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Phylogenetic conservatism of dietary niches in Neotropical leaf-nosed bats

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Abstract

The tendency of lineages to retain their ancestral niche over time is known as phylogenetic niche conservatism (PNC**).** Studies considering Eltonian niche characteristics (i.e. biotic interactions) have increased in recent years. However, the question of whether Eltonian niches are conserved remains largely unexplored. The aim of this study was to test for PNC in the Eltonian niches, namely the dietary niches of phyllostomid bats. More specifically, we look for PNC patterns at three phylogenetic scales: family, subfamily and species levels; and in two features of Eltonian niche: dietary breadth and position. We used phylogenetic comparative methods to test the PNC at family and subfamily levels; for species level, we used an approach that compares the dietary niche similarities between species pairs. Our results are largely consistent with PNC of dietary niches, but different patterns emerged when we assessed dietary niche position or breadth, and at different phylogenetic scales. At family level, we found evidence for PNC in dietary niche breadth, but not for dietary niche position. Conversely, at subfamily level we found evidence for PNC in dietary niche position but not for dietary niche breadth. At species level, we found that dietary niches of sister species resemble each other more than non-sister species do, providing evidence of PNC. Our findings highlight the importance of considering that Eltonian niche do not evolve in the same way over time, nor among subclades. Therefore, not assuming but testing PNC is fundamental for understanding the processes underlying the evolution of dietary niches.

1 Introduction

The ecological niche is a unique trait of species. As with other traits, the ecological niche has been thought of as a heritable among species, but the degree to which niches are conserved over time (niche conservatism; Peterson et al., 1999) has been a key question among ecologists and evolutionary biologist in the last couple of decades (Losos, 2008; Wiens et al., 2010). This tendency of lineages to retain their ancestral niche over time is known as phylogenetic niche conservatism (PNC; Wiens & Graham, 2005). The ecological niche can be viewed from two ways: abiotic characteristics (such as climatic tolerances), called the Grinnellian niche; or biotic characteristics (such as diet), called the Eltonian niche (Soberón, 2007). Both constitute the set of variables in which species can persist and thrive (Hutchinson, 1957). For decades, studies focusing on PNC had concentrated on the characteristics of the Grinnellian niche. However, with the recent development of databases relevant to the biotic interactions related to Eltonian niches (e.g. Wilman et al., 2014), studies considering Eltonian characteristics have increased, but the question of whether Eltonian niches are phylogenetically conserved remains largely unexplored (Olalla-Tárraga et al., 2017).

The study of PNC has been useful for explaining biodiversity patterns (Wiens & Donoghue, 2004), biological invasions (Guisan et al., 2014) or species responses to global climate change (Quiao et al., 2024). However, the way in which it is tested has been debated (Pyron et al., 2014). Traditionally, the use of metrics describing the phylogenetic signal (PS) —the tendency of related species to be more similar to each other than to species randomly selected in the phylogeny (Blomberg & Garland, 2002)— has been the main test for assessing PNC. The resulting pattern under PS is one of closely related species being

more similar than less closely related species, which for some authors was sufficient evidence of PNC (Wiens et al., 2010). However, it has also been argued that the presence of PNC requires additional constraints related to stabilizing selection (Losos, 2008), which promotes slower evolution of niches than simply neutral drift. Currently, it has been shown that PS alone should not be taken as evidence of PNC, as it can lead to misinterpretations (Münkemüller et al., 2015). Alternatively, it has been suggested to compare the relative fit of evolutionary models to the trait of interest (Cooper et al., 2010; Münkemüller et al., 2015). The assumptions of each model regarding the evolution of traits are different, with the most common models being: Brownian motion (BM), related with neutral drift and describing divergence proportional to time; Ornstein-Uhlenbeck (OU), related to stabilizing selection in which traits are attracted to an optimal adaptive value; Early Burst (EB), related to a model of acceleration-deceleration of evolutionary rates early in the history of a clade; White Noise (WN) model related to random variation along the phylogenetic history. Unlike the BM model, in which changes in an trait over time are modeled by a normal distribution with a mean of 0 and a variance (evolutionary rate) σ^2 (Felsestein, 1973), the OU model considers two additional parameters, selection strength (α) and optimum (θ), that together describe a constrained evolution with a certain selection strength in which traits tend to return to optimal values. A result indicating a better fit of an OU model aligns with Losos' (2008) view, given that this model implies evolutionary constraints on traits or evolutionary stasis and can therefore be interpreted as evidence of PNC (Butler & King, 2004).

Regardless of whether a BM or OU model is selected, this model-fitting approach assumes that all model parameters (θ , σ^2, α) remain constant throughout the phylogeny (i.e. phylogenetic stationarity). However, assuming stationarity can hide expected patterns of niche shifts or conservatism and thus lead to erroneous conclusions (Diniz-Filho et al., 2010). Conversely, phylogenetic non-stationarity reflects more complex evolutionary processes by considering that different lineages could follow distinct evolutionary trajectories, responding to environmental pressures through changes towards different adaptive optima or at different rates (Butler & King, 2004; Diniz-Filho et al., 2010; Diniz-Filho et al., 2015). Consequently, less restrictive models have been proposed that allow for shifts in model parameters (θ , σ^2, α) (Butler & King, 2004; Beaulieu et al., 2012). These models were originally developed to test adaptive shifts across specific lineages (regimes) based on clear hypotheses of where adaptive changes might occur (e.g., Rodrigues et al., 2018). However, these models have been criticized precisely for relying on a priori regimes (Uyeda & Harmon, 2014). To address this, automatic detection models have recently been developed to identify shifts in adaptive optima without a prior assumptions (e.g., *l1ou*, Khabbazian et al., 2016). Complementing these full-tree approaches by assessing phylogenetic patterns at shallower phylogenetic scales (e.g., at the species level) could also reveal different PNC patterns (Diniz-Filho et al., 2010; Peixoto et al., 2017). Species level approaches can also be phylogenetically explicit, as they rely on measuring niche overlap between pairs of species and correlating these to their phylogenetic distances. In a PNC scenario, niche similarities between more closely related species should be greater than those between unrelated species. Integrating these complementary approaches across multiple phylogenetic scales, i.e from entire clade and subclades to pairwise species level comparisons, provides a robust way

to test PNC while considering phylogenetic non-stationarity (Cooper et al., 2010; Wiens et al., 2010; Uyeda & Harmon, 2014; Peixoto et al., 2017).

The presence of PNC – at least considering the climatic/Grinnellian aspect of the niche – has been suggested for multiple taxa (e.g. Cooper et al., 2011; Liu et al., 2020). However, the interpretation of the resulting pattern and hypotheses derived from PNC may depend on the degree to which niches are conserved, and this can vary between clades (Buckley et al., 2010) or between groups within the same clade (Peixoto et al., 2017). Therefore, not assuming and testing these patterns is key for informing effective conservation strategies, like when a clade with a high degree of conservatism in its climate tolerances is more vulnerable to climate change (Wiens et al. 2010). In contrast, only a few studies have evaluated PNC in the Eltonian aspect of the niche, mainly its dietary charactersitics. Even in well-studied groups, there are few examples of this type of studies. In birds, there is opposing evidence regarding PNC, where they have been suggested for Passeriformes (Stukenholtz & Stevens, 2024) but not for European avifauna (Pearman et al., 2014). In mammals, Olalla-Tárraga et al. (2017) tested PNC in terms of dietary breadth and their results did not indicate a consistent PNC pattern for the Eltonian niche, and they suggested that future assessments should focus on the use of well-resolved phylogenies and detailed dietary databases.

Within Mammalia, bats (order Chiroptera) constitute a widely studied group, both in relation to the PNC considering the climatic characteristics of ecological niches (Peixoto et al., 2017) and in the associated geographic biodiversity patterns (Ramos-Pereira & Palmeirim, 2013). Of the 1,500 described bat species to date, 231 belong to the family Phyllostomidae (Simmons & Cirranello, 2026). This family has been noted as an example of adaptive radiation (Fleming et al., 2020), a diversification that has been associated with their diets (Rojas et al., 2011; Ochoa-Sanz et al., 2025). The evolution of various morphological traits has allowed phyllostomids to exploit a wide range of resources, from fruit and nectar to vertebrates, arthropods, and even blood (Gardner, 1977, Freeman, 2000), making them the mammal group with the greatest dietary diversity. These morphological changes and the preference for consuming different resources have been widely associated with subfamilies (Wetterer, 2000; Arbour et al., 2019); for example, Stenodermatinae and Glossophaginae have been linked to preferences for consuming fruit and nectar, respectively. Therefore, Phyllostomidae is an ideal group for studying Eltonian niches —specifically its dietary characteristics— at different phylogenetic scales. Phyllostomids are responsible not only for driving the latitudinal diversity gradient in bats, but also in all mammals (Buckley et al., 2010). One explanation for this latitudinal diversity gradient is PNC (Wiens & Donoghue, 2004; Stevens, 2006). It is clear that PNC in phyllostomids is strong, at least in terms of their climatic niches (Villalobos & Arita, 2010; Villalobos et al., 2014; Peixoto et al., 2017; Varzinczak et al., 2019), but little evidence has been presented regarding the PNC in relation to their dietary niches. For Atlantic Forest bats, Stevens (2021) found that dietary niche in phyllostomids is even more conserved than their climatic niches, at least at species level and in that study region. To our knowledge, there is no formal study assessing the PNC in the dietary niche for all bats in the family Phylostomidae.

Here, we evaluated the existence of PNC in the Eltonian (dietary) niches of phyllostomid bats. We explicitly consider the Eltonian niche axis that describes the diet of each bat species, characterized by the dietary niche breadth and position. We considered these two niche characteristics, breadth and position, as suggested by Olalla-Tárraga et al. (2017) that evaluating only one niche component does not provide sufficient information to explore PNC. Moreover, we were interested in evaluating the degree of PNC at different phylogenetic scales. Using phylogenetic comparative methods, we fitted evolutionary models at the family level and multi-optimum, multi-rate evolutionary models at the subfamily level. Furthermore, at species level, we considered a pairwise approach where we measured the dietary similarity of each pair of species and compared it with their phylogenetic similarity. For this study, we considered that PNC requires additional constraints beyond simply neutral drift (Losos, 2008). Therefore, we expected that a) the values corresponding to the dietary niche of phyllostomids would fit a stabilizing selection model, according to an Ornstein-Uhlenbeck model; b) At the subfamily level, we expect a better fit of the multi-optimum and multi-rate models, indicating that the dietary niche of the species in each subfamily is conserved to different degrees; c) we also expect that the models for detecting shifts in the optima will locate such shifts in those nodes where the species had a significant change in the features of the dietary niche, largely coinciding with the ancestral nodes of the subfamilies; and d) sister species will show a greater dietary niche similarities than less related species.

2 Materials and Methods

2.1 Dietary data and phylogenetic information

We obtained the information to characterize dietary niches of phyllostomid species from *PhyllosTrophic*, the most comprehensive and detailed dietary database for phyllostomid bats (Ochoa-Sanz et al., in review). *PhyllosTrophic* compiles primary dietary data for 229 phyllostomid species throughout the American tropics. Unlike other databases such as *EltonTraits* (Wilman et al., 2014), *PhyllosTrophic* contains information on bat-consumed resources at the species level and has the advantage of being updated and taxonomically harmonized for both bat species and the resources they consume. For phylogenetic information on bat relationships, we used the most robust species-level phylogeny for the superfamily Noctilionoidea proposed by Rojas et al. (2016). This phylogenetic hypothesis was estimated with three mitochondrial and seven nuclear markers and was time-calibrated with eight fossils using Bayesian inference. For phyllostomids, this phylogeny contains 163 phyllostomid, all included in *PhyllosTrophic*.

2.2 Family and subfamily level analyses

2.2.1 Dietary niche breadth and position

We used the dietary information for the 163 phyllostomid species included in the phylogeny to characterize their dietary niche in two of their features, breadth and position. First, at family and subfamily levels, we considered the following dietary categories (items): fruits, nectar (and pollen),

arthropods, vertebrates and blood. These five items were originally proposed by MacNab (1971) and have been shown to be closely related to the diverse cranial forms within the family (Freeman, 2000) that in turn reflect the phylogenetic relationships among phyllostomids (Wetterer, 2000). Therefore, they have been widely used in dietary studies of these species (Rex et al., 2010; Rojas et al., 2011).

Accordingly, for each study compiled by *PhyllosTrophic*, we identified which bat species and which of the five items were reported as consumed. Each study resulted in a table with six columns (scientific name of the bat and five item columns). The total number of rows equaled the number of reported bat species, the columns corresponding to the items were filled with values of 1 (item consumed) and 0 (item not consumed). These tables were then combined into a single table and summed for each species, resulting in a table with the same number of columns but with 229 rows (one per bat species). At this point, the item columns indicate the number of studies in which a given item was reported for each species. To account for potential bias due to varying sampling effort and numbers of studies across bat species, we weighted the data by dividing the number of studies reporting each item by the total number of studies. For example, for a bat species with a total of 50 studies, 45 reported fruit, 15 arthropods, 5 nectar, 0 vertebrates, and 0 blood. The result is a frequency vector with values of 0.9, 0.3, 0.1, 0, 0, respectively. Note that the sum of the frequency vectors will not necessarily equal 1, as a single study may report multiple items. Finally, we selected only those phyllostomids with phylogenetic information, our final table contains the frequencies of resources consumed by 163 phyllostomid species (~ 71% of entire family) and was used to measure the dietary niche breadth and position.

We used Levins' index in its raw form to measures the species' dietary niche breadth as follow: $B = 1/\sum_{i=1}^{R}(P_i)^2$ where *B* is the niche breadth, P_i is (in this study) the frequency proportion of the item, i.e. $P_i = \frac{n_i}{N}$ where n_i is the frequency of the item *i* and *N* is the sum of all frequencies, *R* is the total number of items. In this study, Levins' index can take values from 1 (indicating that a species consumes only one item) to 5 (consuming all the five items in the same proportion). This index was measure using the function 'niche.breadth' from the *spaa* R package (Zhang & Zhang, 2013). To measure niche position, we applied an ordination technique called Phylogenetic Principal Component Analysis (pPCA; Revell, 2009) to our item frequency table. pPCA is similar to traditional PCA, but with the advantage of considering the phylogenetic relationships of the species and generating new continuous variables that exclude the effect of phylogeny (Revell, 2009). Our main goal for using pPCA was to position and order the species in a dietary niche space, reflecting their dietary similarity based on the consumption frequency of each item. We are aware that pPCAs in comparative analyses are biased because the first principal components are more influenced by the traits that vary at the base of the tree (Uyeda et al., 2015), which has led to statistical artifacts that can lead to erroneous results, such as favoring an EB model. However, these statistical artifacts are evident when the traits used to construct the pPCs are highly correlated, which is not our case, and when the first principal component (pPC1) explains approximately 75% of the variation (Uyeda et al., 2015). To perform the pPCA, we used the 'phyl.pca' function from the phytools package (Revell, 2024). We retained the first three axes (pPC1,

pPC2, and pPC3), which explained ~ 94% of the variance and formed our niche position metric (see Supplementary Information, Table S1).

2.2.2 Evolutionary model fitting

Following the most recent recommendations (Münkenmüller et al., 2015), we sought evidence of PNC at the family level by fitting of evolutionary models. We used the 'fitContinuous' function from the *Geiger* package (Pennell et al., 2014) to fit four evolutionary models to each trait of interest (pPCs for niche position and Levins' index for niche breadth). We corroborated our results by fitting a multivariate evolutionary model with *mvMORPH* package (Clavel et al., 2015) for niche position (pPC's). These models were: Brownian Motion (BM), a model associated with neutral drift; Ornstein-Uhlenbeck (OU), a model related to stabilizing selection; Early Burst (EB), a model indicating rapid evolution of the trait near the tree root and a subsequent decrease in evolutionary rates; and White Noise (WN), a model of random variation. The selected model was the one with the lowest value on the corrected Akaike Information Criterion (AICc). These models assume that traits evolve at a constant rate throughout the tree. However, it has been shown that throughout the evolutionary history of clades, there can be changes in the optima (θ), selection strength (α) and evolutionary rate (σ^2) of the traits (Hansen, 1997; Butler & King, 2004). This has led to the development of multi-optima and multi-rate OU models that evaluate the relative fit of models in groups (regimes) for which a hypothesis has been previously established (Beaulieu et al., 2012).

Multi-optimum and multi-rate models allow us to test our hypotheses at the subfamily level, where we expect that due to different dietary preferences, each subfamily will evolve under different evolutionary constraints. We use the *OUwie* package (Beaulieu et al., 2012) to fit the following models with variation of the OU parameters: BMs, a BM model with different σ^2; OUm, model with variable θ; OUmv, model whit variable θ and σ^2; OUma, model with variable θ and α; and OUmva, a model with all variable parameters. We compared these models with a single optima, BM and OU and selected the model with lowest AICc.

Although we were interested in evaluating the PNC at the subfamily level, we also took into account the potential bias of selecting groups a priori, the main criticism of models like OUwie (Uyeda & Harmon, 2014). Therefore, we corroborated our results at this level of analysis by using the method *l1ou* (Khabbazian et al., 2016). *l1ou* was developed to automatically detect evolutionary shifts in OU models. Furthermore, thanks to its 'pBIC' criterion, it has proven to be more conservative than other methods such as surface (Ingram & Mahler, 2013) and therefore has a lower false shift detection rate. We used the 'estimate_shift_configuration' function of the l1ou package to perform a multivariate model for niche positon (that includes the three pPC's), and a second univariated model to niche breath.

2.3 Species level analyses

For species level analyses, we considered more detailed information on the dietary preferences of each species, because it has been shown that some phyllostomid genera maintain preferences for certain genera they consume. This has been observed primarily in frugivorous bats where, for example, bats of

the genus *Artibeus* have been observed to prefer *Ficus*, whereas those of the genus *Sturnira* primarily consume *Solanum* (Fleming, 1986). Evaluating dietary niche overlap at this scale allowed us to go beyond the dietary categories that govern at higher taxonomic levels (such as those considered at the family and subfamily levels), providing a more robust analysis for understanding how dietary niches are conserved at this phylogenetic scale. Thus, we established our items as the taxonomic identity at genus level of the consumed resource, and added an indicator of the consumption type, since some bats may consume the same plant species but different parts (fruit or nectar).

Accordingly, for each bat species, we identified the consumed resources that reached the species level, excluding repeated species; we also retained observations that reached the genus level only when no other observation reached the species level within the same genus. The frequency of each item was determined by the number of species consumed within each genus. For example, for a phyllostomid species feeding on the fruit of eight different plant species of the genus *Piper*, an item called 'Piper_fruit' was created with a frequency of 8. If for the same bat species we find five studies that report the consumption of Cecropia fruits, but do not reach the species level, the frequency of the item 'Cecropia_fruit' will only be 1. After applying these filters, 180 species reached our criteria (i.e. with resources consumed identified at the species level) so our final table is given by 180 rows and with the number of columns equal to the number of items (genera) found for the whole family.

We measured the similarity of the dietary niche between each pair of species using the Pianka's index (Pianka, 1973) following the formula: $O_{jk} = \sum_{i}^{n} P_{ij}P_{ik} / \sqrt{\sum_{i}^{n} \left(P_{ij}\right)^2 \sum_{i}^{n} \left(P_{ik}\right)^2}$ where the niche similarity (O_{jk}) of the species *j* and *k* is given by the frequency of shared items (P_i) between them. The Pianka index ranges from 0 to 1, where higher values indicate greater similarity. We used the 'niche.overlap' function from *spaa* (Zhang & Zhang, 2013) to estimate the niche similarity between the 180 phyllostomid species (16,110 species pairs). To include phylogenetic relationships, we used the 'cophenetic.phylo' function from *ape* package to calculate the 13,203 phylogenetic distances conformed for each pair of the 163 species in the phylogeny. Finally, we retained the 147 species (10,731 pairs) shared between both dietary niche and phylogenetic distances matrices, resulting in two matrices of the same length.

To test the existence of PNC, we performed a matrix correlation via Mantel test with *vegan* package (Oksane et al., 2026). Several criticisms have been made regarding the statistical power and high error rate of the Mantel test (Guillot and Rousset, 2013), leading to the suggestion of using niche dissimilarities (1-similarity) instead of similarities (Diniz-Filho et al., 2013; Legendre et al., 2015). Thus, a positive and significant correlation between the dietary niche dissimilarities and phylogenetic distances is a sign of PNC. Additionally, to complement our analysis, we extracted the identity of sister species (cherry pairs) from the phylogeny and estimated the average of the observed dissimilarity, then compared it with a null distribution of niche dissimilarity values between pairs of non-sister species that we constructed from calculating the mean of 100 randomly extracted species pairs and repeating this process 1000 times. Finding a lower value of niche dissimilarity observed between pairs of cherries than

the distribution of dissimilarity values between non-sister species was taken as evidence of PNC. We used dissimilarity matrices for these purposes, but we will refer in terms of similarity for simplicity in our interpretations.

3 Results

3.1 Family and subfamily levels

We retained the first three pPC's that accounted 94% of variation in the dietary niche of phyllostomid bats. The first pPC explained 40.59% of the variation and loaded positively for fruit consumption, separating it from arthropod and nectar consumption. Second pPC explained 36.06% of the variation and separated nectarivory from frugivory and arthropods consumption. The third pPC explained the 17.39% of the variation and loaded positively for the consumption for blood and vertebrates (Fig. 1a, Table S1).

Of the 163 species evaluated, most phyllostomids have their dietary niches in frugivorous diets (positive pPC1 values, Fig. 1b), probably driven by the most diverse subfamily of phyllostomids, Stenodermatinae. Another large group of phyllostomids occupied regions of the dietary niche in nectarivory, represented by the subfamilies Glossophaginae and Lonchophyllinae (Fig. 1c). A smaller proportion were bats that consume arthropods, vertebrates, and blood, represented by less numerous subfamilies such as Micronycterinae, or Desmodontinae (Fig. 1d). Regarding niche breadth, most phyllostomids showed breadths ranging from 1 to 2 on Levins' index. Indicating that most phyllostomids prefer consuming only one dietary category, although they also consume other categories but in a smaller proportion (Fig. S1).

The dietary niche of phyllostomid bats began its diversification around 30 Mya. In terms of niche position, this diversification intensified around 25 Mya (Fig. 2). A very rapid and marked diversification toward positive pPC1 values indicates that frugivory quickly differentiated from other diets and then tended to stabilize (Fig. 2a). pPC2, whose positive values are related to nectar consumption, showed a more pronounced diversification just over 20 Mya (Fig. 2b). Positive pPC3 values, related with the consumption of blood and vertebrates, showed diversification 25Mya (Fig. 2c). The diversification of dietary niche breadth intensified around 20 Mya and showed a tendency for species to move toward values of 1, indicating that species tended toward specialization (Fig. 2d).

Our results at family level from fitting univariate (Table 1) and multivariate (Table S2) evolutionary models for niche position were consistent. None of the univariate models fit an OU model for any of the three pPCs, whereas the multivariate model showed a better fit for BM, thus not supporting PNC. Conversely, for niche breadth, we did find a better fit for the OU model (Table 1), suggesting PNC.

Table 1
Fit of four alternative models of the evolution of dietary niche for family level under corrected Akaike Information Criterion (AICc). ΔAICc = delta AICc, W-AIC = wight AICc. Bold indicates the model with stronger support

	Model	Log-likelihood	AICc	ΔAICc	W-AICc
pPC1[1]					
	BM	24.652	-45.228	0	0.581
	OU	24.686	-43.221	2.01	0.213
	EB	24.652	-43.15235	2.08	0.206
	WN	-106.155	216.384	261.61	0
pPC2[2]					
	BM	29.313	-54.551	0.502	0.379
	OU	30.602	-55.054	0	0.487
	EB	29.313	-52.475	2.58	0.134
	WN	-39.360	82.795	137.85	0
pPC3[3]					
	BM	95.222	-186.369	0	0.467
	OU	95.222	-184.293	2.08	0.165
	EB	96.022	-185.893	0.48	0.368
	WN	2.954	-1.832	184.54	0
levins					
	BM	-115.088	234.25	9.67	0.008
	OU	**-109.214**	**224.579**	**0**	**0.989**
	EB	-115.088	236.326	11.75	0.003
	WN	-146.682	297.439	72.86	0

[1]pPC1 (↑ Fruits, ↓ Arthropods & Nectar); [2]pPC2 (↑ Nectar, ↓ Fruits & Arthropods); [3]pPC1 (↑ Blood & Vertebrates)

Our results at subfamily level of both univariate (Table 2) and multivariate (Table S3) evolutionary models for niche position were consistent. All univariate models fit OU models for the three pPCs, while the multivariate model showed a better fit for multi-optima OUs (Table S3). pPC1 and pPC3 fit an OUmv model, indicating that both traits evolve under different optima θ and at different evolutionary rates σ^2, while for pPC2 the best-fit model was OUma, indicating evolution under different optima and different selection forces. For niche breadth, we also found a better fit for an OUmv model (Table 2), indicating

that the dietary niche breadth of each subfamily evolves under different optima and at different evolutionary rates.

Our results for the automatic shift detection method yielded 17 shifts in optima for niche position (Fig. 3) and 1 shift for niche breadth (Fig. S2). Of the 17 shifts detected for niche position, three of these nodes correspond to the subfamilies Lonchophyllinae, Glossophaginae, and Desmodontinae (Fig. 3). A single shift related to primarily frugivorous diets was also detected; this shift encompassed the subfamilies Stenodermatinae, Carolliinae, Rhinophyllinae, and Glyphonycterinae. One shift detected within the subfamily Phyllostominae corresponded to the genera *Phyllostomus* and *Phyloderma*, whereas the shift detected within Glossophaginae encompassed genera *Phyllonycteris*, *Erophylla*, and *Brachyphylla*. Conversely, the results with the l1ou method did not show adaptive shifts for niche breadth and therefore do not support the results with the OUwie method. Overall, our results at the subfamily level did show evidence of PNC for the position of the dietary niche, but not for its breadth.

Table 2

Fit of seven alternative models of the evolution of dietary niche for subamily level under corrected Akaike Information Criterion (AICc). ΔAICc = delta AICc, W-AIC = wight AICc. Bold indicates the model with stronger support. In models with multi-optimum and multi-rates: m = θ or optimum value of the trait, v = σ^2 evolutionary rate, a = α selection strength

	Model	Log-likelihood	AICc	ΔAICc	W-AICc
pPC1[1]					
	BM	24.65	-45.23	79.43	0
	BMs	46.24	-66.41	58.24	0
	OU	24.69	-43.22	81.43	0
	OUm	51.16	-73.87	50.79	0
	OUmv	**89.29**	**-124.66**	**0**	**0.81**
	OUma	87.86	-121.79	2.87	0.19
	OUmva	92.04	-100.69	23.96	0
pPC2[2]					
	BM	29.31	-54.55	80.01	0
	BMs	41.71	-57.34	77.23	0
	OU	30.60	-55.05	79.52	0
	OUm	59.96	-91.48	43.09	0
	OUmv	89.83	-125.72	8.85	0.01
	OUma	**94.26**	**-134.57**	**0**	**0.99**
	OUmva	98.82	-114.25	20.32	0
pPC3[3]					
	BM	95.22	-186.37	53.64	0
	BMs	115.51	-204.95	35.06	0
	OU	95.22	-184.29	55.72	0
	OUm	117.02	-205.61	34.41	0
	OUmv	**146.98**	**-240.01**	**0**	**0.79**

[1]pPC1 (↑ Fruits, ↓ Arthropods & Nectar); [2]pPC2 (↑ Nectar, ↓ Fruits & Arthropods); [3]pPC1 (↑ Blood & Vertebrates)

	OUma	145.66	-237.38	2.64	0.21
	OUmva	150.31	-217.23	22.78	0
levins					
	BM	-115.09	234.25	37.77	0
	BMs	-102.94	231.96	35.48	0
	OU	-109.21	224.58	28.09	0
	OUm	-94.54	217.51	21.03	0
	OUmv	**-71.27**	**196.48**	**0**	**0.87**
	OUma	-73.20	200.34	3.86	0.13
	OUmva	-69.78	222.96	26.48	0

[1]pPC1 (↑ Fruits, ↓ Arthropods & Nectar); [2]pPC2 (↑ Nectar, ↓ Fruits & Arthropods); [3]pPC1 (↑ Blood & Vertebrates)

3.2 Species level

Our species level analyses covered 10,731 species pairs, corresponding to 147 phyllostomid species with information for both dietary and phylogenetic relationships. Our Mantel test showed a positive and significant relationship ($r = 0.515$, $p = 0.001$) between dietary niche dissimilarities and phylogenetic distances, indicating that species with similar dietary niche are closely related, and that as the dissimilarity of dietary niches increases (i.e., more different diets), the phylogenetic distance between species also increases. In our second test, we identified 46 sister species (cherry pairs), with a observed mean of dissimilarity of 0.585. This mean dissimilarity value observed in sister species was always lower than the mean of random pairs of non-sister species (Fig. 4), indicating that sister species are more similar than species randomly selected from the phylogeny. Taken together, our results can be taken as evidence of PNC at the species level.

4 Discussion

The tendency of species to conserve their ancestral niches over time (PNC) is often assumed but not always tested. Although the importance of studying PNC of Eltonian niche characteristics in phyllostomid bats has been highlighted, mainly regarding their association with the high diversity of the family (Ochoa-Sanz et al., 2025) and their role in delimiting species' geographic ranges (Stevens, 2021), most studies have focused on their Grinnellian niches (Stevens, 2006; Villalobos et al., 2014; Peixoto et al., 2017). Only a few studies have explicitly evaluated the evolutionary pattern of Eltonian niches in this bat family, namely the trophic structure of assemblages at local (Giannini & Kalko, 2004) or regional scales (Stevens, 2021). In this study, our main objective was to test PNC in the Eltonian niche,

specifically the dietary aspect, of phyllostomid bats at the continental scale and at different phylogenetic scales. Overall, our findings were consistent with PNC at the family level but showed distinct patterns at different levels of phylogenetic inclusiveness. Aligning partially with our first hypothesis, we found no evidence of PNC for dietary niche position at family level, but we did find evidence for PNC in niche breadth. Conversely, at the subfamily level, we found evidence of PNC for niche position but not for niche breadth, partially supporting our second and third hypotheses. Meanwhile, at the species level, we demonstrated that closely related species have higher dietary niche similarity than unrelated species, showing evidence of PNC, thus supporting our fourth hypothesis. These results indicate that the evolution of the dietary niche, has not evolved uniformly throughout the evolutionary history of Phyllostomidae, highlighting the importance of considering phylogenetic scale when studying PNC (Diniz-Filho et al., 2010; Peixoto et al., 2017).

In a study on PNC in the dietary niche breadth for all mammals (Olalla-Tárraga et al., 2017), no consistent evidence of PNC was found. Here, we went further by evaluating phyllostomid PNC not only for niche breadth but also for niche position. The dietary niche position provides information about the dietary preference of species, whereas dietary niche breadth provides information about dietary diversity. This is important because two species could have the same dietary niche breadth but not the same dietary position. This, along with considering different phylogenetic scales, allowed us to reveal distinct PNC patterns of dietary niche evolution in phyllostomids. At the family level, our findings showed that the evolution of dietary niche position did not fit an OU model, but rather a BM model, as indicated by the results of our multivariate model fit analysis (Table S2). This does not imply that closely related species lack high similarity; in fact, BM demonstrates precisely that (Felsestein, 1985). Rather, this result indicates an absence of evolutionary constraints, a key assumption for demonstrating PNC at this scale (Losos, 2008). Conversely, our results showed a better fit for the OU model in niche breadth, suggesting that dietary diversity has been conserved around an adaptive optimum for the entire family. Phyllostomid bats are the most dietary diverse group of mammals, and this has been widely associated with its diversification, with frugivorous bats having the highest speciation rates, followed by nectarivorous bats (Rojas et al., 2011, Ochoa-Sanz et al., 2025). Similarly, Grossnickle et al. (2024) found evidence that the evolution of cranial morphology fits an Early Burst model in Phyllostomidae, suggesting early adaptive shift in their evolutionary history that have been linked to their diets (e.g., elongated skulls are associated with nectar consumption). In line with our results, this rapid and early diversification of cranial forms could enabled the exploitation of diverse diets with few evolutionary restrictions. This transition into new adaptive optima in niche position, combined with the phylogenetic conservatism of their niche breadth, may have facilitated dietary specialization and thus generated the dietary preference patterns known among Phyllostomidae subclades.

At the subfamily level, our results did not show consistent evidence of PNC for dietary niche breadth, despite OUwie models favoring the OUmv model for this trait. This result was not supported by our *l1ou* model, so we interpret this as insufficient evidence to suggest PNC for niche breadth at this phylogenetic scale. However, we did find evidence of PNC for dietary niche position, and these results were complementary to those found at the family level. Phyllostomidae subfamilies are known to maintain

preferences for a particular type of diet (Wetterer, 2000). For example, species from Stenodermatinae tend to be frugivorous, while species from Glossophaginae tend to be nectarivorous. Our *l1ou* model for dietary niche position supported evolutionary shifts in three subfamilies: Glossophaginae, Lonchophyllinae (both nectarivorous), and Desmodontinae (hematophagous). and in some lineages within several subfamilies (Fig. 3). Desmodontinae subfamily is composed by only three species, all of which demonstrate a high degree of specialization for blood consumption. Therefore, finding this evolutionary shift reinforces what is obvious but important to demonstrate with evidence. For Glossophaginae and Lonchophyllinae, it had already been suggested that this type of diet arose independently in each subfamily (Datzmann et al., 2010, Rojas et al., 2011), and our results support this hypothesis by detecting two independent shifts in each of their corresponding nodes. Moreover, Rojas et al. (2011) had suggested that frugivory evolved in parallel in five subfamilies. In this study, we found only one evolutionary shift in the common ancestor of the Stenodermatinae, Carolliinae, Rhinophyllinae, and Glyphonycterinae subfamilies. Our results align with the ancestral reconstruction by Ochoa-Sanz et al. (2025) where they found that the common ancestor of these four subfamilies already consumed fruit.

Our *l1ou* model also detected evolutionary shifts in subclades within some subfamilies, further highlighting the importance of phylogenetic non-stationarity (Diniz-Filho et al., 2010). For example, we detected a shift in the common ancestor of the genera *Brachyphylla*, *Phyllonycteris*, and *Erophylla* belonging to the Glossophaginae subfamily and endemic to the West Indies islands. It has been shown that, despite being glossophagines and thus considered nectarivorous, they consume a large quantity of fruit. Indeed, species from these genera exhibit cranial forms with plesiomorphic features (Datzmann et al., 2010) more similar to other genera such as *Phylloderma* or *Sturnira* (Monteiro & Nogueira, 2011), so their dietary niches appear to be evolving toward an evolutionary optimum distinct from that of the other species in their subfamilily. Although we did not find a clear evolutionary shift in dietary niche position for the entire subfamily Phyllostominae, Our *l1ou* model did detect an evolutionary shift in dietary niche position group encompassing the genera *Phyllostomus* and *Phyloderma*. In particular, species of the genus *Phyllostomus* are the only known species of subfamily Phyllostominae that exhibit morphological adaptations for nectar consumption (Quinche et al., 2022), explaining the shift detected in this study.

Our species level analyses focused on comparing dietary niche similarities between pairs of species and their phylogenetic relationships. Our results showed evidence of PNC, with sister species showing higher niche similarity than unrelated species. The same result had already been reported by Stevens (2021), who found that the dietary niches of phyllostomid bats in the Atlantic Forest show a stronger signal of PNC than their climatic (Grinnellian) niches. In our study, we considered 147 phyllostomid species, considering more than 100 species than those evaluated by Stevens (2021), thus extending the results to a generalization beyond the species present in the Atlantic Forest biome into a continental pattern across the American tropics where they family is mostly restricted. At this level of analysis, we considered a much finer resolution of the diet (number of species consumed from each genus) than at the higher levels described above. For phyllostomids, this is important because some bat genera have been observed to prefer the consumption of certain plant genera (Fleming, 1986). The most classic example is that of the genera *Artibeus*, *Sturnira*, and *Carollia*, where preferences for *Ficus*, *Solanum*, and

Piper, respectively, have been reported (Fleming, 1986; Giannini & Kalko, 2004). These findings demonstrate that evaluating dietary niches among phyllostomids using detailed information of species they consume can indeed contribute to a more nuanced understanding of phylogenetic conservatism patterns at a shallower phylogenetic scale.

To our knowledge, our study is one of the few that has comprehensively evaluated the PNC of dietary niches at different phylogenetic scales. This study reveals that PNC is not a homogeneous phenomenon, but rather depends on the phylogenetic scale, where the breadth and position of the dietary niche evolved in different ways. At the deepest level of our analysis (family), phyllostomid species evolved without strong evolutionary constraints on their dietary niche position, allowing for dietary diversification (Grossnickle et al., 2024). However, extrinsic factors such as competition for resources could have acted as an evolutionary constraint on dietary niche breadth, favoring niche partitioning (Schoener, 1974) and thus tending toward specialization. This may have generated the widely known pattern of dietary preferences for the group (Freeman, 2000; Wetterer, 2000; Rojas et al., 2011; Ochoa-Sanz, 2025). Once species specialize toward different optima in their dietary niche position, the PNC pattern shifts to being strongly conserved across subfamilies. Finally, at the most shallow level of our analysis (species pairs), the pattern we currently observe indicates that species tend to maintain their dietary niches among more closely related species (Stevens, 2021). In this study, we evaluated only the phylogenetic conservatism of the dietary niche within the family Phyllostomidae, thus similar studies on other clades are undoubtedly needed. We recommend that future studies consider phylogenetic non-stationarity to more deeply evaluate patterns of PNC across different phylogenetic scales. Furthermore, we strongly suggest that analyses of phylogenetic conservatism regarding the dietary niche evaluate niche position rather than just niche breadth. These considerations may bring us closer to a better understanding the evolution of dietary (Eltonian) niches of species.

Declarations

Declarations

Competing Interests:

The authors declare no competing interests.

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Author Contribution

Conceptualization: G. Dirzo-Uribe & F. Villalobos; Methodology: G. Dirzo-Uribe & F. Villalobos; Formal analysis and investigation: G. Dirzo-Uribe; Writing - original draft preparation: G. Dirzo-Uribe; Writing - review and editing: G. Dirzo-Uribe & F. Villalobos; Supervision: F. Villalobos; Scientific illustrations: G. Dirzo-Uribe.

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Data Availability

Additional processed data and code to repeat the analyses can be accessed at the following repository: https://figshare.com/s/9fc08ad18a3c9bd5fb25

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Figures

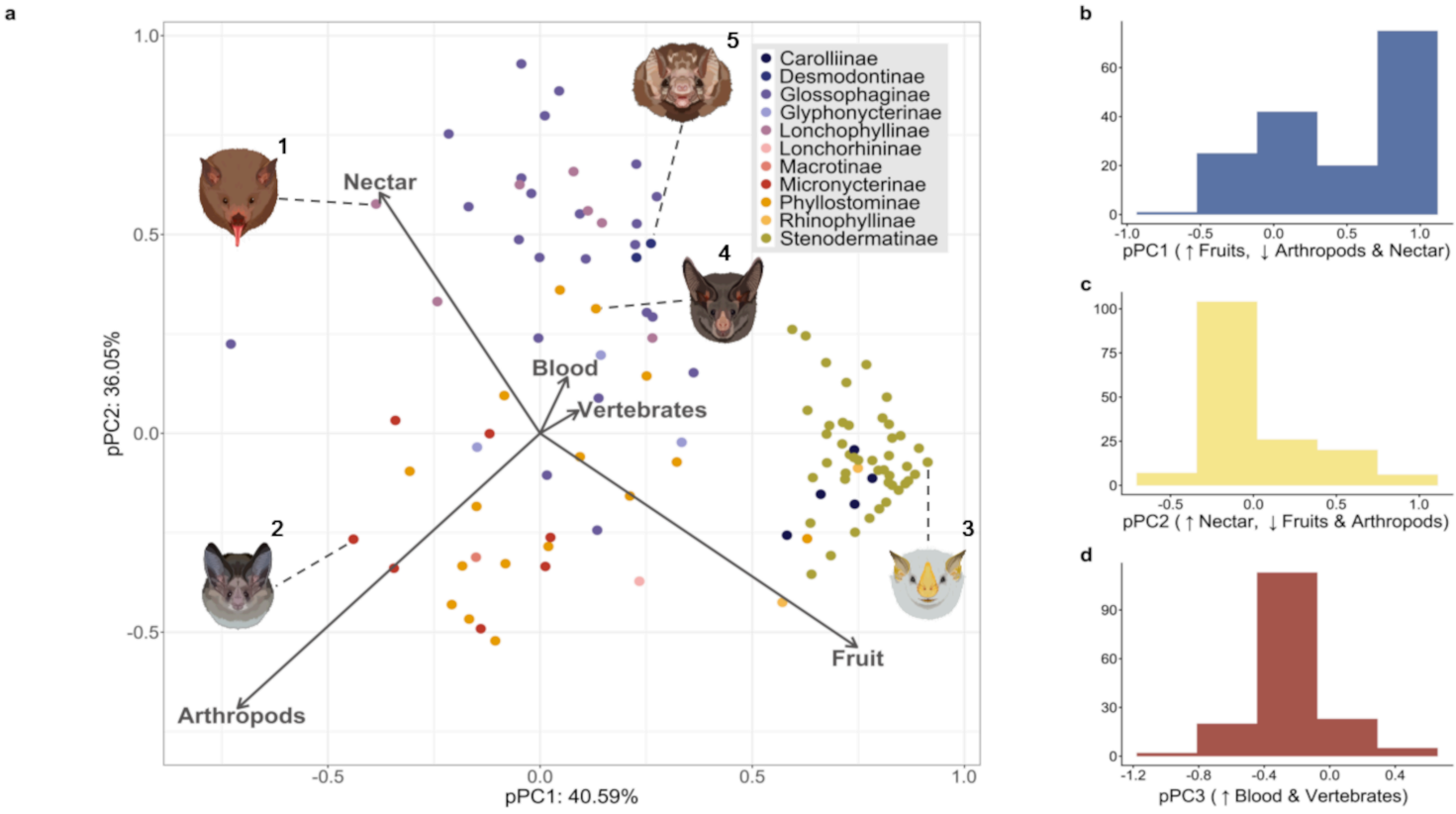


Figure 1

Phylogenetic Principal Component Analyses for dietary axes of dietary niche. **a)** shows the position of the dietary niche for each species. Dots with different colors indicate different subfamilies. **b-d)**Histograms show the frequency distribution across the range of values of each pPC. The illustrations of the bats were based on 1) *Glossophaga morenoi*, 2) *Macrotus waterhousii*, 3) *Ectophylla alba*, 4) *Vampyrum spectrum* and, 5) *Diphylla ecaudata*

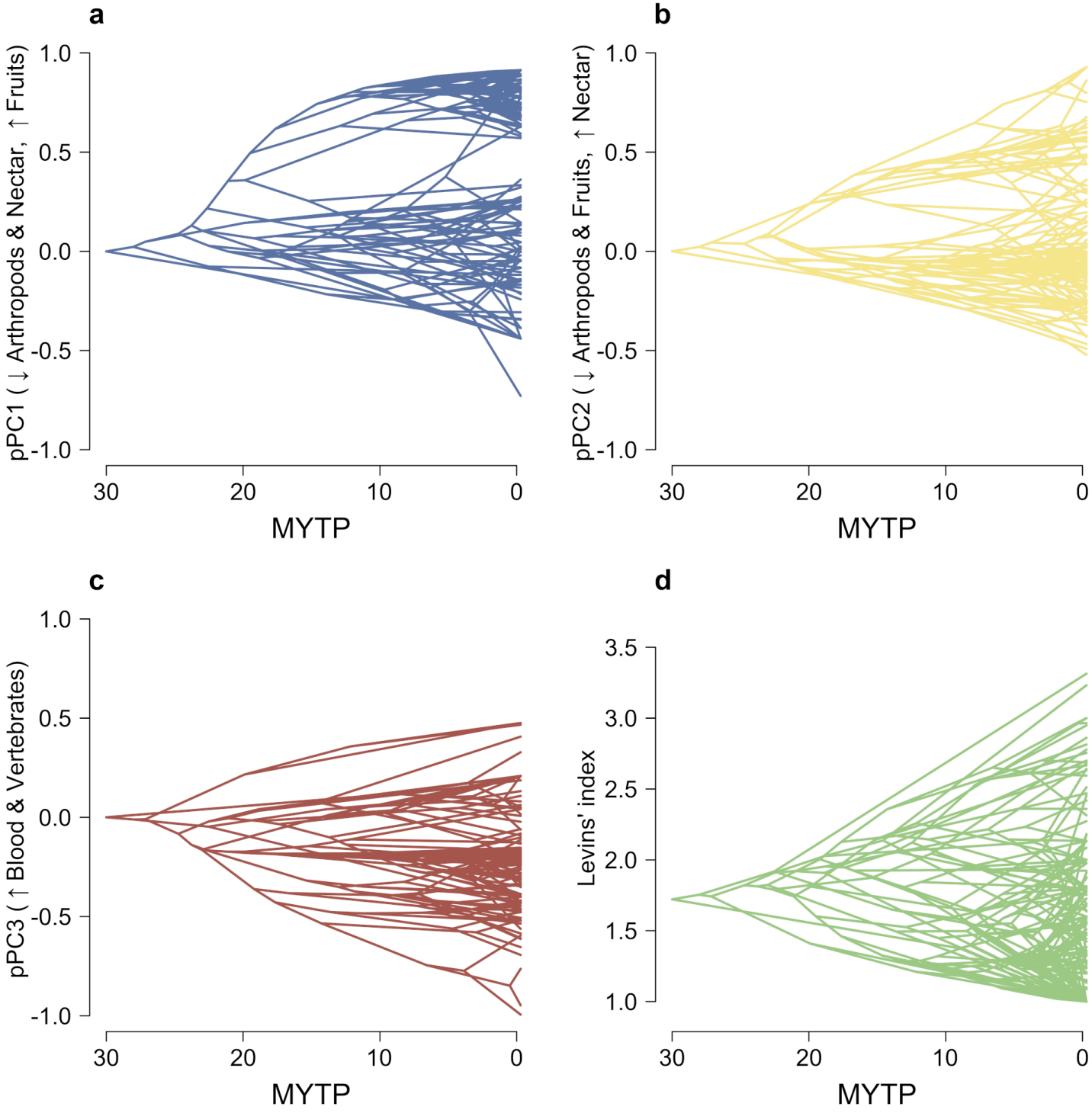


Figure 2

Evolution through time of our three traits for dietary niche position (pPC's) and niche breadth (Levins' index) from. MYTP = Millions of years to the present

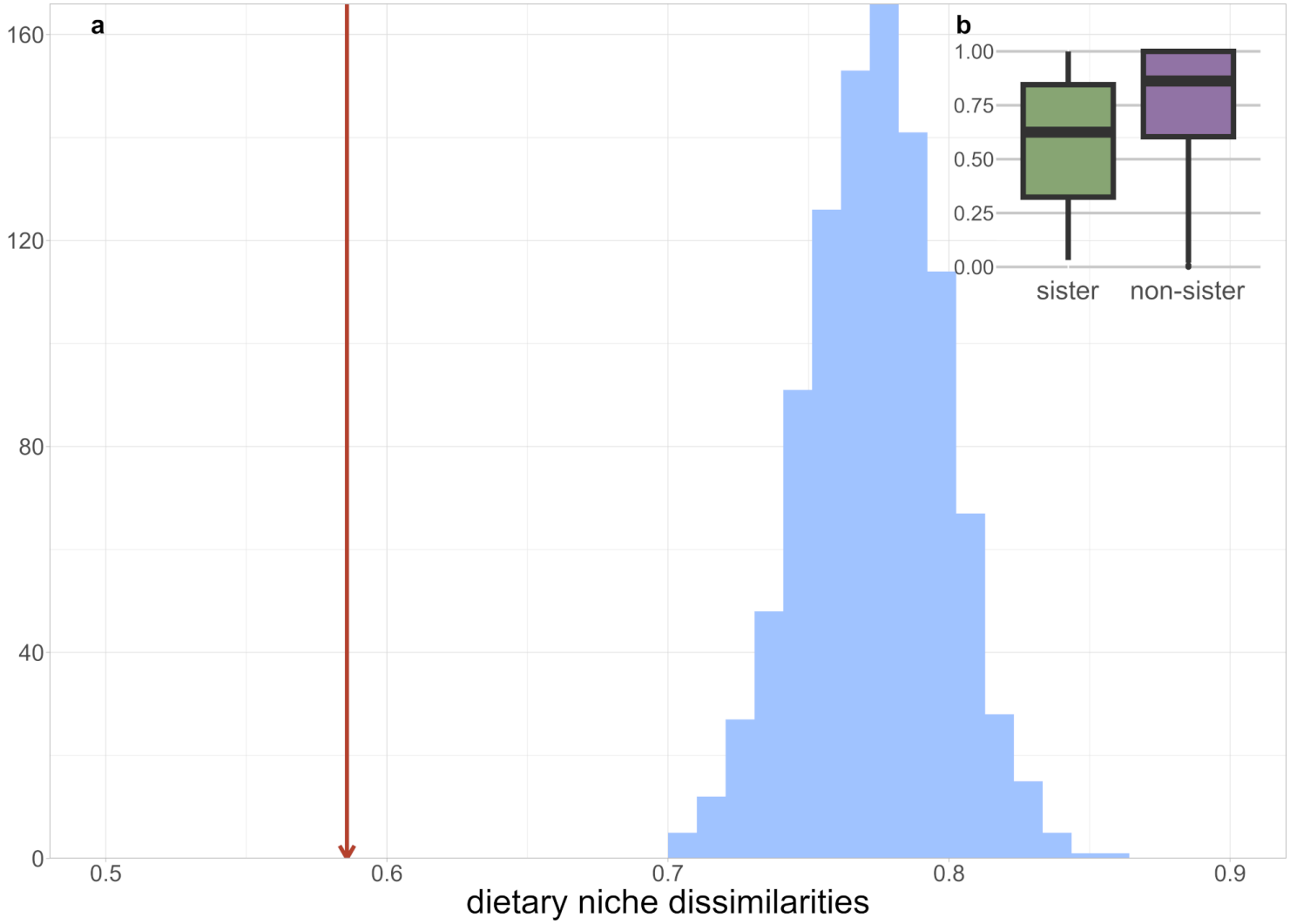


Figure 3

Adaptative shifts for dietary niche position detected by l1ou method. Black dots indicate new adaptative shifts detected for the family Phyllostomidae

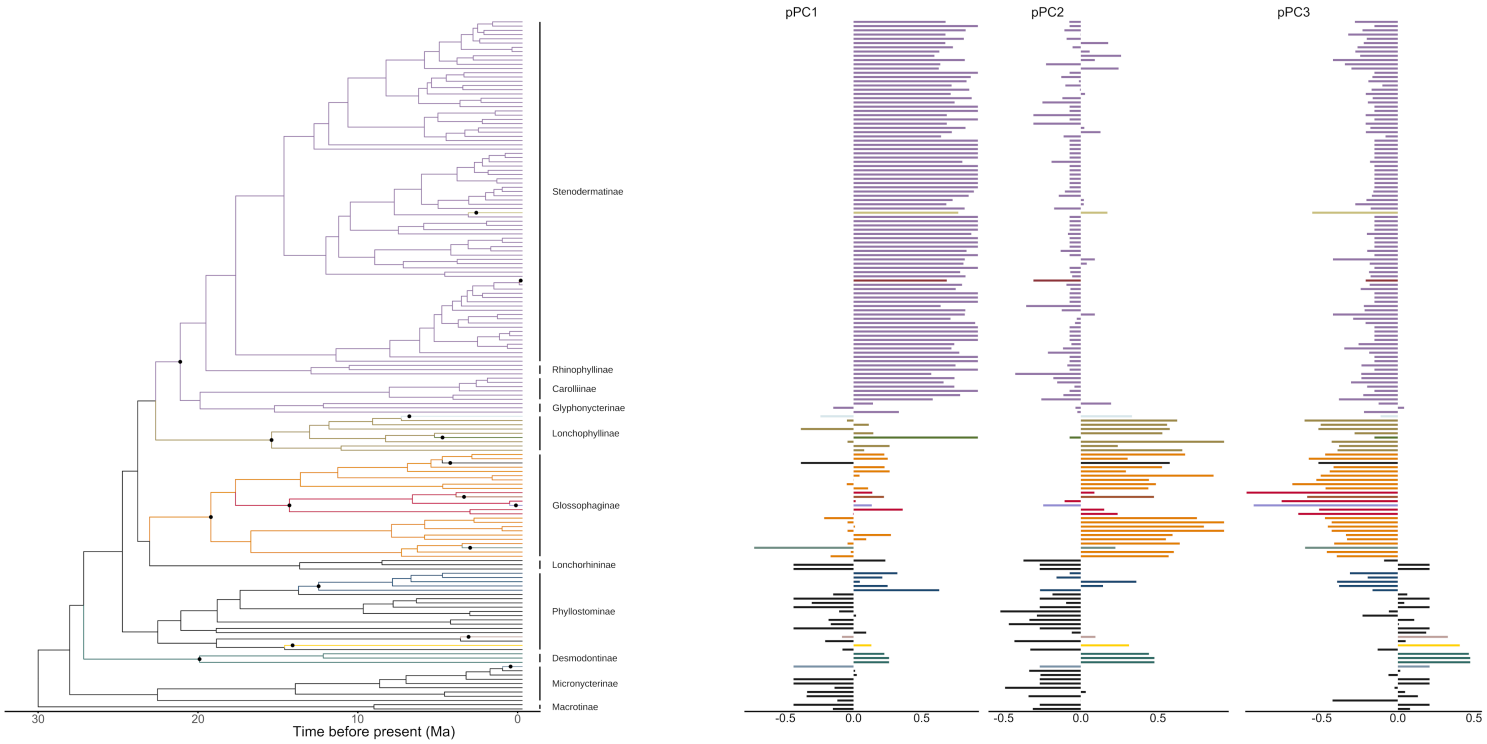


Figure 4

Distribution of values and mean of dietary niche dissimilarities between sister species pairs and non-sister pairs. a) Histogram indicates the null distribution of dissimilarity values out of 1000 iterations of non-species pairs generated. The arrow represents the observed mean dissimilarities for sister pairs. b) Boxplot shows the distribution of values of dissimilarities of sister and non-sister pairs.

Supplementary Files

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