Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Trophic structure of frugivorous bats in the Neotropics: emergent patterns in evolutionary history

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Keywords
bat-plant interactions, bottom-up control, dietary specialisation, evolution, Phyllostomidae

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Submitted: 18 January 2017
Returned for revision: 20 March 2017
Revision accepted: 14 November 2017
Editor: DR

doi: 10.1111/mam.12116

ABSTRACT

1. Knowing the relative importance of phylogeny in dietary specialisation in frugivorous bats is key to understanding the ecological and evolutionary processes that drove their diversification and to elucidating the mechanisms allowing their coexistence in multispecific assemblages.
2. We evaluate the trophic structure of frugivorous phyllostomids using multiple data sets collected throughout the Neotropics. Then, we investigate the relationship between trophic and phylogenetic structure of phyllostomids, and evaluate the evolutionary mechanisms driving current resource partitioning in phyllostomid assemblages.
3. We compiled a data set of 14500 dietary records from 24 well-studied bat communities in the Neotropics. We recoded data at the plant genus level and composed two new data sets including tropical sites only, and tropical and subtropical sites pooled (i.e. including sites where diversity is significantly reduced). We performed multivariate analyses on both data sets and estimated phylogenetic effects on the dietary patterns.
4. Dietary structure in both data sets indicated that bat species remained faithful to their core plant taxa. A phylogenetic comparative method selected only a few basal clades from the entire phyllostomid tree that significantly explained the impact of evolutionary history on the observed multivariate patterns. These clades were dated to the middle Miocene, a period of particularly intense geological and environmental changes in the Neotropics. These clades were always younger than the core plant taxa with which they were strongly associated.
5. Accordingly, the core diet of phyllostomid bats has remained remarkably stable since at least the past 15 My (million years), suggesting a bottom-up control of the evolution of the bat-plant interactions in the Neotropics.

INTRODUCTION

Understanding spatial and temporal variations in the mutualistic interaction between frugivorous vertebrates and the plants they depend upon is key in ecology (Fleming 1986, Fleming & Kress 2011). Central to this interaction is the links between the trophic structure and the phylogenetic structure of frugivores, i.e. variations in their

use of resources at a temporal scale over thousands or millions of years. Estimating the relative importance of phylogeny in dietary specialisations of frugivores is key to unravelling the ecological and evolutionary processes that drove vertebrate diversification and, ultimately, to elucidating the mechanisms allowing the coexistence of species in diverse tropical assemblages. The New World leaf-nosed bats (Phyllostomidae) are suitable models for evaluating the relationship between trophic structure and evolutionary history because their phylogeny is well resolved (e.g. Baker et al. 2012, Dumont et al. 2012, Amador et al. In press, Rojas et al. 2016) and the diets of many lineages in the Neotropics are well known (see Lobova et al. 2009). Moreover, after birds, phyllostomids are the most important vertebrate pollinators and seed dispersers of many Neotropical plant species (at least 549 species in 191 genera; Lobova et al. 2009). The plant–animal mutualisms in which phyllostomids are major participants are key to ecosystem functioning, tropical succession, and the maintenance of tropical forest diversity (Muscarella & Fleming 2007).

From a phylogenetic perspective, Phyllostomidae last shared a common ancestor with its sister family Mormoopidae some 42–36 My (million years ago; stem age), and the divergence of the crown clade (extant phyllostomid subfamilies) seems to have occurred shortly thereafter (Teeling et al. 2005, Datzman et al. 2010, Rojas et al. 2011, 2012, Baker et al. 2012). Members of each subfamily specialised in one major resource type, suggesting an early origin of dietary specialisations in the evolution of this clade (Giannini & Kalko 2004). The oldest lineages are primarily insectivorous (Rojas et al. 2012), as are mormoopids and more external outgroups, which strongly suggests that all feeding strategies evolved from the feeding strategy of a basal insectivore (Baker et al. 2012). Nectarivory probably originated twice independently (Datzman et al. 2010), whereas specialised frugivory evolved just once in the ancestor of the most diverse lineage of phyllostomids, which comprises the Carolliinae, Glyphonycterinae, Rhinophyllinae and Stenodermatinae clades (some 98 species of bats or c. 49% of the species in the family; Simmons 2005, Datzman et al. 2010, Rojas et al. 2011, Baker et al. 2016). This specialisation does not compromise the use of other resources to complement the bats' diet or to survive in time periods when their preferred food is scarce (as stated explicitly by Fleming 1986). The high rate of diversification in frugivorous phyllostomids has been associated with: (1) the adaptive dietary shift to frugivory and the concomitant access to a superabundant resource (Dumont et al. 2012, Rojas et al. 2012); (2) biogeographic effects, including changes in geographical range size and the number of colonised ecoregions, and the differential evolution of island and mainland lineages (Rojas et al. 2012). Major orographic changes and their effects through vicariance and dispersal events may have been crucial for the evolution and current biodiversity patterns of the Amazonian biota in general (Hoorn et al. 2010a), as well as of particular groups, including several lineages of octodontid rodents (Uphan & Patterson 2012), plants, fish and amphibians, all of which underwent a high diversification rate in the Amazon during the Miocene (see Hoorn et al. 2010a). This biogeographical history of the Neotropical region is likely to have had a central role also in the evolution of phyllostomids. For instance, events such as the northern Andean uplift, the formation of the Panama Isthmus, and large-scale landscape changes that occurred during the Miocene and Early Pliocene in South America have been associated with the diversification of *Sturnira*, a Stenodermatinae group of Andean origin and currently the most speciose phyllostomid genus (Velazco & Patterson 2013).

From an ecological perspective, the trophic structure of phytophagous phyllostomids has been broadly studied over the past four decades, and dietary data for several Neotropical communities are available from the literature (e.g. Heithaus et al. 1975, Bonaccorso 1979, Fleming 1986, Palmeirim et al. 1989, Gorchov et al. 1995, Giannini 1999, Giannini & Kalko 2004, Lobova et al. 2009, Sánchez et al. 2012a). Three recent reviews, comprising a network analysis of dietary structure (Mello et al. 2011), a literature and experimental review of diet (Andrade et al. 2013), and a meta-analysis (Saldaña-Vázquez et al. 2013), have largely confirmed the close genus-to-genus relationship between bats and plants that was originally proposed by Fleming (1986) and that was extended by Giannini and Kalko (2004) to the phylogenetic structure of the group. These lines of evidence confirm a strong specialisation of Stenodermatini on fruits of Moraceae *sensu lato* (chiefly *Ficus* and *Cecropia*), of *Carollia* on *Piper* (Piperaceae), and of *Sturnira* on *Solanum* (Solanaceae) and *Piper*. Bat species in these genera consume other bat-dispersed fruits to a lesser extent, as they become seasonally available (e.g. Fleming 1986, Sánchez et al. 2012b), and they also include other resources in their diets, such as pollen, arthropods, leaves and mineral-rich collpa water (e.g. Heithaus et al. 1975, Kunz & Diaz 1995, Giannini 1999, Bravo et al. 2008). Giannini and Kalko (2004) and Sánchez et al. (2012a) detected a strong phylogenetic effect in the diets of species of frugivorous bat assemblages, which indicated a strong link between the evolutionary history of the bats and their trophic ecology. Giannini and Kalko (2004) proposed an evolutionary mechanism of dietary diversification of frugivorous phyllostomids, specifically a dietary shift and specialisation at certain ancestral nodes, followed by a relative stasis within derived clades. If this hypothesis

is correct, extant lineages should exhibit trophic structures that correspond with phylogenetic affinities, and the reconstructed ancestor of each clade should exhibit evidence of a dietary shift with respect to the immediately older nodes.

Some researchers have attempted to address these topics within a phylogenetic framework (e.g. Datzman et al. 2010, Rojas et al. 2011, Baker et al. 2012) or through an extensive analysis of the trophic structure of bats (Lobova et al. 2009, Mello et al. 2011, Andrade et al. 2013, Saldaña-Vázquez et al. 2013). However, a synthesis involving both evolutionary and ecological patterns remains elusive. Here, we dissect those patterns via an analysis that includes dietary information as well as evolutionary data from phytophagous phyllostomids. Specifically, the goals of our study were: (1) to determine the trophic structure of frugivorous phyllostomids at large geographical and temporal scales through a review of data from sites throughout the Neotropics, testing the relationship between the trophic and phylogenetic structures of phyllostomids, in order to assess the evolutionary mechanisms driving the current resource partitioning among them; (2) to assess the expected congruence between the geological age of bat clades and clades of their food plants, in order to explore the evolutionary mechanism underlying the plant–bat interaction (see Fleming & Kress 2011). Thus, we attempted to provide a wide spatiotemporal framework to analyse the evolution of these interactions. First, we chose a continental geographical scale and considered the main heterogeneity found at this level, i.e. the contrast in biodiversity between tropical and subtropical sites, the latter being replicated in the Northern and Southern hemispheres. Second, to help us interpret the pattern of frugivorous bat diversification, we considered the major landscape features and events that configured the evolutionary scenario of phyllostomid diversification. At this spatiotemporal scale, members of phyllostomid assemblages may have remained faithful to their phylogenetic roots and their original ecological adaptations (Prediction 1), or may have responded patchily to resource diversity and availability throughout the highly variable Neotropical landscape (Prediction 2). Sánchez et al. (2012a) showed that in the subtropics of Argentina, despite more limited fruit diversity than in tropical South America, phyllostomids from different genera retained consumption preferences for their respective core plant taxa, with few exceptions. We extend this analysis to 24 bat communities throughout the Neotropics, from Mexico to Argentina, and report new evidence linking the evolutionary history of bats with their dietary patterns, suggesting the mechanisms underlying the stability of fruit preferences at a specific taxonomic level for some 15 My.

METHODS

Data sets

We compiled 24 data sets from published studies on the diets of phyllostomid bats in 13 ecoregions of Central and South America (Fig. 1, Table 1). We summarised data from the literature dealing with community surveys of chiropteran frugivores and their food plants, both in tropical and subtropical forests (12 studies from each forest type; a list of data sources is available in Appendices S1 and S2). We focused on assemblage-level studies conducted for at least one year or one complete field season (comprising dry and wet periods), disregarding short-term studies and those focused on small subsets of phyllostomid assemblages. We used data sets that were built on records from mist-netting and faecal sampling at ground or subcanopy level; this method to obtain dietary data has been found to be useful for phyllostomid bats (e.g. Palmeirim et al. 1989, Gorchov et al. 1995). With this information, we generated two new data sets, one comprising data from the tropical region, located between latitudes c. 20° S and c. 17° N (hereafter "Tropics"), and the other comprising data from all 24 studies, i.e. including subtropical sites that are marginal areas in the distribution of many species (hereafter "Tropics and Subtropics"). Within this data set we separated a Tropical region, a Northern Subtropical region (data from Mexico), and a Southern Subtropical region (data from northern Argentina and southern Brazil). While somewhat arbitrary, the distinction between these three regions reflects compositional and diversity differences in their respective phyllostomid assemblages (see Ramos-Pereira & Palmeirim 2013).

Data sets were arranged in bat-by-item matrices, as follows. For each data set (Tropics or Tropics and Subtropics), the total list of bat species and food items reported in the studies were arranged in row and column sets, respectively. Dietary data were entered into the matrix cells once discrepancies between studies due to ecological differences in communities were resolved. We established a common comparative ordinal scale of originally quantitative dietary data. This approach was developed by Giannini and Kalko (2005) and is akin to the practice in macroecological research in which information from wide geographical and temporal scales is incorporated, at the expense of reducing the level of detail (see Brown 1999). Specifically, a new ordinal scale from 0 to 4 was defined for dietary data, in which 0 corresponded to a dietary item that was absent from records in the data sets; 1 to an item that was present in low percentages (10% or less of total diet); 2 to an item that was present in 10.1–25% of the total diet; 3 to an item that was present in 25.1–50% of the total diet; and 4 to an item that was present in 50.1% or more of the

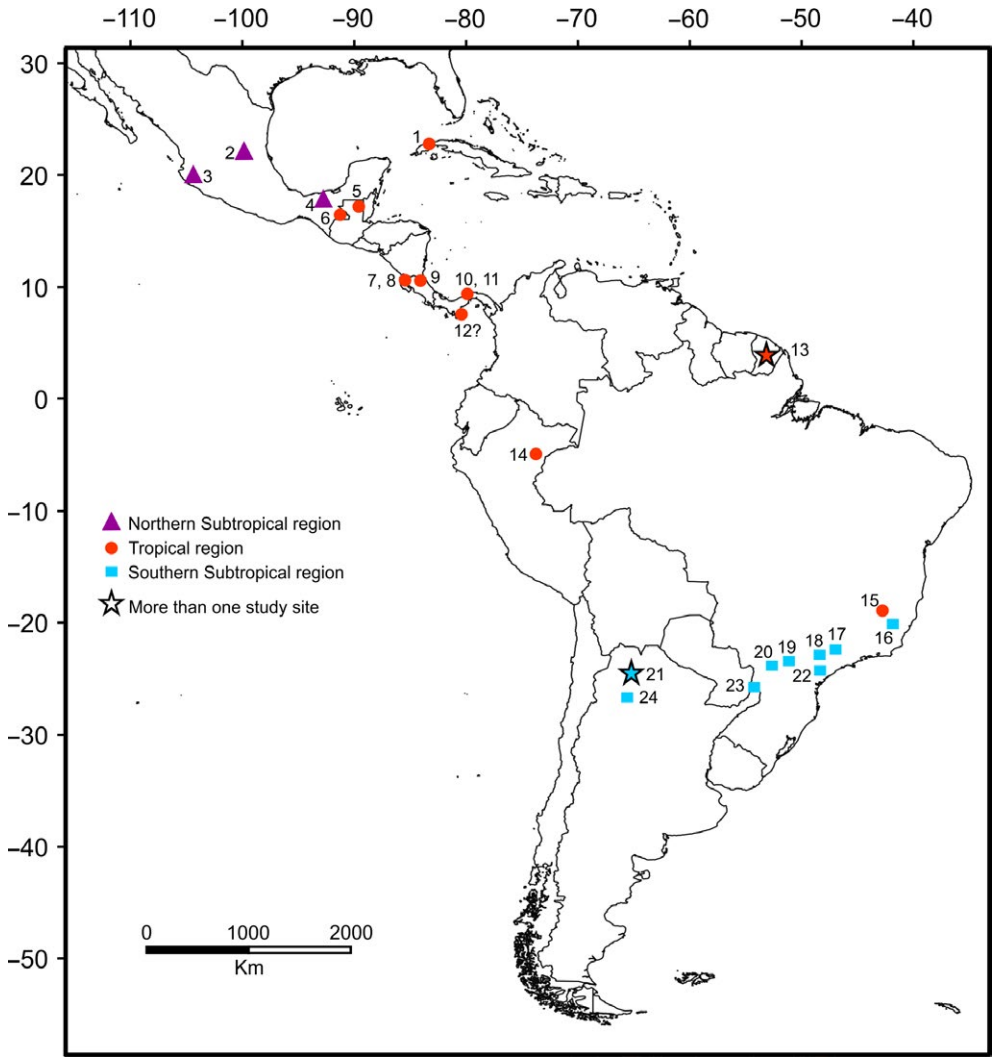

Fig. 1. Map of Central and South America, showing the locations of source studies (triangles, dots, squares and stars). All numbered study sites are listed with details in Table 1. Stars indicate locations of more than one study site close together. [Colour figure can be viewed at wileyonlinelibrary.com]

total diet. After recoding each data set, a consensus among studies was reached for each bat species and dietary item. Conflicts between data sets were resolved by calculating the mode value of the non-zero scores; if the dietary item was represented by only two values (e.g. 3 and 2), we scored it by assigning the code from the study with the greatest sample size. Because dietary profiles are vectors composed of percentages of disjointed categories that amount to 100%, it was not possible to apply the maximum score of 4 (frequency ≥50.1% of the diet) to more than one item for a given frugivorous species; this conflict was solved by assigning a value of 3 to all the dietary items that had a maximum score of 4 in more than one individual study. In our matrices, this procedure was applied only to 13 data entries out of 258 (or 5% in the Tropics) and 15 of 382 (or 4% in the Tropics and Subtropics; cells marked * in Appendices S1 and S2). We considered the following dietary items: pollen, arthropods, and genera of fruit plants; thus, in the latter category we pooled records of several different species. This decision was made to avoid signal deletion due to geographical turnover of plant species at a continental scale, therefore ensuring comparability in distant sites with few or no species in common, and because we only assessed the structure of the frugivorous part of the diet of all the bat species we included. In addition, the plant genus matches the taxonomic level at which the hypotheses of fruit selection were proposed (see Fleming 1986).

Focal bat species

We adopted the scientific nomenclature for species following Simmons (2005), but we recognised *Vampyriscus*

Table 1. Details of the study sites from which the data analysed in this study originated. Negative latitudes are south of the equator (all longitudes are west). Each site was assigned to an ecoregion of the World Wildlife Fund. Locality numbers match the geographic locations shown on the map (Fig. 1).

No.	Source	Country	Latitude	Longitude	Elevation (m a.s.l.)	Annual rainfall (mm)	Ecoregion
1	Mancina et al. (2007)	Cuba	22°52′	83°05′	140*	2208	Cuba moist forests
2	García-Morales et al. (2012)	Mexico	21°57′10.3″ *	99°33′43.2″ *	50–1500	700–1000	Veracruz moist forests
3	Hernández-Conrique et al. (1997)	Mexico	19°35′ 10.1″ *	104°16′ 27.3″ *	1950*		Trans-Mexican volcanic belt pine-oak forests
4	Castro-Luna and Galindo-González (2012)	Mexico	17°35′52.1″	92°27′3.4′	185	3500	Péten-Veracruz moist forests
5	Lou and Yurrita (2005)	Guatemala	17° 04′ 10″	89° 24′ 00″	247*	1500	Péten-Veracruz moist forests
6	Gonçalves da Silva et al. (2008)	Mexico	16°06′	90°56′	120		Péten-Veracruz moist forests
7	Fleming (1988)	Costa Rica	10°45′	85°30′	45	1617	Central American dry forests
8	Heithaus et al. (1975)	Costa Rica	10°27′2.1″ *	85°7′39.1″ *	43*	1562	Central American dry forests
9	Palmeirim et al. (1989)	Costa Rica	10°26′	83°59′	50	4000	Isthmian-Atlantic moist forests
10	Bonaccorso (1979)	Panama	9°09′	79°51′	148	2600	Isthmian-Atlantic moist forests
11	Giannini and Kalko (2004)	Panama	9°09′	79°51′	148	2600	Isthmian-Atlantic moist forests
12	Griscom et al. (2007)	Panama	7°15′30′?	80°00′15″?	?	1300	Panamanian dry forests
13	Lobova et al. (2009)	French Guiana	†	†	†	2417	Guiana moist forests
14	Gorchov et al. (1995)	Peru	–4°55′	73°45′	130	2521	Southwest Amazon moist forests
15	Tavares et al. (2007)	Brazil	–19°29′	42°28′	515	1478	Bahia interior forests
16	Aguiar and Marinho-Filho (2007)	Brazil	–19°50′	41°50′	628	1100	Bahia interior forests
17	Silveira et al. (2011)	Brazil	–22°22′	46°58′	600*	1062	Cerrado
18	De Carvalho (2008)	Brazil	–22°48′	48o24′	577	1300	Cerrado
19	Muller and dos Reis (1992)	Brazil	–23°23′30″	51°11′5″	700	1615	Alto Paraná Atlantic forests
20	Pinto and Filho (2006)	Brazil	–23°40′	52°38′	530		Alto Paraná Atlantic forests
21	Sánchez (2011)	Argentina	‡	‡	‡	‡	Southern Andean Yungas
22	Passos et al. (2003)	Brazil	–24°16′	48°24′	898	2000	Alto Paraná Atlantic forests
23	Sánchez et al. (2012a)	Argentina	–25°40′	54°27′	200	2000	Alto Paraná Atlantic forests
24	Giannini (1999)	Argentina	–26°47′	65°21′	600–1850	1200–1500	Southern Andean Yungas

*Geographic coordinates or elevation were not indicated in the original source, so they were estimated by using Google Earth software.
†More than three sampling sites pooled, see details in Lobova et al. (2009).
‡More than three sampling sites pooled, see details in Sánchez (2011).
?Geographic coordinates given in the source do not correspond with a land point.

and *Artibeus planirostris* as a valid genus and species, respectively, and treated *Dermanura* and *Artibeus* as synonyms (see Gardner 2007). Thus, we included the following species, arranged in subfamilies and tribes after Baker et al. (2016):

Lampronycteris brachyotis (Micronycterinae); *Phyllostomus discolor* and *Phyllostomus hastatus* (Phyllostominae: Phyllostomini); *Glossophaga commissarisi*, *Glossophaga soricina*, *Monophyllus redmani* (Glossophaginae: Glossophagini); *Brachyphylla nana* (Glossophaginae: Brachyphyllini:

Brachyphyllina); *Erophylla sezekorni*, *Phyllonycteris poeyi* (Glossophaginae: Brachyphyllini: Phyllonycterina); *Anoura caudifer* (Glossophaginae: Choeronycterini: Anourina); *Choeroniscus minor*, *Hylonycteris underwoodi* (Glossophaginae: Choeronycterini: Choeronycterina); *Carollia brevicauda*, *Carollia castanea*, *Carollia perspicillata*, *Carollia sowelli* and *Carollia subrufa* (Carolliinae); *Rhinophylla pumilio* (Rhinophyllinae); *Sturnira erythromos*, *Sturnira lilium*, *Sturnira ludovici*, *Sturnira oporaphilum* and *Sturnira tildae* (Stenodermatinae: Sturnirini); *Chiroderma trinitatum*, *Chiroderma villosum*, *Platyrrhinus helleri*, *Platyrrhinus lineatus, Platyrrhinus recifinus*, *Uroderma bilobatum*, *Vampyressa pusilla*, *Vampyressa thyone*, *Vampyriscus nymphaea* and *Vampyrodes caraccioli* (Stenodermatinae: Stenodermatini: Vampyressina); *Artibeus concolor*, *Artibeus fimbriatus*, *Artibeus gnomus*, *Artibeus jamaicensis*, *Artibeus intermedius*, *Artibeus lituratus*, *Artibeus obscurus*, *Artibeus phaeotis*, *Artibeus planirostris*, *Artibeus toltecus*, *Artibeus watsoni* (Stenodermatinae: Stenodermatini: Artibeina); *Centurio senex*, *Pygoderma bilabiatum* and *Phyllops falcatus* (Stenodermatinae: Stenodermatina).

Statistical analysis

We used Correspondence Analysis (CA) to analyse the recoded matrices Tropics or Tropics and Subtropics (hereafter "CA 1″ and "CA 2", respectively). CA generates a simultaneous ordination of row and column elements (bats and food items) of the dietary matrix. This multivariate technique is appropriate for frequency data treated as proportions or percentages, with many zeroes (see ter Braak 1995). We used CA ordination diagrams to identify dietary structure in the form of trophic groups or gradients of bats. From the joint plots of bat-dietary items, we draw conclusions regarding structural patterns among bats (i.e. the presence and composition of either groups or gradients of bat species), and the plants that were associated with each bat's dietary structure. We assessed the fit of bat and plant genus as the cumulative fraction of variance of species accounted for by the axes chosen for interpretation; fit was represented graphically by circles of proportional size (the greater the circle, the better the fit; Figs 2 and 3 and Appendix S4). In CA 2, for bats occurring in both tropical and subtropical regions, individual species with dietary data from more than one region were represented by more than one row in the matrix. For instance, *Sturnira lilium* was represented by three rows corresponding with the dietary data of the species in the Northern Subtropics, the Tropics, and the Southern Subtropics. All the species and their regional subdivisions were included in the same analysis. Species were connected with arrows, which represented the dietary shift from tropical to subtropical regions, as depicted in multivariate space (see Fig. 4).

We subjected our data to a Detrended Correspondence Analysis in order to detect the presence of the arch effect, which is known to affect CA ordinations occasionally (see ter Braak & Šmilauer 2002). Detrending was carried out using fourth-order polynomials. All multivariate analyses were done using CANOCO 4.5 (ter Braak & Šmilauer 2002) with down-weighting of rare species and symmetrical bi-plot scaling.

We estimated phylogenetic effects on present-day dietary patterns using Canonical Phylogenetic Ordination (Giannini 2003), a phylogenetic comparative method derived from linear regression models and canonical ordinations (Giannini 2003). This method uses the nested set of clades to which the taxa of the main matrix belongs as an external matrix. In this setting, Canonical Phylogenetic Ordination is a CA controlled by phylogeny. The main matrices were the same as in CA 1 and 2, whereas the external matrix consisted of a set of binary variables coding clade membership for each species (the 'tree matrix'). We used the phylogenetic tree from Rojas et al. (2016) as a reference to construct our tree matrix, which was pruned to include only the phytophagous bats included in CA 1 and 2 (see Figs 5 and 6). To build a tree that included CA 2, we added a terminal branch for tropical and subtropical populations in a node that represented a polytomy. These nodes were not considered in the analyses and they were not named in Fig. 6. Clade significance ($\alpha \leq 0.01$) was assessed individually using 9999 unrestricted Monte Carlo permutations. A forward stepwise selection of clades from the tree matrix was performed to obtain a reduced tree matrix that explained the share of dietary variation in evolutionary history to the maximum possible extent without redundancy (see Giannini 2003).

RESULTS

The compilation of our data set resulted in 14500 dietary records reported from studies of phyllostomid assemblages throughout the Neotropics, and included 47 species of phytophagous bats with fruit consumption records from 63 plant genera. From this list, we excluded nine species from the analyses (*Brachyphylla nana, Centurio senex, Erophylla sezekorni, Pygoderma bilabiatum, Platyrrhinus recifinus*, *Choeroniscus minor*, *Phyllops falcatus*, *Anoura caudifer* and *Hylonycteris underwoodi*) due to their small sample size (N = 3, 4, 1, 1, 1, 6, 5, 4 and 2, respectively) and their behaviour as outliers. *Artibeus concolor* was also excluded because the available dietary samples were unidentified. Three additional species were excluded due to their lack of frugivorous dietary records in the communities we analysed (*Lampronycteris brachyotis*, *Monophyllus redmani* and *Phyllonycteris poeyi*). All these species were removed

together with their exclusive food items. The final data set included 34 phyllostomid species and their diets.

For analysis in the CA 1, the data matrix comprised 49 dietary items (47 plant genera, pollen and arthropods) and 26 phytophagous bats (Appendix S1), whereas in the CA 2 the data set contained 62 items (60 plant genera, pollen and arthropods) and 34 phytophagous bats (Appendix S2).

Tropics

In the Tropics, the first two CA 1 axes explained c. 28% of the total variation in bat diet (c. 46% in the first four axes; Table 2). Considering the best-fitted bat species, the plane of CA Axes 1 and 2 defined a dietary structure with a gradient: bats eating *Solanum, Piper* and other plants (such as *Philodendron*, *Vismia* and *Evodianthus*) dominated the positive side of Axis 1, and bats eating a high percentage of Moraceae (*Ficus*, *Cecropia* and *Maclura*) and *Muntingia* were located toward the negative side of Axis 1 (Fig. 2). Axis 2 was mainly a pollen-vs.-fruit axis, due to the fit of *Phyllostomus discolor* on the positive side of the axis. *Glossophaga* species and some Stenodermatini that also consume some pollen (e.g. *Artibeus jamaicensis* and *Artibeus phaeotis*) were also located near this resource in the ordination diagram. In this plane, *Piper* took a central position (Fig. 2). The species on the positive end of Axis 1 were *Sturnira tildae* (which exhibited a low level of *Piper* consumption at c. 10%) and *Rhinophylla pumilio*; together they were the main consumers of *Philodendron* (35% and 26% of the diet, respectively; Appendix S1). *Carollia subrufa* and *Sturnira tildae* defined the positive variation along Axis 3; also, the genera *Piper*, *Solanum* and *Muntingia* were located on the positive side of the axis (Fig. 3). By contrast, another species of *Carollia* (*Carollia perspicillata*) was a more generalist frugivore that

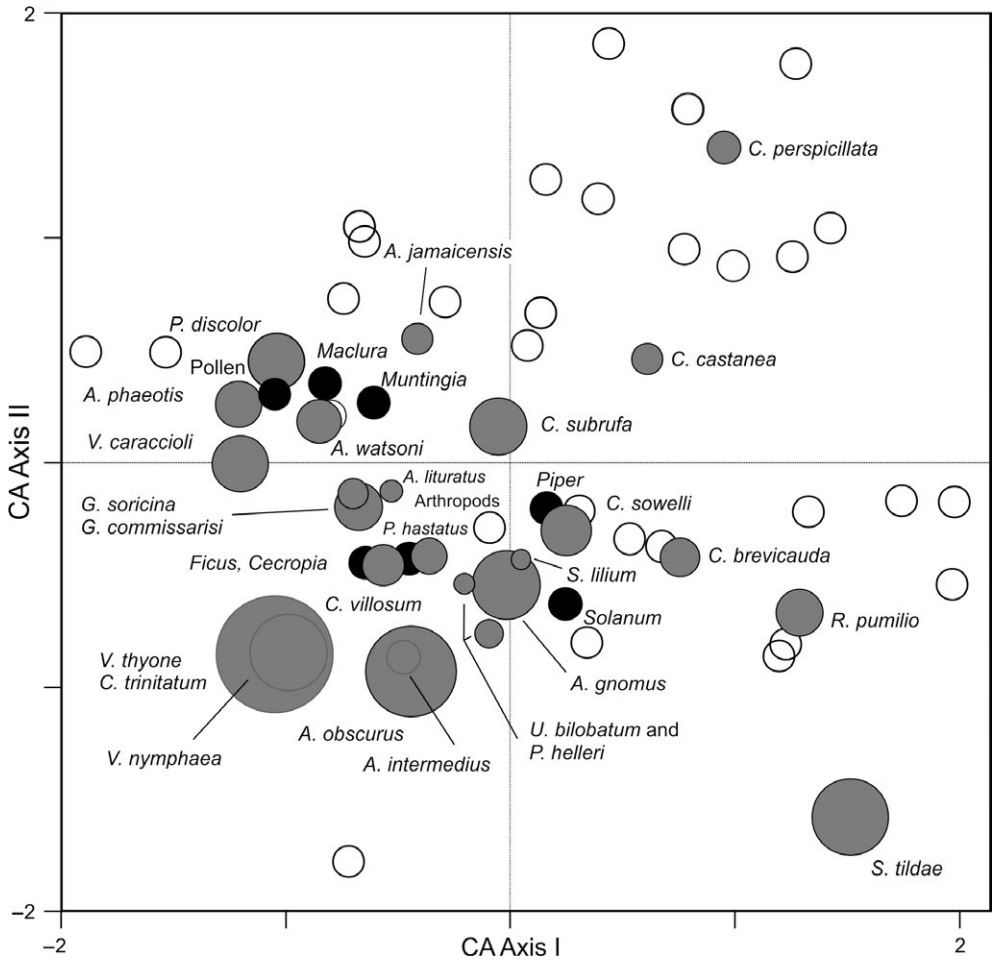

Fig. 2. Ordination diagram of the first and second axes of Correspondence Analysis based on the Tropics data set. Bat species are represented by solid grey circles; the size of each circle is proportional to the fit of bat species in the plane of the CA axes. Dietary items are indicated in named black circles (items that scored 3 or 4 in bat diets) or unnamed open circles (items that sored 0 to 2 in bat diets).

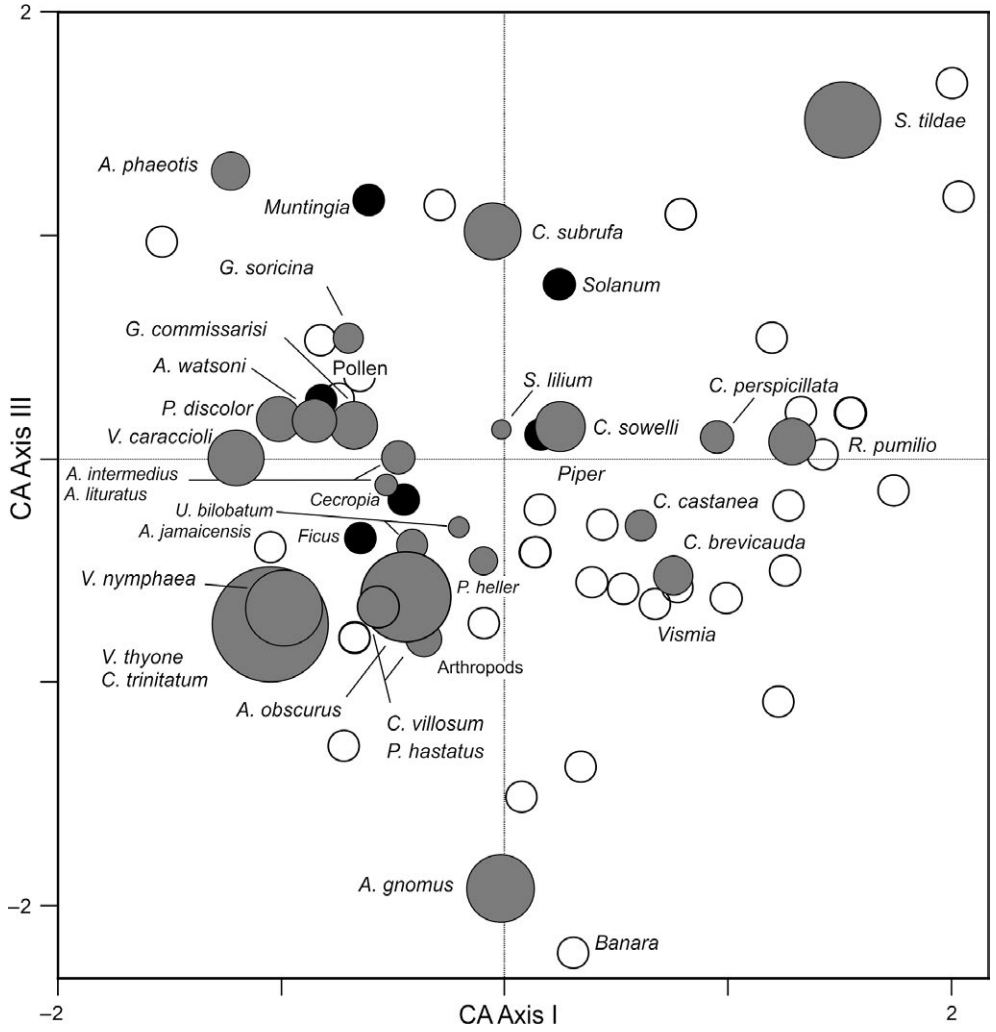

Fig. 3. Ordination diagram of the first and third axes of Correspondence Analysis based on the Tropics data set. Bat species are represented by solid grey circles; the size of each circle is proportional to the fit of bat species in the plane of the CA Axes. Dietary items are indicated in named black circles (items that scored 3 or 4 in bat diets) or unnamed open circles (items that sored 0 to 2 in bat diets).

used many other plant genera in addition to *Piper*; in this data set, the following genera were consumed exclusively by *Carollia perspicillata*: *Acacia*, *Eugenia*, *Gustavia*, *Henriettea*, *Phytolacca*, *Potalia*, *Rollinia* and *Carludovica*. The negative side of Axis 3 was defined by the high fit of *Artibeus gnomus,* which ate a high percentage of *Banara* (Fig. 3, Appendix S1). A separation of the consumers of *Piper* and *Solanum* (species of *Carollia*, *Rhinophylla* and *Sturnira*) was evident toward the positive quadrant in the plane of Axes 1 and 3 (Fig. 3). Genera of Stenodermatini clustered around the consumption of *Ficus*, *Cecropia*, *Maclura* and pollen, and were joined by eclectic plant-eating bats (*Phyllostomus* and *Glossophaga*). Regarding plants, genera exhibited a good fit to the ordination planes, especially those that were key to each group of frugivores (Appendix S4).

Tropics and subtropics

We subjected the Tropics and Subtropics data set to a Detrended Correspondence Analysis to assess possible arch effects in the CA 2 analysis. However, both the diagram and eigenvalues were similar to those in CA 2 (see Fig. 4, Appendices S3 and S5); therefore, we discarded this effect and report here results from CA.

In CA 2, the first two axes explained 21% of total variation in the diet (c. 35% for the first four axes; Table 2). The first two axes displayed a subtle gradient from bats with data from just the Tropics to bats with data from the Northern and Southern Subtropics (Fig. 4). Thus, this axis represented the variation in diet between Tropical and Subtropical regions, associated with botanical composition changes. Among the arrows linking points of species with

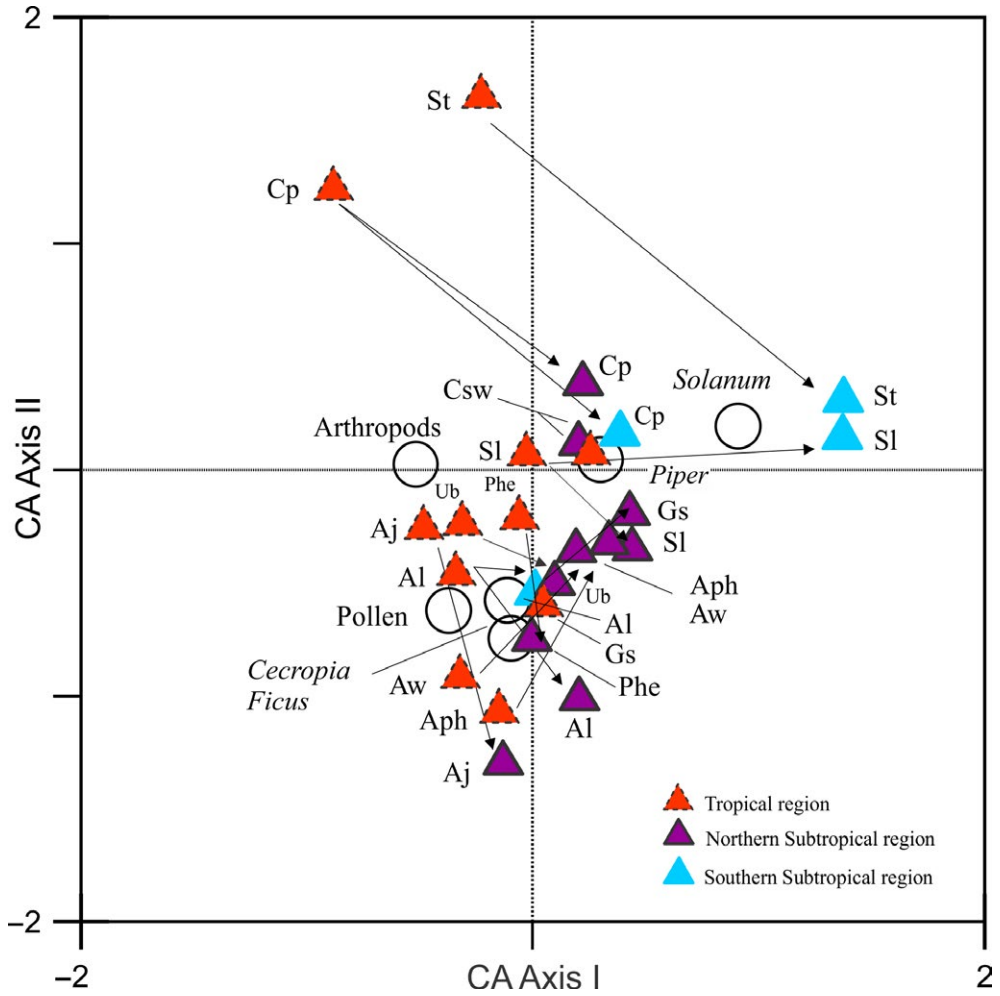

Fig. 4. Ordination diagram of Correspondence Analysis for the Tropics and Subtropics data set. Dietary items are represented by open circles and bat species by triangles. Only bats found in all three regions are included in the figure. Arrows represent the dietary shift from tropical to subtropical regions. Abbreviations for bat species: Aj, *Artibeus jamaicensis*; Al, *Artibeus lituratus*; Aw, *Artibeus watsoni*; Aph, *Artibeus phaeotis*; Cp, *Carollia perspicillata*; Csw, *Carollia sowelli*; Gs, *Glossophaga soricina*; Phe, *Platyrrhinus helleri*; Sl, *Sturnira lilium*; St, *Sturnira tildae*; Ub, *Uroderma bilobatum*. [Colour figure can be viewed at wileyonlinelibrary.com]

both Tropical and Subtropical distributions, those of *Carollia perspicillata* and *Sturnira tildae* were the longest and depicted a major change in diet between regions. These two bats exhibited broad diets in the Tropics and this diagram revealed both a dietary shift from Tropical to Subtropical regions and a strong decrease in fruit diversity. Likewise, another common species, *Sturnira lilium*, showed an increase in its use of *Solanum* fruits in Subtropical regions; its Tropical diet was dominated by *Piper*. *Glossophaga soricina* showed a decrease in its use of pollen and an increase in its consumption of fruits such as *Piper*, *Cecropia* or *Muntingia* toward Subtropical regions (Fig. 4; Appendix S2). Arrows in Stenodermatini tended to be shorter, indicating that these bats were less flexible and exhibited little change in their use of fruits between regions (Fig. 4). Overall, most arrows indicate a shift in diet from Tropical to Subtropical regions, towards the positive side of Axis 1, indicating a shift towards the consumption of certain key plants, particularly *Solanum*.

Evolutionary patterns

Only six clades were individually significant at $\alpha \leq 0.01$ for the Tropical data set (Table 3), all of which were important to explain dietary patterns (see below). After selection of clades, the reduced tree matrix resulted in a model of five clades that together explained, without redundancy, 48% of the dietary variation ($F = 1.97$, $P = 0.0087$; Table 3). The model successively incorporated the clade Stenodermatini (marked 39 in Fig. 5), followed by the basal unranked clade Nullicauda (clade 31); the next clade up the tree, *Artibeus watsoni* and *Artibeus phaeotis* (clade 48); Carolliinae (clade 32); and

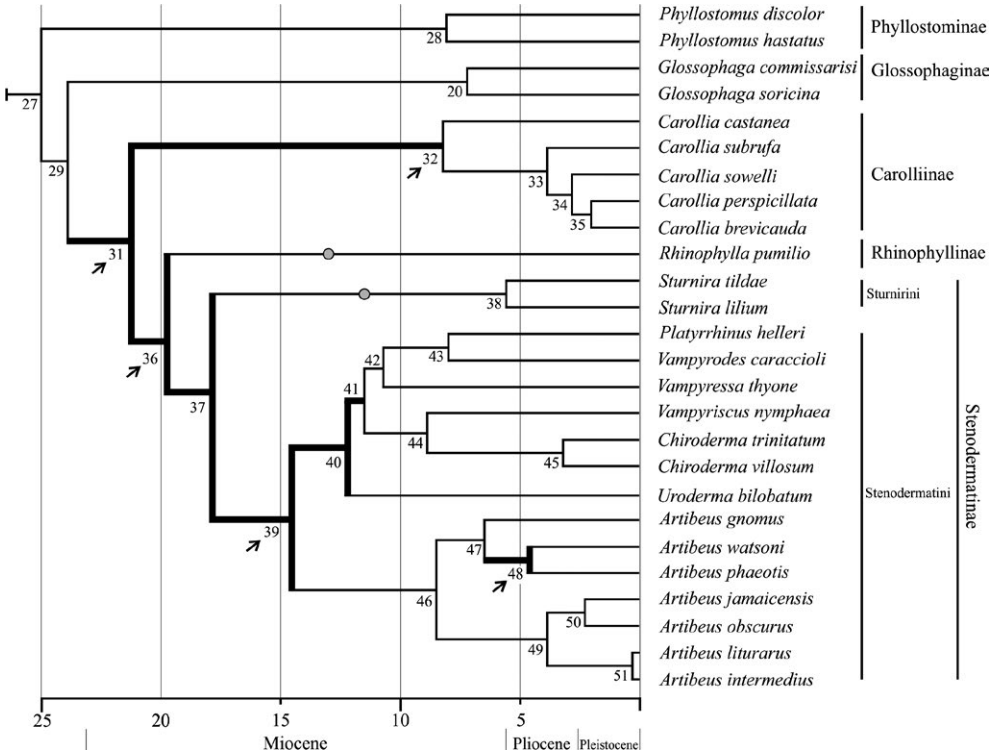

Fig. 5. Cladogram of Neotropical phyllostomid bats, based on Rojas et al. (2016). This pruned tree includes only those phytophagous bats included in CA 1. The origins of Rhinophyllinae and Sturnirini clades are indicated with solid grey circles.

finally the clades Rhinophyllinae and Stenodermatinae (clade 36 in Fig. 5).

In the Tropics and Subtropics data set, 12 clades were individually significant at $\alpha \leq 0.01$ and selection of clades via forward stepwise selection retained only three clades in the model (Table 3): Stenodermatini (marked 51 in Fig. 6), Nullicauda (clade 40) and Stenodermatinae (clade 46), which together explained 29% of the total dietary variation ($F = 2.66$, $P = 0.0001$; Table 3).

DISCUSSION

The tropical pattern of bat frugivory

Using a data set of over 14500 dietary records, we evaluated the trophic structure in frugivorous phyllostomids in the Tropical and Subtropical regions with the expectation (Prediction 1) that bat species would remain faithful to their original core resources (Fleming 1986, Giannini & Kalko 2004, Mello et al. 2011, Andrade et al. 2013, Saldaña-Vázquez et al. 2013). Alternatively, we postulate that bats could respond patchily to resource diversity and availability throughout the highly variable Neotropical landscape (Prediction 2). In the data set from the Tropical region, the trophic structure of phyllostomid bats showed gradients of species with two main trends: (1) bats that consume mainly *Solanum* and *Piper* vs. bats that eat Moraceae *sensu lato* (*Ficus*, *Maclura* and *Cecropia*) most frequently; and (2) bats that consume a high percentage of pollen compared to fruits (Fig. 2). In the plane of Axes 1 and 3, the *Piper* and *Solanum* specialists (Carolliinae and Sturnirini) were clearly separated from Moraceae-eating bats (Stenodermatini) as well as from eclectic plant-eating bats (Glossophaginae and Phyllostominae; Fig. 3). Thus, at the macro-geographical scale, tropical phyllostomid assemblages exhibited a trophic structure consisting of bat species groups strongly linked to specific plant resources. This supports our Prediction 1 and agrees with current hypotheses stating that bat species groups specialise in specific core plant taxa (Fleming 1986, Giannini & Kalko 2004), also called genus-to-genus specialisation in recent reviews (Mello et al. 2011, Andrade et al. 2013, Saldaña-Vázquez et al. 2013). A few plant genera accounted for a high proportion of records in our data set: only four and five plant genera scored values of 25.1–50% and <50.1%, respectively (Appendix S1). Nevertheless, less frequently eaten plant genera seemed to have important roles in the diets of some bat species. For instance, *Acacia*, *Eugenia*, *Gustavia*, and *Carludovica* were relatively infrequently found in the diets of bats (always scoring values <10% in the Tropical data set; Appendix S1), but as a

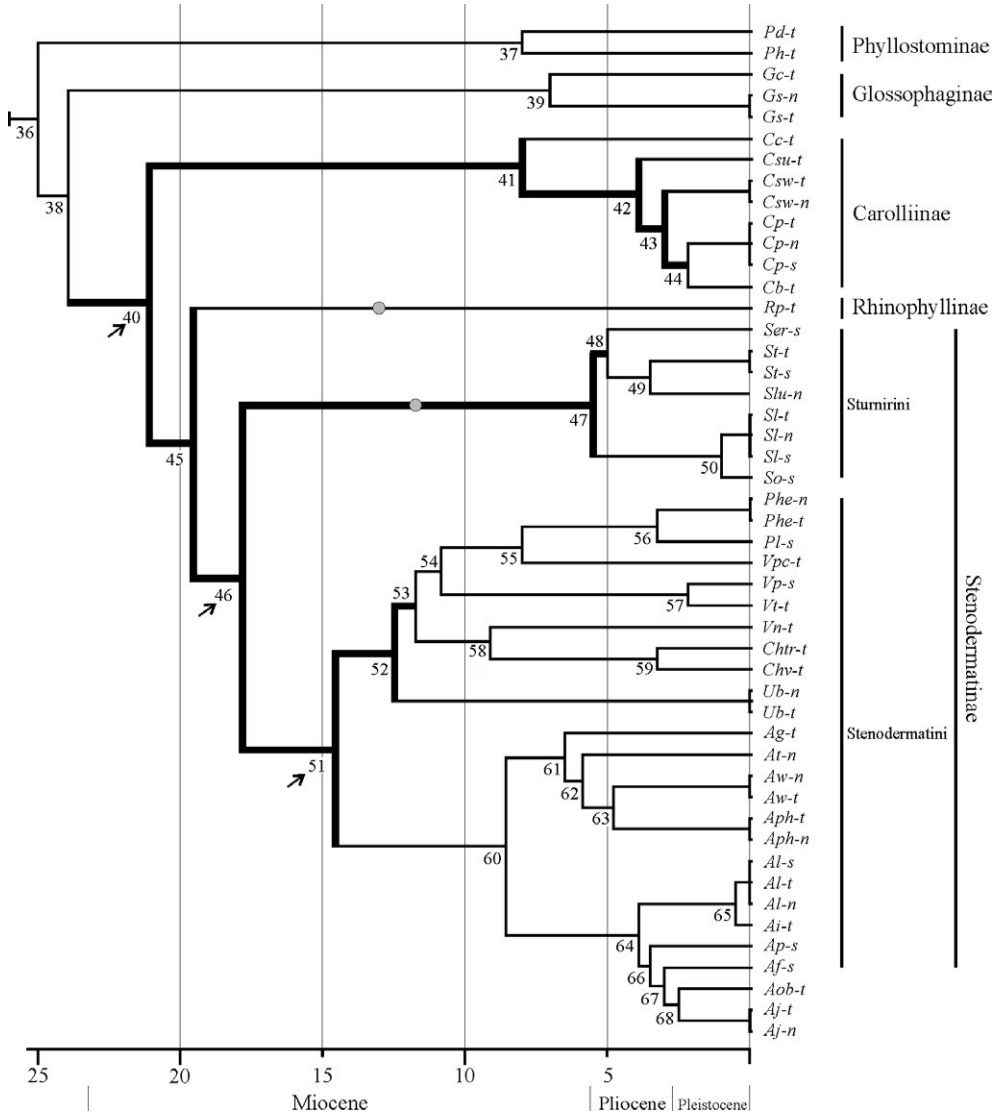

Fig. 6. Cladogram of Neotropical phyllostomid bats, based on Rojas et al. (2016). This pruned tree includes only those phytophagous bats included in CA 2. The origins of Rhinophyllinae and Sturnirini clades are indicated with grey solid circles. Polytomies are not numbered. Abbreviations for regions: -n, Northern Subtropical region; -s, Southern Subtropical region; -t, Tropical region. Abbreviations for bat species: Af, *Artibeus fimbriatus*; Ag, *Artibeus gnomus*; Aj, *Artibeus jamaicensis*; Ai, *Artibeus intermedius*; Al, *Artibeus lituratus*; Aob, *Artibeus obscurus*; Aph, *Artibeus phaeotis*; Ap, *Artibeus planirostris*; At, *Artibeus toltecus*; Aw, *Artibeus watsoni*; Cb, *Carollia brevicauda*; Cc, *Carollia castanea*; Cp, *Carollia perspicillata*; Csu, *Carollia subrufa*; Csw, *Carollia sowelli*; Chtr, *Chiroderma trinitatum*; Chv, *Chiroderma villosum*; Gc, *Glossophaga commissarisi*; Gs, *Glossophaga soricina*; Pd, *Phyllostomus discolor*; Ph, *Phyllostomus hastatus*; Phe, *Platyrrhinus helleri*; Pl, *Platyrrhinus lineatus*; Rp, *Rhinophylla pumilio*; Ser, *Sturnira erythromos*; Sl, *Sturnira lilium*; Slu, *Sturnira ludovici*; So, *Sturnira oporaphilum*; St, *Sturnira tildae*; Ub, *Uroderma bilobatum*; Vn, *Vampyriscus nymphaea*; Vp, *Vampyressa pusilla*; Vt, *Vampyressa thyone;* Vpc, *Vampyrodes caraccioli*.

group they characterised the diet of *Carollia perspicillata* (a relative generalist) and differentiated it from the diet of the relative *Piper* specialists *Carollia subrufa* and *Carollia sowelli* (see Thies & Kalko 2004, Andrade et al. 2013). In addition, *Rhodospatha*, *Thoracocarpus*, and *Philodendron* helped to differentiate the diet of *Sturnira tildae* from that of *Sturnira lilium* (two syntopic and similar lowland forest bats; see Velazco & Patterson 2013). Furthermore, *Rhinophylla pumilio* consumed a high percentage of *Philodendron* and, to a lesser extent, fruits of *Evodianthus* and *Anthurium* (spikes of Araceae), which differentiated its diet from that of *Carollia* (specialised on spikes of *Piper*). Both bat genera are highly similar in morphology and size, and are syntopic in most Neotropical forests (see Gardner 2007). *Philodendron, Evodianthus* and *Anthurium* are root-climbing vines that colonise rocks or,

Table 2. Results of Correspondence Analysis for the Tropics data set (CA 1) and the Tropics and Subtropics data set (CA 2). The corresponding eigenvalues, percentage of total variation per axis and cumulative percentage of successive axes are indicated. Inertia of matrix was Σ λi = 2.37 in CA 1 and Σ λi = 3.90 in CA 2.

	CA 1 Axis				CA 2 Axis			
Eigenvalues	1	2	3	4	1	2	3	4
λ_i	0.38	0.27	0.23	0.20	0.44	0.38	0.28	0.25
%	16.0	11.6	9.7	8.6	11.2	9.8	7.2	6.4
% cum	16.0	27.6	37.3	45.9	11.2	21.0	28.2	34.6

Table 3. Results of Canonical Phylogenetic Ordination for both bat dietary data sets. Significant *P*-values for each clade at $\alpha \leq 0.01$ are indicated in bold; *F*, statistic value of permutations test; V%, percentage variance. Numbers with asterisks represent groups that are integrated in the optimal model (after forward stepwise selection of variables). As this table shows two trees, a dash indicates inapplicable data because the clades are not included in the tree. Clades are numbered as in Figs 5 and 6, respectively.

	Tropics				Tropics and Subtropics			
Test	Clade	*F*	*P*	V%	Clade	*F*	*P*	V%
Individual	39	2.90	**0.0001**	15.2	51	3.63	**0.0001**	11.9
	32	2.62	**0.0006**	13.8	41	3.08	**0.0002**	10.2
	37	2.30	**0.0009**	12.4	46	3.02	**0.0001**	10.0
	41	2.17	**0.0024**	11.7	45	2.64	**0.0008**	8.8
	40	2.05	**0.0044**	11.1	47	2.51	**0.0015**	8.4
	31	2.03	**0.0128**	11.0	53	2.44	**0.0008**	8.2
	36	2.02	0.0760	11.0	43	2.40	**0.0050**	8.1
	33	1.94	0.0181	10.6	42	2.37	**0.0027**	8.0
	35	1.94	0.0179	10.6	52	2.33	**0.0012**	7.8
	48	1.91	0.0296	10.4	44	2.30	**0.0071**	7.8
	34	1.86	0.0200	10.1	48	2.18	**0.0101**	7.4
	47	1.53	0.0787	8.5	40	2.17	**0.0100**	7.3
	44	1.52	0.0788	8.4	37	1.65	0.0783	5.7
	30	1.43	0.1354	8.0	38	1.65	0.0725	5.7
	38	1.41	0.1262	7.8	60	1.62	0.0348	5.5
	46	1.36	0.1208	7.5	49	1.60	0.0809	5.5
	28	1.28	0.2018	7.1	63	1.53	0.0826	5.2
	29	1.28	0.1910	7.1	39	1.43	0.1266	4.9
	45	1.00	0.4447	5.6	62	1.40	0.1203	4.8
	42	0.95	0.5000	5.4	58	1.37	0.1617	4.7
	49	0.87	0.5910	5.0	57	1.35	0.1842	4.6
	50	0.86	0.5563	4.9	54	1.29	0.1549	4.4
	43	0.66	0.8195	3.8	64	1.27	0.1681	4.4
	51	0.58	0.8854	3.3	61	1.21	0.2122	4.2
	—	—	—	—	68	1.22	0.2564	4.2
	—	—	—	—	50	1.14	0.2992	3.9
	—	—	—	—	67	1.09	0.3356	3.8
	—	—	—	—	65	0.99	0.4268	3.5
	—	—	—	—	66	0.96	0.4677	3.3
	—	—	—	—	59	0.93	0.4992	3.2
	—	—	—	—	56	0.74	0.7453	2.6
	—	—	—	—	55	0.73	0.7800	2.5
Forward stepwise	39*, 31*	2.89	0.0001	29.2	51*, 40*	2.91	0.0005	21.1
	39*, 31*, 48*	2.08	0.1240	38.9	51*, 40*, 46*	2.66	0.0001	29.2
	39*, 31*, 48*, 32*, 36*	1.97	0.0087	47.6				

more frequently, tree trunks in the rainforest understory (Cockle 2001), whereas *Piper* species are mainly shrubs, herbs, or treelets that inhabit the understory (Jaramillo et al. 2008). These plant characteristics suggest a spatial segregation in feeding between the clades Rhinophyllinae and Carolliinae, which are successive branches in the phyllostomid tree, driven by the use of spikes of root-climbing vines vs. spikes of understory shrubs, herbs, or treelets, respectively. So, changes in dietary composition with respect to the core diet in *Carollia perspicillata*, *Rhinophylla pumilio* and *Sturnira tildae* can be interpreted as evidence of a mechanism of dietary or spatial segregation.

The subtropical dietary shift

Climate, and especially temperature, plays a strong role in governing tropical forest diversity, affecting within-clade diversity and intrafamily abundance and richness (Punyasena et al. 2008); due to this, plant diversity drops dramatically outside the tropical belt worldwide (Lomolino et al. 2010). This critically affects resource availability for fruit-eating bats (e.g. Giannini 1999). Previous researchers (e.g. Giannini 1999, Sánchez et al. 2012a) reported the diet of phyllostomid bats from a few subtropical sites. This study provides a unique opportunity to test the evolutionary response of phyllostomids to a low-diversity spectrum of fruits, as well as the plasticity of their preferences as specialists, with data from many independent sites in both the Northern and Southern Subtropics. We showed that different bat species exhibited distinct responses to the strong decrease in fruit diversity in Subtropical regions. The dietary diversity of members of the Carolliinae and Sturnirini clades was reduced, whereas their use of their core plant genera, especially *Solanum* in the case of *Sturnira,* was intensified. This trend was apparent in the ordination diagram in the form of long arrows departing from *Carollia perspicillata*, *Sturnira tildae* and *Sturnira lilium* sampled in tropical sites, toward their subtropical conspecifics with a more restricted diet. These species converged in dietary space in their increased use of *Solanum* (Fig. 4). By contrast, Stenodermatini species showed only modest changes in their diets, as shown by short arrows in the ordination space (Fig. 4). Finally, *Glossophaga soricina* showed a pronounced decrease in the percentage of pollen it consumed and a concomitant increase in its use of fruits, towards the Subtropics (Fig. 4). Species from both Northern and Southern Subtropical regions converged in the same dietary trends or directions over space, indicating a particular dominance of *Solanum* (an Andean-centred plant genus; D'Arcy 1991) and a decrease in the use of tropical resources as they disappear toward both the Northern and Southern Subtropical regions (e.g. Hernández-Conrique et al. 1997, Giannini 1999, Sánchez et al. 2012a). Saldaña-Vázquez et al. (2013) also found an association between Southern and Northern Subtropical ecoregions (e.g. Yungas or Pine-oak) and an increase in the use of *Solanum* by *Sturnira* bats, indicating the dominance of this bat-fruit system that is replicated in the Subtropical regions of both hemispheres. Pollen seems to be a less important resource in the Subtropics than in the Tropics, where it represented 10–50% of the diets of many different species of primarily frugivorous bats (e.g. Heithaus et al. 1975, see Appendix S2). In fact, pollen was recorded just once in the diets of obligate frugivorous bats in each of the Southern Subtropical region (Argentina; Giannini 1999) and the Northern Subtropical region (Mexico; Flores-Martínez et al. 1999).

The response of Stenodermatini to decreased resources toward the Subtropics was more evident at the level of their diversity (fewer bat species present) than in the intensity of their dietary shifts (short arrows in Fig. 4). A few examples of rather generalist species, such as *Artibeus planirostris,* a common bat in subtropical sites of in northwestern Argentina, where *Ficus* and *Cecropia* are missing, and where it ate fruits from Celtidaceae, Solanaceae, Piperaceae and Urticaceae (see Sánchez et al. 2012b). As a consequence, *Artibeus planirostris* represented the exception in this tropical-centred group specialised in fruits of *Ficus* and *Cecropia* (Fleming 1986, Giannini & Kalko 2004).

Evolutionary patterns

The trophic structure described in the preceding sections was statistically associated with major clades of the phyllostomid phylogenetic tree, considering both strictly Tropical sites and the entire dietary data set including Subtropical sites. The phylogenetic effect, which was first detected by Giannini and Kalko (2004) as a global correlation between a dietary phenogram and the phylogenetic tree, is here shown with greater precision, given that for our analysis we selected only a few tree partitions (clades in the rooted tree) that together explained up to 48% of the use of plants by bats. Except for the clade formed by *Artibeus watsoni* and *Artibeus phaeotis* (clade 48 in Fig. 5), all the important clades are basal: Nullicauda, which contains all the predominantly frugivorous phyllostomids (i.e. Carolliinae, Rhinophyllinae, and Stenodermatinae), Carolliinae, Stenodermatinae, and Stenodermatini. These groups, particularly Stenodermatinae, experienced a pronounced shift in diversification rate (Rojas et al. 2016), which was associated with significant morpho-functional evolution (Dumont et al. 2012).

Molecular dating of the selected groups (Fig. 5; Table 4) placed the point estimates of stem ages of these four major clades between approximately 17 and 7 My. This additional

insight from the analysis indicates a middle Miocene diversification, at a time during which significant biogeographic events were recorded in the Neotropics. During this temporal span, one of the most intense peaks of Andean mountain-building events on record occurred, resulting in an increase in 20–50% of the current elevation (~2000 m above sea level, Hoorn et al. 2010a). This event resulted in significant shifts in atmospheric circulation, rainfall, nutrient deposition patterns, and formation of riverine systems of lowland habitats (Hoorn et al. 2010a). Andean orogeny had a great impact on Amazonian forests and their drainage basin, favouring the development of a complex mega-wetland system with marginal marine influence (Hoorn et al. 2010a,b, Vonhof & Kaandorp 2010). Consequently, Amazonian landscapes changed dramatically from lowland Neotropical rainforests that date back to at least the middle Paleocene, to a system of wetlands of shallow lakes and swamps, the Pebas and Acre systems, during the Miocene and Pleistocene, respectively (Hoorn et al. 2010a,b). Climate also contributed to the development of the mega-wetland systems through the occurrence of a global Middle Miocene Climate Optimum (Hoorn et al. 2010a). In this context, the Paleogene continuous lowland rainforest, which had characteristics of the present-day Amazonian forest but with lower diversity, was substantially fragmented, and plant communities subsequently experienced increased diversification, especially during the Middle Miocene Climate Optimum (Hoorn et al. 2010a, Wesselingh et al. 2010).

Important food plants for bats also underwent high diversification rates during the Middle Miocene. These speciose plant genera did not seem to respond to bat interactions as a whole, but did so only in some of their sections or species groups. For example, *Solanum* originated at c. 17 My; its main lineages started to diversify at c. 16 My, and those lineages containing the species that are important for frugivorous bats diverged between 10 and 8 My (e.g. sections Torva, Acanthophora, Geminata, Brevantherum and Cyphomandra; see Särkinen et al. 2013, Additional file 3). *Ficus* split into major lineages in Late Cretaceous times (86 to 79 My; Xu et al. 2011), and Neotropical clades, sections Pharmacosycea and Americana, emerged at c. 86 and 30 My. However, the intense diversification of these groups did not begin until the early Middle Miocene (c. 20 My; Xu et al. 2011). Pollen of the Moraceae dominated, and therefore characterised, a palynological zone from Early to Middle Miocene of the Pebas system (Jaramillo et al. 2010), evidencing the importance of this family in Amazonian mega-wetland systems. Furthermore, since *Cecropia* is an Andean-centred genus, it had an important representation in palynological and fossil seed records from the Middle to Late Miocene of Central Andes (Franco-Rosselli 1997, Hooghiemstra et al. 2006). Similarly to *Ficus*, the Neotropical lineage of *Piper* originated during the Late Cretaceous (~70 My) and its divergence from Paleotropical clades also seemed to coincide with the breakup of Gondwana during the Cretaceous terrestrial revolution (see Martínez et al. 2015). However,

Table 4. Crown ages of plants and their respective main disperser groups. Values of clade (crown, genera, basal ancestor and stems) originations are given as averages and ranges. Plant clade ages were obtained from: Martínez et al. (2015) for *Piper,* Xu et al. (2011) for *Ficus,* and Särkinen et al. (2013) for *Solanum*; ages of bat clades were obtained from Rojas et al. (2016). Note that in all cases, the plant group origination preceded the emergence of its main frugivorous disperser.

Plants		Bats	
Major clade / Section	Age in My (range)	Ancestral node / crown	Age in My (range)
Piper	111.8 (116.2–109.0)		
Netropical *Piper*	76.1 (85.0–66.5)		
Basal Radula	44.3(53.0–32.0)	Stem *Carollia*	8.3 (10.5–7.0)
Crown Radula	11.0 (22.5–7.5)	Crown *Carollia*	4.3–4.0
Basal Macrostachys	45.8 (57.0–31.0)		
Crown Macrostachys	7.0 (12.5–6.0)		
Ficus	74.9 (101.9–60.0)		
Stem *Pharmacosycea*	74.9 (101.9–60.0)		
Stem *Americana*	32.3 (46.1–22.1)		
Crown *Americana*	20.5 (29.3–13.1)	Stem Stenodermatini	16.8 (17.8–13.0)
Crown *Pharmacosycea*	16.2 (25.7–8.2)	Crown Stenodermatini	13.0–12.5
Solanum	17.0 (18.5–14.0)		
Solanum clade II	13.0 (14.5–11.5)	Stem Sturnirini	11.5 (14.0–9.0)
Brevantherum	8.0 (10.0–6.0)	Crown *Sturnira*	5.0–2.9
Geminata	7.0 (9.0–5.0)		
Cyphomandra	5.5 (7.0–4.7)		
Torva	5.5 (6.5–4.5)		
Acanthophora	5.0 (6.0–4.0)		

its diversification coincided with the onset and later development of both the Andean uplift and the rise of Central America c. 25 My (Martínez et al. 2015). In fact, the two most speciose clades, Macrostachys and Radula (see Jaramillo et al. 2008), diverged at c. 45 My and diversified between c. 7 and 11 My (Martínez et al. 2015). For this highly diverse genus (there are ~1300 spp. of *Piper*; Jaramillo et al. 2008), the centre of endemism is in Central America, the Caribbean and the Chocó region of South America, and the centre of richness is in the contact region between the Amazonia and the Andes. The biogeographical history of *Piper* was associated with both pre-and post-Andean events (Quijano-Abril et al. 2006).

Our results suggest that the different lineages of frugivorous bats emerged and specialised in the context of high diversification of the Neotropical flora, following a specific pattern. Table 4 compares the crown ages of plant groups and their respective main dispersers. Each plant group originated least one million years before the emergence of its main frugivorous bat dispersers; moreover, some fruit plant groups existed for many millions of years before the present-day dispersers originated. Assuming adequate comparability of the various sources of molecular dating involved, these temporal differences between the emergence of plant and bat clades suggests a bottom-up evolutionary control of the mutualistic interaction between plants and bats: the fruit resources were available first, then, bats from successive sister clades took over the seed disperser niche of each plant group. This indicates that other groups (e.g. arboreal mammals or birds) may have dispersed these fruits before bats entered the guild.

CONCLUSIONS

On the basis of a large data set of 14500 dietary records, pooled from 24 independent community studies from sites throughout the Neotropics, we confirm the pattern of genus-to-genus specialisation of the mutualistic plant-bat interactions in the system of frugivory and seed dispersal that has often been found (e.g. Fleming 1986, Giannini & Kalko 2004, Mello et al. 2011, Sánchez et al. 2012a, Andrade et al. 2013, Saldaña-Vázquez et al. 2013). This pattern was confirmed in core tropical areas, and also in subtropical sites sampled in both the Northern and Southern Subtropics, where the availability of resources for bats decreases sharply. Bats responded to low diversity of fruit resources by shifting in diet within their preferred plant groups, or by reducing the species richness of bat groups. Results from a phylogenetic comparative method significantly associated dietary patterns with just three or four basal clades of the frugivorous phyllostomid tree, all dated to the Middle Miocene. During this epoch, environmental changes in the Amazon basin, the Caribbean and especially the Andes were very intense, and heavily fragmented landscapes probably favoured speciation of both plants and bats. Dating of the important clades strongly suggests that fruit plants originated first and were available as resources millions of years before they were adopted by bats as mutualistic interacting partners. The major patterns of Neotropical bat frugivory have remained stable at a specific taxonomic level of response for some 15 My.

ACKNOWLEDGEMENTS

We especially thank Theodore Fleming for valuable suggestions and insight on previous versions of the manuscript. We thank Leticia Moyers Arévalo for helping with the first version of the manuscript and Roman Sánchez for helping with figures edition. Three anonymous reviewer significantly improved the scope and quality of the manuscript. The study was partially supported by Consejo Nacional de Investigaciones Científicas y Técnicas and Agencia Nacional de Promoción Científica y Tecnológica through the research grants (PICT2013-2759 and PICT2016-0608) given to Mariano Sánchez.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Dietary matrix of composite data from quantitative sources for the Tropical region.

Appendix S2. Dietary matrix of composite data from quantitative sources for the Tropical and Subtropical regions.

Appendix S3. Results of Correspondence Analysis and Detrended Correspondence Analysis for the Tropics and Subtropics data set.

Appendix S4. Ordination diagram of Correspondence Analysis for the Tropics data set; fit of dietary items.

Appendix S5. Ordination diagram of Detrended Correspondence Analysis for the Tropics and Subtropics data set.