

Research



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Community ecology

Annual precipitation predicts the phylogenetic signal in bat–fruit interaction networks across the Neotropics

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Closely related species tend to be more similar than randomly selected species from the same phylogenetic tree. This pattern, known as a phylogenetic signal, has been extensively studied for intrinsic (e.g. morphology), as well as extrinsic (e.g. climatic preferences), properties but less so for ecological interactions. Phylogenetic signals of species interactions (i.e. resource use) can vary across time and space, but the causes behind such variations across broader spatial extents remain elusive. Here, we evaluated how current and historical climates influence phylogenetic signals of bat–fruit interaction networks across the Neotropics. We performed a model selection relating the phylogenetic signals of each trophic level (bats and plants) with a set of current and historical climatic factors deemed ecologically important in shaping biotic interactions. Bat and plant phylogenetic signals in bat–fruit interaction networks varied little with climatic factors, although bat phylogenetic signals positively covaried with annual precipitation. These findings indicated that water availability could increase resource availability, favouring higher niche partitioning of trophic resources among bat species and hence bat phylogenetic signals across bat–fruit interaction networks. Overall, our study advances our understanding of the spatial dynamics of bat–fruit interactions by highlighting the association of current climatic factors with phylogenetic patterns of biotic interactions.

1. Introduction

The central goal of macroecology is to understand the mechanisms that determine species distributions and their co-occurrence across spatial and environmental gradients. Phylogenetically closely related species share similar traits and tend to occur at sites with similar geographical and environmental factors [1]. One of the primary explanations of such phylogenetic signals (i.e. the tendency of related species to be more similar to each other than to randomly selected species from the same phylogenetic tree [2]) in the distribution of species in similar environments is the conservatism of their ancestral niches [2]. Because phylogenetically closely related species share traits and environmental preferences, they also display similar roles in ecosystems (i.e. ways in which species use resources) and engage in similar biotic interactions [3]. However, compared to the climatic and geographical aspects of species niches, the study of species' trophic niches on a network level and their phylogenetic patterns of resource use are still very limited [3].

Studies have shown that biotic interactions exhibit phylogenetic signals, where closely related species of one trophic level interact with a set of similar

species of another trophic level [4]. Such phylogenetic signals potentially result from the evolutionary conservation of their ancestral trophic niches among species (i.e. trophic niche conservatism) [4]. Given the spatial and temporal co-occurrence of two or more species required for a biotic interaction to occur, phylogenetic patterns in biotic interactions can be more sensitive to climate than species' geographic distributions alone. Moreover, climatic and geographic variation across space and time may affect biological processes, such as dispersion and speciation rates [5], influencing the phylogenetic relatedness among species [6]. Consequently, the phylogenetic signal of biotic interactions would presumably be strongly modulated by spatial heterogeneity and current and historical environmental gradients [7].

Some of the most useful tools to study the organization of biotic interactions are derived from network analysis [8]. Studies dealing with species' interaction networks have provided new insights into the ecological and evolutionary processes structuring biotic interactions and their role in maintaining biodiversity [9]. For instance, the organization of interaction networks over spatial gradients is driven by both deterministic (e.g. niche-based assembly environmental factors, such as morphological matching) and stochastic factors (e.g. neutral-based assembly and dispersal, such as the probability of an interaction occurring as a function of species abundances) [10]. However, despite some evidence showing that the phylogenetic signals of pollination and seed-dispersal networks mediated by birds vary across space at the regional scale [11,12], the amount of theoretical and empirical information about the underlying drivers of trophic phylogenetic signals is still limited in the literature, mainly regarding other biotic interactions, such as bat frugivory.

Bats, namely from the family Phyllostomidae, disperse the seeds of plants from a variety of families and are key elements in the regeneration of tropical forests in the Neotropics [13]. Moreover, there is strong empirical evidence that phyllostomid bats have marked preferences for fruits of specific plant genera [14], which provides us with an excellent framework for studying the phylogenetic signal in bat–fruit interaction networks over large spatial scales. Phyllostomidae bat communities in warmer sites with lower climatic variability and closer to the equator tend to be more ecologically and phylogenetically similar than those in sites far from the equator, resulting in higher levels of diversity towards their tropical centre of origin (i.e. tropical niche conservatism) [15,16]. There are two main non-mutually exclusive hypotheses that posit explanations for bat diversity patterns on regional scales [17,18]. First, the energy hypothesis posits that sites with higher precipitation or temperature harbour species-rich communities, a large number of biotic interactions and a high division of trophic niches [12,19,20]. Second, the climatic stability hypothesis posits that sites with more current (annual) and historical (since the last glacial maximum) climatic stability have high species richness and biotic interactions [11,12,20]. Therefore, given that climatic factors and their geographic variation modulate the distribution of both bats and fruit, these factors were also expected to affect the phylogenetic signal of bat–fruit interaction networks, as previously reported for hummingbird–plant interaction networks [11]. To fill this research gap, we investigated how current and historical climatic variations shape phylogenetic signals in bat–fruit interaction networks across the Neotropics. We hypothesized

that bat–fruit interaction networks would exhibit an environmentally structured phylogenetic signal pattern, with a higher phylogenetic signal in sites with higher energy and climatic stability.

2. Material and methods

(a) Dataset

We compiled a dataset of 44 bat–plant interaction networks distributed across the Neotropics. Most records came from primary publications, and some grey literature datasets (e.g. theses) were also included. The dataset covered a range between 1975 and 2017 (figure 1; electronic supplementary material, appendix S1). To compile this dataset, we used the main scientific search engines (i.e. Google Scholar, Web of Science and Scielo), and all studies reporting the diet of local phyllostomid bat communities were compiled. Our search was done in the three predominant languages within the Neotropical region: Spanish, English and Portuguese (electronic supplementary material, appendix S2).

For each study, we built an interaction matrix A , in which the element a_{ij} equalled 1 if there was a recorded interaction between a plant species i and a bat species j , while zero values represented non-observed interactions. The use of binary networks responded to our focus on the breadth of interactions between bats and fruit and not on the intensity of these relationships, while acknowledging the difficulty of accurately measuring the difference in the frequency of resource consumption among plant species and across studies [21].

(b) Phylogenetic signal in bat–fruit interaction networks

We measured the phylogenetic signal in bat–fruit networks using the framework proposed by Ives & Godfray [22] that evaluates the effect of phylogeny on species' interaction patterns by quantifying the degree to which phylogenetically closely related species are more likely to share similar interaction partners than distantly related species. The phylogenetic signal of bat–fruit interaction networks was obtained using the bat phylogeny (Chiroptera: Noctilionoidea) from Rojas *et al.* [23] and the seed plant phylogeny (ALLMB) from Smith & Brown [24], following the backbone provided by Magallón *et al.* [25]. For both plant and bat phylogenies, we calculated the variance–covariance matrices as a measure of the phylogenetic distances between species [26]. This analytical framework uses variance–covariance and interaction matrices, based on an Ornstein–Uhlenbeck evolutionary model with stabilizing selection, presuming that the product of phylogenetic distances gives the strength of interactions between bats and fruit [22].

We performed phylogenetic bipartite linear models to obtain the phylogenetic signal from both bat (d_{bats}) and plant (d_{plants}) trophic levels for each of the 44 bat–fruit interaction networks [27]. The ' d ' parameter determines the strength of the phylogenetic signal on species' interaction patterns, varying from 0 (no effect of phylogeny on interactions), with values increasingly higher than 0 implying weak to strong phylogenetic signals. This parameter was calculated by an estimated generalized least square model, which does not assume normally distributed phylogenetic distances and biotic interactions [22] (electronic supplementary material, appendix S3). The percentage of fruits/seeds consumed by bats identified up to the species level varied greatly among the 44 networks. Thus, to avoid comparing networks with different taxonomic resolutions, we performed phylogenetic signal analyses at the genus level on the phylogeny for plants and the species level for bats. In other words, all plant morpho-species interactions were pooled at the genus level over all 44 networks.

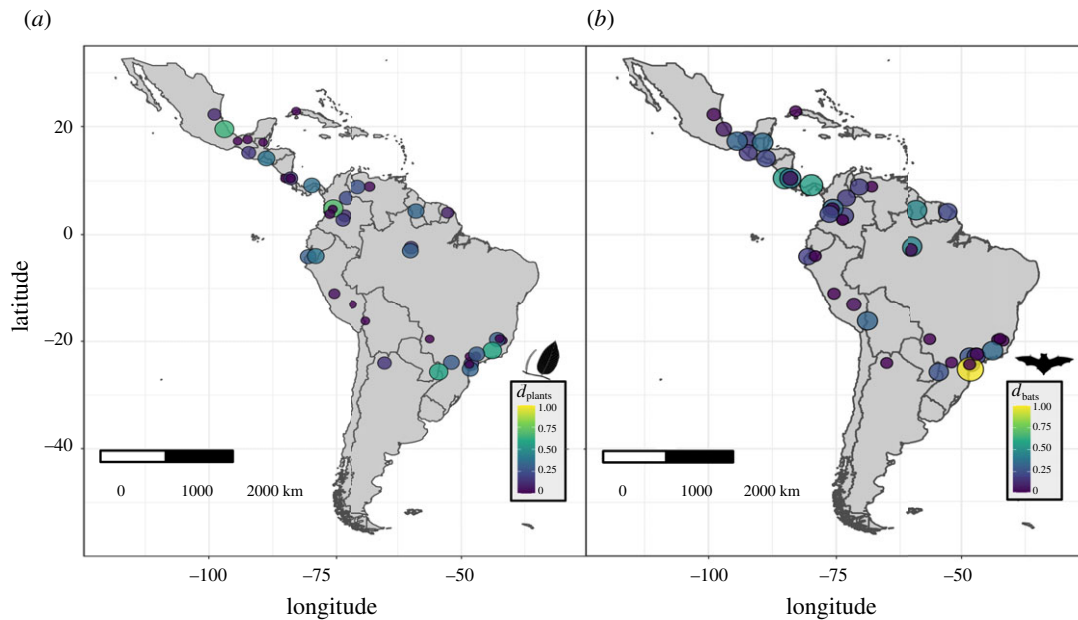


Figure 1. Geographic distribution of the 44 bat–fruit interaction networks throughout the Neotropical region. Circle size and colour intensity are proportional to the phylogenetic signal for (a) plants and (b) bats.

Therefore, higher values of d_{bats} and d_{plants} represent a stronger phylogenetic signal of bat species and plant genera, respectively, where phylogenetically close operational taxonomic units (OTUs) interacted with more similar OTUs from the other trophic level [22]. Following the approach proposed by Schleuning *et al.* 2012 [28], we found no evidence that sampling intensity was related to plant and bat phylogenetic signals ($d_{\text{bats}} r = 0.12$, $p = 0.42$; $d_{\text{plants}} r = -0.20$, $p = 0.17$).

(c) Climatic predictors

We evaluated the relative influence of current climate factors on the phylogenetic signal of bats and plants within their interaction networks across the Neotropical region. Based on the energy and seasonality hypotheses, suggested as explanations for the structure of mutualistic pollination and seed-dispersal networks [12,20,29], as well as bat species richness [17,18], the following climatic variables were considered: mean annual temperature, mean annual precipitation, temperature seasonality and precipitation seasonality [30]. Historical climate variations influenced the current distribution and evolutionary paths of species from both trophic levels, consequently affecting interactions and the phylogenetic signal of the networks. Thus, we also used historical climatic predictors (i.e. temperature instability and precipitation instability from the maximum glaciation), which are usually related to the structure of the mutualistic networks over broad spatial scales [11,12,28]. The climatic values of each network were obtained from the coordinates where each study was performed. Climatic predictors were extracted from the Worldclim v. 2.0 dataset at a 2.5° resolution per pixel [30]. The historical climatic predictors were obtained with the library climateStability [31], which represented the inverse of the standard deviation of the temperature and precipitation from 20 100 years ago and were calculated in slices of 1000 years from the RaCE21 ka experiments using the CCSM 3.0 climate model.

(d) Statistical analyses

First, we tested whether bat and plant phylogenetic signals were spatially correlated using a modified correlation test that controls the spatial autocorrelation of two geographically structured variables [32]. The relationships between phylogenetic signals and current and historical climatic factors were evaluated using

saturated models consisting of compound Poisson generalized linear models with all additive combinations of the predictor factors. Subsequently, we adjusted the models with a Tweedie distribution because our data are continuous, strictly positive and included many zeros [33]. For this, we used the Akaike Information Criterion for small samples (AICc). Models with a $\Delta\text{AICc} \leq 2$ and a $\omega\text{AICc} \geq 0.1$ were selected as the best models from all additive combinations (electronic supplementary material, appendixes S4 and S5). The models were averaged with the predicting factors selected within the best models to obtain the relative importance of each predictor. Good predictors of the phylogenetic signal of bat–fruit networks were considered those with a relative importance ($\sum \omega\text{AICc}$) ≥ 0.8 [34]. We evaluated the spatial autocorrelation in the residuals of global models using Moran's I index, and none of these models showed spatial autocorrelation [26].

3. Results

Overall, the 44 analysed networks covered a geographic range of 48° of latitude from Argentina to Mexico, covering most of the distribution of the bat family Phyllostomidae across the Neotropics. Our study included 79 bat species and 119 plant genera (electronic supplementary material, appendix S1). The bat species with the highest frequency in the networks were *Artibeus lituratus* (81% of the networks, $n = 36$), followed by *Carollia perspicillata* (77% of the networks, $n = 34$) and *Sturnira lilium* (77% of the networks, $n = 34$). The most common plant species was *Piper aduncum* (Piperaceae) (47% of the networks, $n = 21$), followed by *Ficus insipida* (Moraceae) (29% of the networks, $n = 13$) and *Piper amalago* (Piperaceae) (29% of the networks, $n = 9$). The most common plant genera were *Piper* (97% of the networks, $n = 43$), *Cecropia* (93% of the networks, $n = 42$) and *Ficus* (90% of the networks, $n = 40$).

In general, bat and plant phylogenetic signals exhibited similar values (d_{bats} : mean \pm s.d.: 0.17 ± 0.20 , ranging from 0 to 0.98; d_{plants} : 0.17 ± 0.19 , ranging from 0 to 0.68) throughout the Neotropical region. However, we found that neither bat (d_{bats}) nor plant (d_{plants}) phylogenetic signals were spatially

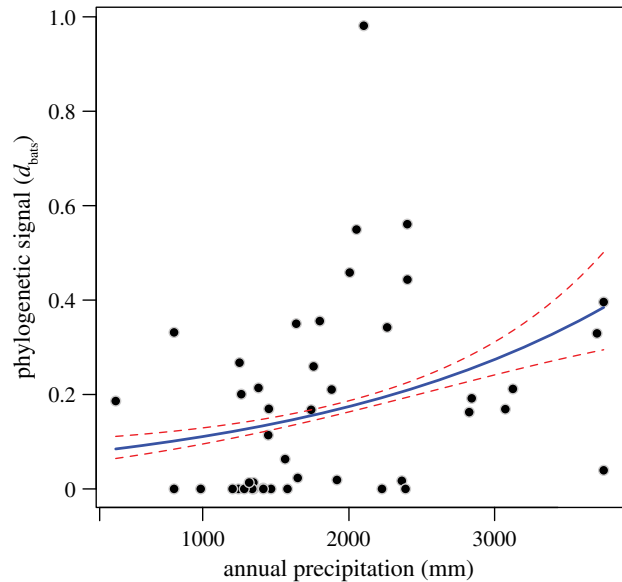


Figure 2. Relationship between bat phylogenetic signal (d_{bats}) and mean annual precipitation (mm). Solid line represents the predicted curve and dotted lines represent the best fit model with a 95% confidence interval ($p_{\text{pseudo}}r^2=0.11$). Confidence intervals were estimated with 1000 bootstrapped (with replacement) samples of the dataset and model fitting.

correlated ($r=0.22$, $p=0.14$). Additionally, we observed that the bat phylogenetic signal (d_{bats}) was only positively associated with mean annual precipitation (figure 2). Specifically, we observed that sites with a higher mean annual precipitation presented a stronger bat phylogenetic signal (d_{bats}) within bat–fruit interaction networks (table 1 and figure 1). Furthermore, there was no evidence that the plant phylogenetic signal (d_{plants}) was associated with any of the predictor variables studied (table 1).

4. Discussion

Here, we observed that bat and plant phylogenetic signals in bat–fruit interaction networks varied little with current and historical factors throughout the Neotropics. However, we found that mean annual precipitation was positively related to the strength of bat phylogenetic signals in bat–fruit interaction networks. Moreover, there was no evidence of any current or historical climatic factor structuring plant phylogenetic signals in these networks.

Some studies have shown that sites with greater species richness and abundance increase phenotypic matching between two trophic levels, reducing the generalization and increasing the phylogenetic signal in species’ interaction networks [35]. In this sense, a higher water availability (i.e. high accumulated precipitation) within ecosystems can increase fruiting species richness [36] and thus increase frugivory events by vertebrates [37]. In this study, closely related bats tended to share more resources among them (in terms of plant genera) in those sites with higher precipitation. Sites with high precipitation tend to exhibit large pools of fleshy fruit plants, mainly given by these plants’ need for high amounts of water to grow [38]. Therefore, high values of annual precipitation can be related to a large diversity of food resources for bats, shaping bat–fruit interactions. Moreover, frugivorous bats tend to shift their diet in sites with low

Table 1. Model averaging of the phylogenetic signal in bat–fruit interaction networks and Moran’s index (I) and its statistical significance (P). β represents the averaged estimated parameters of each predictor and the positive or negative values represent the direction of the association. Σwi represents the relative importance of each predictor. MAT, mean annual temperature; AP, annual precipitation; PS, precipitation seasonality; HTI, historical temperature instability; HPI, historical precipitation instability. Numbers in *italic* and with a single asterisk (*) indicate the best predictor (i.e. relative importance ≥ 0.8) of the phylogenetic signal.

phylogenetic signal	distribution family	MAT		AP		PS		HTI		HPI		Moran’s I		full model R^2
		Σwi	β	Σwi	β	Σwi	β	Σwi	β	Σwi	β	I	p	
plants (d_{plants})	Tweedie	0.37	−0.22	—	—	—	—	—	—	0.19	−0.04	−0.008	0.39	0.30
bats (d_{bats})	Tweedie	—	—	0.83*	0.09	0.15	0.03	0.22	0.04	0.14	0.04	0.005	0.31	0.34

resource availability, such as those with low precipitation, reducing diet partitioning among coexisting bats and thus decreasing the phylogenetic signal within their interaction networks [39].

The absence of association of plant phylogenetic signal with any climatic predictor may be caused by the genus level resolution of the phylogenetic hypothesis used for this trophic level. In our analyses, plants were considered only at the genus level because in the original sources of information, this was the finest level of identification of many fruits/seeds consumed by bats. This fact reveals the challenging nature of the task of identifying plants at the species level even when direct evidence is available (e.g. defecated seeds by bats). Accordingly, phylogenetic signal of plant species may still be related to climatic factors, but this is not evident at the genus level because of their species richness differences (species-rich versus species-poor genera) and broad geographic distributions. Indeed, the geographic distribution and taxonomic variation of both trophic levels may obscure the identification of plant species' distribution and interaction patterns. For instance, New World frugivorous bats are mostly restricted to the Neotropical region and to one particular family (Phyllostomidae) [13], which could increase diet partitioning among closely related bats by selecting plants based on their fruit similarity [40]. Conversely, plant genera consumed by bats are more widely distributed and represented by a much larger taxonomic diversity of plants (62 plant families), from which only a few species are exclusively consumed by bats [41]. As such, fruit plants may depend less on specific frugivores, such as bats, across their entire distribution, showing different levels of interaction intimacy [42], probably related to different selection pressures and environmental effects on the distinct

ways plants interact with animals compared to the more restricted way in which animals interact with plants (e.g. a frugivore only consumes plant fruits, but plants are not only 'used' by frugivores but also by herbivores and pollinators) [43]. In consequence, fruit traits may not be as phylogenetically conserved as bat traits [43,44]. Therefore, presumably, plant phylogenetic signals within the networks should be more diffuse and less likely to be associated with abiotic factors.

Here, we showed that bat–plant interaction networks are phylogenetically structured and shaped by mean annual precipitation, indicating that part of the bat–fruit interaction network organization could be explained by trophic niche conservatism, where closely related species shared similar dietary preferences and thus tended to interact with a similar set of species. In short, our findings advance our understanding of the spatial dynamics of bat–fruit interaction networks by demonstrating that the phylogenetic structure of such networks can be associated with current climatic factors over broad spatial gradients.

Data accessibility. Data were sourced from literature and uploaded as part of the electronic supplementary material [45].

Authors' contributions. The study was designed by E.J.C., F.V., A.L.-N., R.G., P.R.G. Jr and W.D. Data collection was carried out by E.J.C.. Data analyses were performed by E.J.C. E.J.C. drafted the manuscript with help from F.V. and W.D. All authors contributed to the final draft and editing, giving their approval for publication, and agreeing to be held accountable for the work performed herein.

Competing interests. We declare we have no competing interests.

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