colorado Island, Panama, revisited. *Acta Chiropterologica* 7, 131–146.
- Gorchov, D.L., Cornejo, F., Ascorra, C.F., Jaramillo, M., 1995. Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. *Oikos* 74, 235–250.
- Gotelli, N.J., Entsminger, G.L., 2006. *EcoSim: null models software for ecology*. Version 7.72. Acquired Intelligence and Kesey-Bear, Jericho, VT05465. Available from: <<http://garyentsminger.com/ecosim/index.htm>>.
- Hernández-Conrique, D., Iñiguez-Dávalos, L.I., Storz, J.F., 1997. Selective feeding by phyllostomid fruit bats in a subtropical montane cloud forest. *Biotropica* 29, 376–379.
- Herrera, C.M., 1987. Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs* 57, 305–331.
- Horn, H.S., 1966. Measurement of “overlap” in comparative ecological studies. *The American Naturalist* 100, 419–424.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–228.
- Hueck, K., 1978. *Los bosques de Sudamérica*. GTZ, Eschborn, Germany.
- Humphrey, S.R., Bonaccorso, F.J., Zinn, T.L., 1983. Guild structure of surface-gleaning bats in Panama. *Ecology* 64, 284–294.
- Jordano, P., 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *The American Naturalist* 145, 163–191.
- Kalko, M.B., Smith, A.R., Kalko, E.K.V., 2008. Bats limit arthropods and herbivory in a tropical forest. *Science* 320, 71.
- Kalko, E.K.V., 1997. Diversity in tropical bats. In: Ulrich, H. (Ed.), *Tropical Diversity and Systematics*. Proc. Int. Symp. Biodiv. Syst. Tropical Ecosystems, Bonn 1994. Zool. Forschungsinstitut Mus. Alexander Koenig, Bonn.
- Kalko, E.K.V., Condon, M.A., 1998. Echolocation, olfaction and fruit display: how bats find fruit of flagelliferous cucurbits. *Functional Ecology* 12, 364–372.
- Kalko, E.K.V., Handley Jr., C.O., 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology* 153, 319–333.
- Kalko, E.K.V., Handley Jr., C.O., Handley, D., 1996a. Organization, diversity and long-term dynamics of a Neotropical bat community. In: Cody, M., Smallwood, J. (Eds.), *Long-term Studies in Vertebrate Communities*. Academic Press, Los Angeles, pp. 503–553.
- Kalko, E.K.V., Herre, E.A., Handley Jr., C.O., 1996b. Relation of fig fruit characteristics to fruit-eating bats in the new and old world tropics. *Journal of Biogeography* 23, 565–576.
- Klingbeil, B.T., Willig, M.R., 2009. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. *Journal of Applied Ecology* 46, 203–213.
- Krebs, C.J., 1999. *Ecological Methodology*, 2nd ed. Addison-Wesley Educational Publishers Inc., Menlo Park, Calif.
- Lang, A.B., Kalko, E.K.V., Römer, H., Bockholdt, C., Dechmann, D.K.N., 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146, 659–666.
- Lawlor, L.R., 1980. Structure and stability in natural and randomly constructed competitive communities. *The American Naturalist* 116, 394–408.
- Lim, B.K., Engstrom, M.D., Lee Jr., T.E., Patton, J.C., Bickham, J.W., 2004. Molecular differentiation of large species of fruit-eating bats (*Artibeus*) and phylogenetic relationships based on the cytochrome b gene. *Acta Chiropterologica* 6, 1–12.
- Lobova, T.A., Geiselman, C.K., Moris, S.A., 2009. Seed dispersal by bats in the Neotropics. *Memoirs of the New York Botanical Garden*, vol. 101. The New York Botanical Garden.
- Lomáscolo, S.B., Schaefer, H.M., 2010. Signal convergence in fruits: a result of selection by frugivores? *Journal of Evolutionary Biology* 23, 614–624.
- Lomáscolo, S.B., Speranza, P., Kimball, R.T., 2008. Correlated evolution of fig size and color supports the dispersal syndromes hypothesis. *Oecologia* 156, 783–796.
- Lopez, J.E., Vaughan, C., 2007. Food niche overlap among neotropical frugivorous bats in Costa Rica. *Revista Biología Tropical* 55, 301–313.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd ed. Chapman and Hall, London, United Kingdom.
- Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27, 209–220.
- Marinho-Filho, J.S., 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. *Journal of Tropical Ecology* 7, 59–67.
- Mello, M.A.R., Kalko, E.K.V., Silva, W.R., 2008. Diet and abundance of the bat *Sturnira lilium* (Chiroptera) in a Brazilian montane Atlantic forest. *Journal of Mammalogy* 89, 485–492.
- Minetti, J.L., Bobba, M.E., Hernández, C., 2005. Régimen espacial de temperaturas en el Noroeste de Argentina. In: Minetti, J.L. (Ed.), *El Clima del Noroeste Argentino Laboratorio Climatológico Sudamericano (LCS)*. Editorial Magna, pp. 141–161.
- Palmeirim, J.M., Gorchov, D.L., Stoleson, S., 1989. Trophic structure of neotropical frugivore community: is there competitions between birds and bats? *Oecologia* 79, 403–411.
- Pianka, E.R., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4, 53–74.
- R Development Core Team, 2004. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Available from: <<http://www.Rproject.org>>.
- Sampaio, E.M., Kalko, E.K.V., Bernard, E., Rodríguez-Herrera, B., Handley Jr., C.O., 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland rainforest of central Amazonia, including methodological and conservation considerations. *Studies on Neotropical Fauna and Environment* 38, 17–31.
- Simmons, N.B., Voss, R.S., 1998. The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna. Part 1. Bats. *Bulletin of the American Museum of Natural History* 237, 1–219.

- Srur, M., Gatti, F., Benesovsky, V., Herrera, J., Melzew, R., Camposano, M., 2007. Identificación, caracterización y mapeo de los ambientes del Parque Nacional Iguazú. Informe final. Centro de Investigaciones Ecológicas Subtropicales, Delegación Técnica Regional NEA. A.P.N. Parques Nacionales, Argentina.
- Pijl van der, L., 1972. Principles of Dispersal in Higher Plants. Springer-Verlag.
- Villalobos, F., Valerio, A.A., 2002. The phylogenetic relationships of the bat genus *Sturnira* Gray, 1842 (Chiroptera: Phyllostomidae). *Mammalian Biology* 67, 268–275.
- Wetterer, A.L., Rockman, M.V., Simmons, N.B., 2000. Phylogeny of Phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. *Bulletin of the American Museum of Natural History* 248, 1–200.
- Zuloaga, F.O., Morrone, O. (Eds.), 1999. Catálogo de las Plantas Vasculares de la República Argentina II. Dicotyledoneae. Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 74, pp. 1–1246.