



Understanding the spatial variations in the diets of two *Sturnira* bats (Chiroptera: Phyllostomidae) in Argentina

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Frugivorous phyllostomid bats are a diverse group and one of the major partners of fleshy-fruited plants in seed dispersal mutualisms. The first step towards comprehension of mechanisms shaping the structure of highly diverse phyllostomids assemblages is to gather information about diet composition and to study the variations in the use of fruits across space. Herein we tested whether frugivorous phyllostomids changes the use of its fruits where fruit offer may change with the altitude and latitude. Particularity, using 1,525 dietary records from 20 sites, we evaluated the spatial use of *Solanum*, *Piper* and other fruits by two syntopic and similar species of *Sturnira* bats from Northwestern Argentina. The relationship between dietary compositions and spatial variables was studied through Dirichlet statistical regressions. Additionally, we constructed predictive models of diets in function of latitude and altitude by estimating the parameters of Dirichlet distributions, and compared then their behavior. Both bats showed spatial changes in the diets. However, in taking into account the overall pattern of predicted diets throughout the space, inter-specific differences were detected. While both species increased the use of *Solanum* with altitude, only *Sturnira erythromos* showed a meaningful altitudinal and latitudinal response concerning to the use of *Piper* and other fruits or *Solanum*, respectively. Our predictive models for diets enable us to split the space into two sectors, one characterized by a high dietary overlap and another with the salient feature of dissimilar preference towards the subsidiary resources. These findings call for a model of spatial segregation, acting at a regional scale, as a hypothetical mechanism allowing the coexistence of both species.

Los murciélagos filostómidos frugívoros son un grupo diverso y uno de los mayores socios de las plantas con frutos carnosos en los sistemas mutualistas de dispersión de semillas. El primer paso para comprender los mecanismos detrás de las estructura en los diversos ensambles de filostómidos es reunir información acerca de la composición de las dietas y estudiar la variación en el uso de los frutos a través del espacio. Aquí evaluamos si los filostómidos frugívoros cambian el uso de sus frutos en lugares donde la oferta de fruta puede cambiar con la altitud y latitud. Particularmente, usando 1,525 registros de dieta de 20 sitios, evaluamos el uso espacial de *Solanum*, *Piper* y otros frutos por dos especies sintópicas y similares de *Sturnira* que habitan el Noroeste de Argentina. Las relaciones entre dietas y variables espaciales fueron estudiadas a través de regresiones estadísticas de Dirichlet. Además, construimos un modelo predictivo de dietas en función de la latitud y la altitud mediante estimación de los parámetros de las distribuciones de Dirichlet, y comparamos luego su desenvolvimiento. Ambos murciélagos exhibieron cambios espaciales en las dietas. Sin embargo, cuando tomamos en cuenta la superposición de los patrones del modelo predictivo de dietas a través del espacio, diferencias interespecíficas fueron detectadas. Mientras ambas especies incrementan el uso de *Solanum* con la altitud, sólo *Sturnira erythromos* mostró una respuesta altitudinal y latitudinal significativa en relación al uso de *Piper* y otros frutos o *Solanum*, respectivamente. Nuestros modelos predictivo de dietas pueden dividir el espacio en dos sectores, uno caracterizado por una alta superposición en las dietas y otro donde se destacan preferencias diferenciales hacia los recursos subsidiarios. Estos resultados sugieren un modelo de segregación espacial, actuando a escala regional, como un mecanismo hipotético que permite la coexistencia de ambas especies.

Key words: altitude, dietary simulations, Dirichlet regression, latitude, spatial segregation, *Sturnira erythromos*, *S. liliium*

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Seed dispersal mediated by vertebrates is an outstanding process in tropical and subtropical forests which involve up to 90% of woody plant species that can support up to 80% of the vertebrate biomass (Terborgh 1986; Fleming et al. 1987). Fruits are strongly heterogeneous resources whose availability can change among successive scales of analysis (among individuals, sites, or landscape—García and Ortiz-Pulido 2004). To cope with this scale-dependent heterogeneity of fruits, frugivores might show different strategies or behavioral mechanisms including migration to track fruit production (e.g., Blendinger et al. 2012; Tellería et al. 2014), switch to less preferred but more abundant fruits (Fleming 1986), or the use of other resources such as arthropods or leaves in times of scarcity of their preferred fruits (e.g., Heithaus et al. 1975; Kunz and Diaz 1995; Blendinger et al. 2012). These strategies and their capacity to exploit a specific resource may have a strong phylogenetic constraint, which may result in similar diets for closely related species (e.g., Giannini and Kalko 2004; Sánchez et al. 2012a), or may be limited by negative interactions such as competitive segregation (e.g., Ricklefs 1987; Bonaccorso et al. 2006).

One of the main challenges we face in analyzing patterns of fruit consumption across spatial dimensions is the quantitative nature of diet composition data (or dietary profiles). Dietary profiles are vectors composed of proportions (or percentages) of disjoint categories adding to one (or 100%). For this reason, to assess the individual changes of each dietary item and their covariation with spatial variables such as latitude, longitude, or altitude, it is imperative to fulfill the numerical restrictions imposed by the dependence between data and the intrinsic heteroscedasticity. This explains why the traditional linear regression analysis is discouraged to address the analysis of compositional vectors (see Zar 1996; Hijazi and Jernigan 2009). Ordination methods like Correspondence Analysis dealt in part with this constraint since it only allows the analysis of diet in an assemblage perspective (e.g., Gorchoy et al. 1995; Giannini and Kalko 2004; Gonçalves Da Silva et al. 2008). However, new methods of analysis, such as the Dirichlet regression (Hijazi and Jernigan 2009), open the possibility to assess changes across samples (including nonlinearities) in each component from a compositional vector, providing us with a fresh statistical framework to understand the structure of frugivorous diets and their variations across space.

Phyllostomids fruit-bats are a specious group that ordinarily co-occur in rich multispecies assemblages and dominate mist net bats captures (Kalko et al. 1996). These bats are among the most abundant seed-dispersing vertebrates in the Neotropics (Muscarella and Fleming 2007; Lobova et al. 2009). Their interactions with plants are old in the time and can go back to late Oligocene (25–22 million years—Baker et al. 2012; Rojas et al. 2012). These bats may disperse seeds of 549 species in 191 genera (Lobova et al. 2009). However, their evolutions seem to be characterized by a close genus-to-genus relationship, particularly those species belonging to *Artibeus*, *Carollia*, and *Sturnira* genus feeding primarily on fruits of *Moraceae sensu lato* (*Ficus* and *Cecropia*), *Piper* (*Piperaceae*), and *Solanum* (*Solanaceae*) plus *Piper*, respectively (Fleming

1986). Extrinsic and intrinsic factors seem to be also crucial in the structure of mutualistic bat–plant interactions (Saldaña-Vázquez et al. 2013). These hypothesis states that latitude, altitude, and ecoregion or body size (extrinsic and intrinsic factors, respectively) determine the relative preference of fruits by *Sturnira* and *Artibeus* genera, whereas these factors do not seem to be important for *Carollia*–*Piper* interaction (Saldaña-Vázquez et al. 2013). There also seems to be differences in the use of fruits at different taxonomic resolutions among phyllostomids. For instance, bats from *Carollia* and *Sturnira* genera showed differences in the use of fruits among species as well as among individuals of the same species producing generalists or specialists trends among them (Andrade et al. 2013; Muylaert et al. 2014).

Sturnira is an Andean genus of frugivorous phyllostomids comprising 21 putative species (Velazco and Patterson 2013). These bats are distributed in tropical and subtropical forests, and peaks of diversity occur in the eastern slopes of the Andes (Velazco and Patterson 2013). In Argentina, this genus occurs in NW and NE rain forests (see Gardner 2007). In the mountain rain forests of NW Argentina, 3 species occur syntopically: *Sturnira lilium*, *Sturnira erythromos*, and *Sturnira oporaphilum* (Gardner 2007). The latter is rare, but the first 2 species are extremely abundant and account for at least 50%, and up to 95% of mist net bat captures across localities (Giannini 1999; Sánchez in press). Abundances of these bats change differentially in response to climatic conditions across latitudinal and altitudinal gradients in NW Argentina (Sánchez and Giannini 2014). In the same line, diversity of plants also changes across these gradients (see Brown et al. 2001). Observations about diet of bats throughout the sampling sites suggest spatial changes in its plants abundance. These data indicate that the diversity and abundance of *Solanum* increase with altitude, whereas *Piper* is very common at lower altitude and latitude (see Giannini 1999; Sánchez et al. 2012b). Hypothetical statements regarding the use of fruits by *Sturnira* bats in NW Argentina are thus generated: 1. both *Sturnira* bats show changes in the use of their core plants associated with altitude and latitude (e.g., Giannini 1999; Saldaña-Vázquez et al. 2013), or alternatively, 2. *Sturnira* bats do not show changes or differ in their response to the spatial gradients. This last can derivate in generalist or specialist tendencies between them (e.g., Andrade et al. 2013; Muylaert et al. 2014). Specifically, the main goal of our research is to evaluate, via Dirichlet regressions, the spatial use of fruits by 2 similar and syntopic species of *S. erythromos* and *S. lilium*. Additionally, using altitude and latitude as predictors, we will construct predictive models for compositional dietary vectors and compare them to assess the influence of phylogenetic constraint (closely related species share their resources because of recency of common ancestry—Blomberg and Garland 2002; Giannini and Kalko 2004) and competitive exclusion principle (co-occurring species differ in the resource usage—Ricklefs 1987). Therefore, through an analysis of the diets across space and using our predictive models, we hope to get clues about the usage of fruits and the mechanisms that allow the coexistence of these frugivores.

MATERIALS AND METHODS

Study area.—Our general study area corresponds to the biogeographic province of Southern Andean Yungas, NW Argentina (Cabrera and Willink 1980). In Argentina, these forests form a long and narrow E-W strip on the Eastern slopes of the Andes between 22° and 28° S (Brown et al. 2001). The area is bordered to the east by the phytogeographic province of Chaco and to the west with the Monte, Prepuna, and Puna provinces (Cabrera 1976; Cabrera and Willink 1980). These mountain rain forests range from 400 to 3,000 meters above sea level (hereafter masl). Climate is subtropical and annual rainfall varies between 1,000 and 2,000 mm with altitude (Cabrera 1976; Brown et al. 2001). Mean annual temperature is 19°C (Minetti et al. 2005). Additional details of these forests are given in Brown et al. (2001) and a detailed description of some sites can be found in Giannini (1999), Sánchez (2011), and Sánchez et al. (2012a, 2012b).

The dietary data set was developed from successive field research projects carried out in NW Argentina between March 2004 and November 2012 (e.g., Sandoval et al. 2010; Barquez et al. 2011; Sánchez 2011; Sánchez et al. 2012a, 2012b; Blendinger et al. in press). We studied 17 sites scattered throughout the provinces of Jujuy, Salta, Tucumán, and Catamarca, all of them included into the elevation interval ranging from 380 to 1,200 masl (Appendix S1). In our analyses, we also included dietary data from another study carried out by Giannini (1999) in Sierra de San Javier, Tucumán, NW Argentina.

Bat sampling and diet.—At each site, we sampled bats using 10 mist nets 40–50 m apart from each other, half placed at ground level and half at the subcanopy level in suitable locations (e.g., intercepting flight pathways). We sampled each site by 3–5 consecutive nights, changing net location frequently. We operated all mist nets for approximately 6 h from sunset. Nets were checked every 30 min and were closed in response to bad weather. Each bat was removed from the net and placed in an individual cloth bag for about 1 h. On each specimen, we recorded body mass to the nearest 0.5 g using a spring scale PESOLA, forearm length to the nearest 0.1 mm using a digital caliper, sex, and age (juvenile or adult). Bats were marked by trimming the hair on the back to avoid multiple counting of recaptures and were released near the capture site. Voucher specimens were deposited in Colección Mamíferos Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina. We preserved dietary samples as individually labeled dry pellets. The plant dietary items were identified using a reference collection of seeds that was initiated by Giannini (1999) and continued by Sánchez et al. (2012a). Each plant species present in a fecal sample, irrespective of their abundance, was considered a dietary record (i.e., a separate event of feeding). For our analyses, we considered the following dietary items: *Solanum*, *Piper*, and other fruits. This decision obeys to the fact that these genera are important items in the diets of *Sturnira* in Argentina (Giannini 1999; Sánchez et al. 2012a) and constitute the core plant taxa at which the hypotheses of fruit selection were proposed (see Fleming 1986). Giannini (1999) studied *Sturnira* bats in 3 sites along an

altitudinal transect (800–1,600 masl). In this study, 596 dietary records were reported for 2 species of *Sturnira*, which showed a strong selection of Solanaceae and Piperaceae fruits (97–99% of diet—Giannini 1999).

Compositional nature of dietary data.—The dietary profile reflects how the feeding habit is spread across the alimentary choices. For each sampling site, the values of such compositional vector were inferred from the relative frequency of food items across the studied specimens. The diet was thus treated as a compositional data since it is composed by a set of variables (food items) whose contents are bounded in an interval and sum up to constant for each observation (here, summing up to the unity). Since we are interested in the relationship between dietary profiles with the spatial variables altitude and latitude, we performed a multiple Dirichlet regression on the available data because this technique can handle complex, even non-linear, relationships between several quantitative independent variables and a response variable encoded in a compositional vector (i.e., dietary vector). For *S. erythromos*, the 3 geographical points with a single diet observation were excluded from the analyses due to the small sample size (Table 1). The statistical analysis was implemented through the package DirichletReg (Maier 2013) of the software R (R Development Core Team 2014). Next, we provide a synthetic theoretical background to grip the fundamentals of Dirichlet regression and we develop a predictive model about diet composition in function of latitude and altitude.

Modeling compositions using Dirichlet regression.—Compositional data consists of vectors which D components are proportions or percentages. The overall sum of their elements yields a constant c (equals to 1 in case of proportions). For composition vectors provided of strictly positive entries, the respective sample space is given by the simplex S^D .

For the particular case of $D = 3$, the simplex S^3 can be graphically represented with a ternary plot. This plot is an equilateral triangle where tripartite compositional data are unequivocally represented on it through a point. A given compositional datum $x = [x_1, x_2, x_3]^T$ corresponds with the point that is d_1 , d_2 , and d_3 from the opposite sides to the respective apexes 1, 2, and 3 (Fig. 1), being d_1 , d_2 , and d_3 distances linearly proportional to x_1 , x_2 , and x_3 , respectively.

Let $x = [x_{i1}, x_{i2}, \dots, x_{iD}]$ be an observation i from a compositional vector, that is, $x_{ij} \geq 0$ and $\sum_j x_{ij} = 1$ for $j = 1, 2, \dots, D$. In addition, suppose that $\alpha = [\alpha_1, \alpha_2, \dots, \alpha_D]$ with $\alpha_i > 0$ for each i , and let $\alpha_0 = \sum_i \alpha_i$. The x is said to be a Dirichlet distribution with parameter α , denoted as $x \sim \text{Dir}(\alpha)$, if it has $f(q; \alpha) = 0$ if q is not a compositional vector, and if q is a compositional vector:

$$f(q; \alpha) = (\Gamma(\alpha_0) / \prod_{i=1, D} \Gamma(\alpha_i)) \prod_{i=1, D} q_i^{\alpha_i - 1} \quad (1)$$

where $\Gamma(s)$ denotes the gamma function evaluated at s . The mean of a Dirichlet distribution is defined as α/α_0 . Note that the support of the Dirichlet is open and does not include the vertices or edge of the simplex, that is, no component of a compositional vector drawn from a Dirichlet will ever be zero. A Dirichlet regression model is obtained by allowing the parameters of a

Table 1.—Data set about diet composition used in statistical analyses. Location of study sites in [Appendix S1](#). Data given as percentage of dietary items for each bat species (with number of observed samples between brackets). NA: data not available. Sites 13–15 were studied by [Giannini \(1999\)](#). masl: meters above sea level.

Site	Altitude (masl)	Latitude (degree)	<i>Sturnira erythromos</i>			<i>Sturnira lilium</i>		
			<i>Solanum</i>	<i>Piper</i>	Other fruits	<i>Solanum</i>	<i>Piper</i>	Other fruits
1	450	-22.65	0.0	100.0 (1)	0.0	0.0	100.0 (16)	0.0
2	650	-23.00	0.0	100.0 (1)	0.0	75.0 (27)	22.2 (8)	2.8 (1)
3	385	-23.09	100.0 (1)	0.0	0.0	71.9 (23)	28.1 (9)	0.0
4	1,008	-23.10	75.0 (3)	25.0 (1)	0.0	83.3 (5)	16.7 (1)	0.0
5	613	-23.13	0.0	0.0	0.0	73.9 (99)	22.4 (30)	3.7 (5)
6	500	-23.11	0.0	0.0	0.0	62.5 (5)	37.5 (3)	0.0
7	542	-23.10	0.0	0.0	0.0	40.0 (8)	60.0 (12)	0.0
8	1,200	-24.07	50.7 (38)	18.7 (14)	30.7 (23)	62.5 (65)	31.7 (33)	5.8 (6)
9	1,000	-24.04	36.4 (4)	18.2 (2)	45.5 (5)	39.4 (26)	33.3 (22)	27.3 (18)
10	817	-25.40	95.3 (41)	2.3 (1)	2.3 (1)	98.4 (60)	1.6 (1)	0.0
11	986	-25.40	0.0	0.0	0.0	100.0 (14)	0.0	0.0
12	900	-25.47	88.2 (15)	0.0	11.8 (2)	94.7 (71)	2.7 (2)	2.7 (2)
13	1,600	-26.70	96.0 (192)	4.0 (8)	0.0	100.0 (2)	0.0	0.0
14	1,200	-26.73	80.1 (NA)	19.2 (NA)	0.7 (NA)	83.3 (NA)	16.7 (NA)	0.0 (NA)
15	800	-26.77	41.5 (NA)	54.7 (NA)	3.8 (NA)	43.7 (NA)	50.0 (NA)	6.2 (NA)
16	920	-26.77	95.5 (21)	0.0	4.5 (1)	100.0 (2)	0.0	0.0
17	700	-26.78	50.0 (1)	50.0 (1)	0.0	44.4 (4)	55.6 (5)	0.0
18	825	-26.77	66.7 (2)	33.3 (1)	0.0	52.8 (28)	45.3 (24)	1.9 (1)
19	600	-26.60	0.0	0.0	0.0	0.0	100.0 (35)	0.0
20	760	-28.10	83.6 (56)	4.5 (3)	11.9 (8)	94.5 (52)	5.5 (3)	0.0

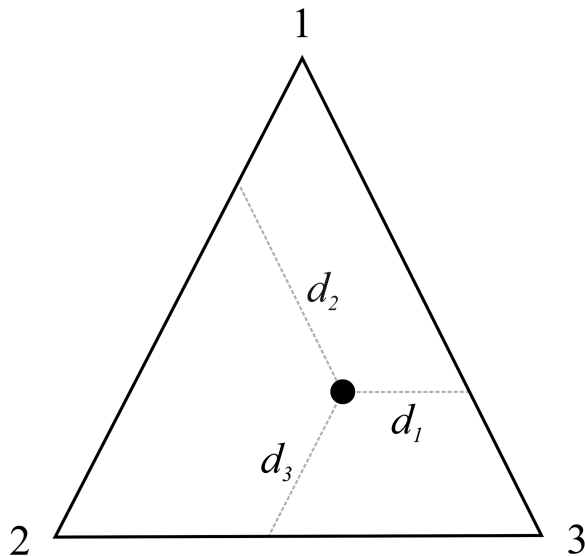


Fig. 1.—Basics about ternary plots. Vectors containing 3 components (d_1 , d_2 , and d_3) are conveniently represented as a single point in these triangular diagrams. Such diagrams are based on the property of equilateral triangles that the sum of the perpendicular distances from any point to each side of the diagram is a constant equal to the length of any of the sides. For points lying along any line parallel to a side of the diagram, the fraction of the component of the corner opposite to that side is constant.

Dirichlet distribution to change with a covariate ([Hijazi and Jernigan 2009](#)). The general purpose of Dirichlet regression is to predict the alphas for each component by a set of variables. A log-link function can be used because parameters to be estimated must be greater than zero. In this respect, the work of [Hijazi \(2003\)](#) and [Hijazi and Jernigan \(2009\)](#) are relevant since the Dirichlet distribution's parameters are directly modeled by

covariates using a log-link. Since the different α parameters are modeled individually, heteroscedasticity is accounted for implicitly. This method, using maximum likelihood estimation, is implemented in the R package *DirichletReg* ([Maier 2013](#)) via the procedure called common parameterization. Stable versions of this package can be obtained from the Comprehensive R Archive Network (CRAN; <http://cran.r-project.org>) and development versions are hosted at R-Forge (<http://r-forge.r-project.org>).

Lastly, we explored emergent patterns in the geographical variation of diets by running the inferred statistical model. We assume that the different combinations of altitude and latitude define an ecospace that shapes indirectly the pattern of frugivory. Once the models of diet were constructed, we extracted predictions from them, using as input values those of latitude and altitude within the respective ranges applicable to the Southern Andean Yungas. The predicted compositional dietary profiles were projected onto the ecospace using their components (fractions of food items) as elements in the Red, Green, and Blue (RGB) color system. This enables us to map each dietary profile onto its unequivocal image in the RGB color system. To compare the behavior of the inferred models across the ecospace, we project in a ternary plot the dietary compositional vectors predicted for both species of bats. In our case, the fractions of the following food items are represented in the ternary plot: *Solanum*, *Piper*, and other fruits. The R script to perform all these procedures is available in [Appendix S2](#).

RESULTS

We obtained 1,569 dietary records: 973 obtained directly from our 17 studied sites ([Table 1](#)) and 596 gathered from literature ([Giannini 1999](#)) corresponding to 3 additional sites. *Solanum*

accounted for 69.0% of total dietary records, whereas *Piper* and other comprised 23.4% and 7.6%, respectively. At each locality, bats mainly choose fruits of *Solanum* (from 39.0% to 100.0% of diet; Table 1), followed by *Piper*, which can represent between 2.0% and 100.0% of diets. Separately, other resources accounted for less than 11.0% of diets in general; only in 3 sites other resources were important and contributed between 30.0% and 45.0% of diets (see Table 1).

Multiple Dirichlet regression for each bat species showed spatial differences in the use of their resources. As the altitude increases, *S. erythromos* consumed more *Solanum* fruits at the expense of *Piper* and other fruits. Additionally, *Solanum* consumption decreased at lower latitudes (Fig. 2; Table 2). On the other hand, *S. lilium* only showed a positive increase in the use of *Solanum* with altitude, whereas the remainder associations were nonsignificant (Fig. 3; Table 2).

The graphical representation of model predictions highlights 2 main trends in the spatial use of fruits. When mapped onto the RGB color system, the outcome for *S. erythromos* shows clearly the joint effect of altitude and latitude on its diet, being other fruits and *Piper* preferred over *Solanum* in lower latitudes and altitudes (Fig. S1), while the pattern retrieved for *S. lilium* is mainly driven by the turnover between *Solanum* and *Piper* coupled with changes in altitude

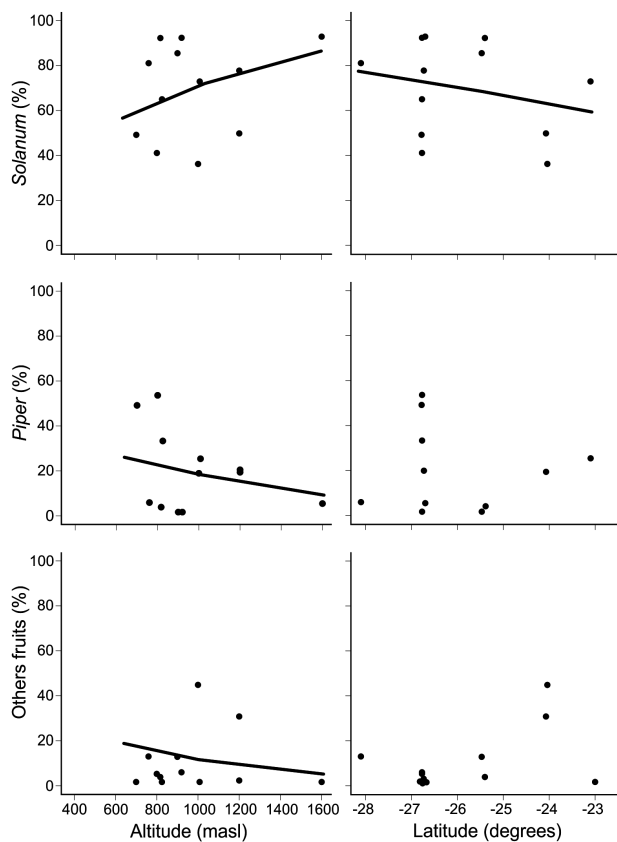


Fig. 2.—Scatterplots of the use of *Solanum*, *Piper*, and other fruits against 2 spatial sources of variability explored with the Dirichlet regression analysis for *Sturnira erythromos*. Continuous regression lines indicate significant relationships at $\alpha = 0.05$. Full regression models listed in Table 2.

(Fig. S1). When dietary predictions are projected onto a ternary plot (Fig. 4; Fig. S2), we observed a high overlap between both model outputs in the ecospace where *Solanum* is the dominant item, but predicted diets diverge each other when the prevalence of *Solanum* is lower. Specifically, the diet of *S. erythromos* is biased toward other fruits plus *Piper*, whereas *S. lilium* is deflected toward *Piper* (Fig. 4; Fig. S2). Compositions of dietary profiles derived from our statistical models under combinations of latitude and altitude are available in Appendix S3.

DISCUSSION

We evaluated the spatial structure associated to diet data retrieved from 2 common, similar, and syntopic species of frugivorous bats belonging to the genus *Sturnira*. For that purpose, we defined statistical models for diets on the grounds of the independent variables latitude and altitude. Both species exhibited dietary changes throughout the space, although following a diverging pattern in the relative allocation of fruit resources. While both species increased the use of *Solanum* with altitude, only *S. erythromos* showed a meaningful altitudinal response concerning to the use of *Piper* and other fruits and displayed latitudinal differences in the use of *Solanum*, supporting in part our prediction 1 due to the differences between them (see above). Remarkably, altitude is highly correlated with climatic variables such as annual mean temperature, maximum temperature, and minimum temperature (see Sánchez and Giannini 2014), all of them able to shape the composition and floristic structure across the Yungas forests where 3 altitudinal districts can be recognized (Cabrera 1976; Brown et al. 2001). This suggests us that dietary changes could mirror changes in vegetal community (i.e., bats respond accordingly to the changes in the availability of their resources) shaped by the environmental gradients. For example, Giannini (1999) reported an altitudinal turnover pattern in the use of Solanaceae and Piperaceae performed by both *S. erythromos* and *S. lilium*. This finding was related with the concurring loss of Piperaceae and increasing diversity of Solanaceae at higher altitudes in 3 sites of NW Argentina. In a similar way, Sánchez et al. (2012b) found that the use of *Solanum*, *Piper*, and other fruits by *S. lilium* appeared to be coupled with diversity and density of these resources in both lowland and highland sites. Likewise, bats of the genus *Carollia* and *Phyllostomus* were sensitive to experimental relocations and offer of their preferred plant genera in other regions (Fleming et al. 1977; Kalko and Condon 1998; Andrade et al. 2013). Meanwhile, Saldaña-Vázquez et al. (2013) reported that ecoregion, latitude, and altitude affect the use of *Solanum* by *Sturnira* and the use of *Ficus-Cecropia* by *Artibeus*. Altogether, these lines of evidence indicate that phyllostomids are flexible and capable of tracking variations in the availability and diversity of fruits at different geographical scale; dietary changes operate mainly at the usage fraction of the core plant taxa; in other words, some of their core plants are always dominant in the diet and this dominance depends upon the spatial availability of them.

Table 2.—Results of Dirichlet regression analyses of diet composition versus latitude and altitude for both species of bats. Information about models include: β , beta coefficient for the intercept and each variable; Z , statistic; P , statistical significance. Significant responses are indicated with an asterisk.

	Statistic	<i>Sturnira erythromos</i>			<i>Sturnira lilium</i>		
		<i>Solanum</i>	<i>Piper</i>	Other fruits	<i>Solanum</i>	<i>Piper</i>	Other fruits
Intercept	β_0	-25.594	-15.989	-9.372	-0.008	5.181	1.160
	Z	-3.549	-2.311	-1.590	-0.002	1.170	0.338
	P	0.000*	0.021*	0.112	0.998	0.242	0.736
Latitude	β_1	-0.755	-0.416	-0.173	0.086	0.231	0.130
	Z	-3.182	-1.780	-0.832	0.523	1.203	0.888
	P	0.001*	0.075	0.405	0.601	0.229	0.375
Altitude	β_2	0.008	0.006	0.005	0.004	0.001	0.002
	Z	3.700	3.161	2.421	3.836	0.832	1.865
	P	0.000*	0.002*	0.015*	0.001*	0.405	0.062

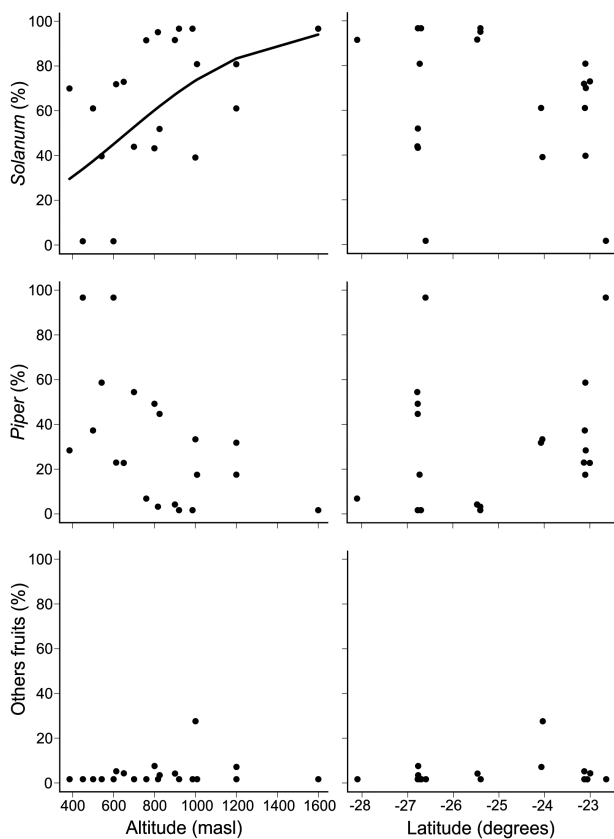


Fig. 3.—Scatterplots of the use of *Solanum*, *Piper*, and other fruits against 2 spatial sources of variability explored with the Dirichlet regression analysis for *Sturnira lilium*. Continuous regression lines indicate significant relationships at $\alpha = 0.05$. Full regression models listed in Table 2.

Predictions of diets, once projected onto the ternary plot, highlights interspecific differences between *S. erythromos* and *S. lilium* in the use of fruits. These differences come from a diverging pattern in the allocation of resources and are hard to be detected through pairwise comparisons such as those carried out with indices of niche overlap. Moreover, Sánchez (2011) and Sánchez et al. (2012a) detected a significant feeding niche overlap between these bats ranging from 69.0% to 99.0%. At a first glance, we could expect to find a complex competitive segregation scenario as those described

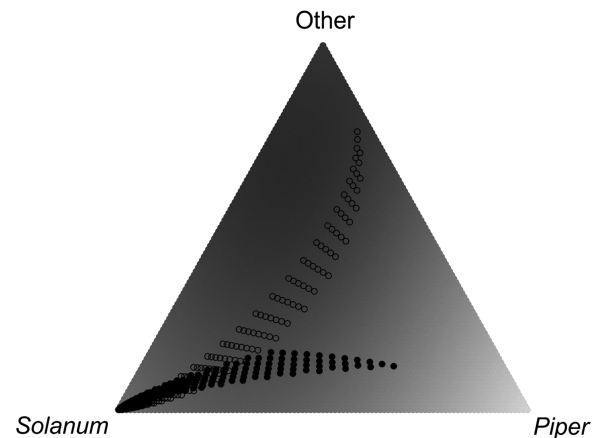


Fig. 4.—Ternary plot with predicted diets of *Sturnira erythromos* (open circles) and *S. lilium* (solid circles) for some input values taken as combinations of latitude and altitude within the range of interest. Leftmost, rightmost, and upper corners correspond, respectively, to the dietary items *Solanum*, *Piper*, and other fruits. Note the diverging pattern between diets.

for *Carollia perspicillata* and *C. castanea* or *Artibeus jamaicensis* and *A. obscurus* (e.g., Bonaccorso et al. 2006; Henry et al. 2007). However, patterns of captures and responses to geographic and environmental conditions for *S. erythromos* and *S. lilium* point to an autoecological model of spatial segregation acting at a regional scale instead of a scenario of mutual exclusion (Sánchez and Giannini 2014). These patterns may be driven by the physiological capacity of each bat to cope with different environmental conditions (see Soriano et al. 2002). Differences in the use of fruits can be also a consequence of physiological differences between bats. For example, Saldaña-Vázquez et al. (2015) found that the diversity and nutritional quality of the fruits used by *S. lilium* and *S. ludovici* depends on their digestive capacity. So, the diverging pattern observed in our diet models could be associated with differences in the digestive capacity of *S. erythromos* and *S. lilium*, supporting the hypothesis of spatial segregation among closely related frugivorous bats (Sánchez and Giannini 2014). These strategies of segregation may modify the seed dispersal patterns stressing the importance of understanding the geographical changes in diets to assess properly the

contribution of these bats to the ecosystem service of seed dispersal, a service of paramount importance in Neotropical rainforests (Howe and Smallwood 1982; Kunz et al. 2011). Lastly, diet predictions for *S. erythromos* indicate that other fruits are mainly eaten that *Piper* below the level of 600 masl. This prediction disagrees with the hypotheses about diets of *Sturnira* genus at continental scale (see Fleming 1986; Giannini and Kalko 2004; Sánchez et al. 2012a; Saldaña-Vázquez et al. 2013). This could result of biases in our models due to the scarce information in the altitudinal range from 400 to 600 masl (Fig. 2); in fact, the few samples for *S. erythromos* below the 600 masl indicate that *Piper* fruits are also consumed at lowland (see Table 1). An important task to perform at the near future is to validate our predictive models with a more complete data set of field observations. Effort should be concentrated in sites at lower altitude where dietary divergence starts to appear. This is an outstanding subject to understand better the kind of results issued by the models.

Compositional data, such as dietary profiles, can be encoded into arrays whose components represent percentages of a total. The quantitative peculiarity of these vectors is that they add to a constant. Consequently, the corresponding sample space is the simplex, a formal construct that is very distinct to the real Euclidean space associated with unconstrained data (Camargo et al. 2012). For that reason, statistical models specially conceived for compositional data should be implemented instead of applying statistical methods for unconstrained data; otherwise, misleading inferences can be derived (Aitchison 1982). Given a response variable conformed by the proportions of some whole, the Dirichlet regression constitutes a useful technique to model it in the presence of observed covariates and facilitates an alternative view about the structure of a composition (Hijazi and Jernigan 2009). Our manuscript represents the first attempt to assess changes of diet across space (more precisely, ecospace delimited by altitude and latitude) via Dirichlet regression. With this approach, we gain knowledge about the trophic behaviors of involved bats and we could perform an overall comparison between them after projecting predicted values of diet onto the simplex.

In conclusion, our study from Southern Yungas reveals spatial differences in the foraging patterns of frugivorous bats. We could detect here interspecific differences in the use of fruits, otherwise hardly to be detected through focal pairwise comparisons (i.e., centered at single localities). Predictive models suggest us to split the ecospace into 2 sectors matching, in turn, the highland and lowland portions of the Yungas. Despite depending on a narrow set of plant genera, these bats exhibit spatial variations in their pattern of relative fruit consumption. Dietary segregation arises at certain portions of the ecospace (jointly defined by latitude and altitude). This mechanism, in addition to others already proposed (see Fleming 1986; Giannini and Kalko 2004; Thies and Kalko 2004; Bonaccorso et al. 2006; Henry et al. 2007; Sánchez and Giannini 2014), may help to explain the coexistence of species in diverse assemblages of frugivorous bats.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (j mammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Fig. S1.—Predicted diets for *Sturnira erythromos* (a) and *S. lilium* (b) mapped onto the ecospace following the RGB color system.

Fig. S2.—Predicted diet compositions for *Sturnira erythromos* and *S. lilium*. Points correspond to predictions for some combinations of latitude and latitude, projected onto a colored ternary plot following the RGB color system.

Appendix S1.—Gazetteer of 20 localities studied in NW Argentina.

Appendix S2.—R scripts for diet predictions and graphical representations.

Appendix S3.—Dietary profiles (composition vectors) derived from predictive models for both frugivorous bats.

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