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Ecological function over evolutionary legacy: The limited role of shared evolutionary history in shaping modern frugivory interactions

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Abstract

1. Frugivory, encompassing interactions between vertebrates and plants that range from mutualistic to antagonistic, drives seed dispersal and underpins the structure and resilience of tropical ecosystems. However, the relative importance of shared evolutionary history versus present-day functional traits in shaping these interactions remains unresolved.
2. Here, we analyse frugivory networks involving bats, birds and primates across the Neotropics through a comprehensive framework that evaluates the interplay between evolutionary constraints and ecological sorting in mutualistic networks.
3. Using the Procrustean Approach to Cophylogeny, we detect a weak but significant cophylogenetic signal, suggesting that evolutionary history leaves a detectable, though limited, imprint on network structure. In contrast, ecological and functional traits—particularly dietary specialization, network connectivity and fruit characteristics such as husk presence, type, colour and size—emerge as dominant drivers of interaction patterns.
4. Species with similar ecological roles tend to cluster within modules, especially among primates and bats, reflecting strong trait-mediated filtering rather than phylogenetic conservatism. Moreover, we document contrasting evolutionary patterns between interaction partners, as vertebrate traits exhibit strong phylogenetic signal, while fruit traits are more evolutionarily labile, indicating that plant traits may respond more rapidly to ecological pressures.
5. These findings suggest that evolutionary legacy provides a scaffold for frugivory interactions, but contemporary ecological processes more strongly shape their assembly and modular structure. This asymmetry challenges assumptions about strict coevolutionary matching and highlights the flexibility of plant–animal interactions under ecological change.
6. The framework offers a roadmap for disentangling drivers of interaction patterns in other mutualisms, with broad applications to community ecology, trait evolution, and conservation biology. Understanding how trait matching, often influenced by conserved traits, and shared evolutionary history interact to

structure mutualistic networks is essential for predicting their resilience under global change, emphasizing the need to conserve not only species but also the interactions that sustain tropical biodiversity and ecosystem functioning.

KEYWORDS
cophylogenetic signal, ecological filtering, mutualistic networks, network modularity, seed dispersal dynamics

1 | INTRODUCTION

Mutualistic interactions between vertebrates and plants form complex ecological networks that drive key processes in tropical ecosystems, including seed dispersal, plant recruitment and biodiversity maintenance (Bascompte & Jordano, 2007). Understanding how these mutualisms are structured requires disentangling the contributions of present-day trait matching—through which biotic interactions are assembled—and shared evolutionary history, which reflects phylogenetic conservatism, codiversification or coevolutionary processes (Agrawal & Zhang, 2021; Thompson, 1994). Importantly, trait matching is often shaped by evolutionary history, as traits involved in interactions tend to be phylogenetically conserved. Despite growing interest in the eco-evolutionary dynamics of interactions, distinguishing codiversification from trait-mediated ecological filtering remains a central challenge (Perez-Lamarque & Morlon, 2024). This calls for an integrative framework to assess the relative contributions of evolutionary legacy and contemporary ecological processes in shaping frugivory networks. Frugivores, including bats, birds and primates, consume fruits and disperse seeds across landscapes, facilitating gene flow, habitat colonization, and the regeneration of plant communities (Fleming & Kress, 2013; Howe & Smallwood, 1982). In turn, plants offer nutritional rewards, creating a reciprocal relationship and raising questions about the evolutionary mechanisms underlying the patterns that drive present-day dynamics of frugivory networks.

A central question in the study of frugivory is whether phylogenetic relationships among species constrain their ecological interactions. Cophylogenetic signal—the tendency for closely related species in one clade to interact with closely related species in the other (Perez-Lamarque & Morlon, 2024)—can emerge through a variety of mechanisms, including phylogenetic conservatism of interaction-mediating traits, ecological filtering of pre-existing traits, or true coevolutionary processes involving reciprocal adaptation (Blasco-Costa et al., 2021). In frugivory networks, a strong phylogenetic signal may reflect deep coevolutionary relationships in tightly specialized interactions. However, such signal can also arise from conserved traits that mediate interactions, such as fruit and seed size or animal body mass, that are shaped by shared evolutionary histories and conserved ecological niches, without necessarily involving reciprocal adaptation (Blasco-Costa et al., 2021; Perez-Lamarque & Morlon, 2024). Disentangling these scenarios is particularly challenging in tropical systems, where high species diversity and generalized interactions may obscure phylogenetic patterns (Fuzessy, Silveira, et al., 2022), even when traits themselves are evolutionarily conserved.

While strong signals may suggest coevolution in tightly specialized interactions, it may also result from ecological sorting of traits shaped by past evolution (Perez-Lamarque & Morlon, 2024). Distinguishing these alternatives is particularly important in hyperdiverse tropical systems, where diffuse interactions and trait lability may obscure evolutionary pathways (Blasco-Costa et al., 2021). In frugivores, traits such as body size, dietary breadth and foraging strategies influence their capacity to access and disperse seeds (Dehling et al., 2016). For plants, fruit traits including nutritional value, size, colour and seed number mediate attractiveness to different dispersers and the outcomes of seed dispersal (Lomáscolo & Schaefer, 2010).

Frugivorous vertebrates offer a powerful comparative framework for investigating eco-evolutionary dynamics. Bats, birds and primates, representing distinct evolutionary lineages, exhibit unique morphological, behavioural and ecological adaptations, together accounting for the majority of frugivory interactions in the Neotropics (Fuzessy & Pizo, 2025b). Although other vertebrate groups (e.g. rodents, ungulates) also participate in seed dispersal, their interactions are less frequently documented and tend to involve phylogenetically diverse lineages. This combination of limited data availability and diffuse phylogenetic patterns reduces the power of cophylogenetic approaches for these groups. Several frugivorous bat species, such as those in the genus *Artibeus*, display nocturnal foraging adaptations, for example acute olfaction, and contribute significantly to long-distance seed dispersal (Fleming et al., 2009), although this specialization is not uniform across all bat taxa. Birds rely predominantly on visual cues and exhibit diverse morphologies, exhibiting a wide range of dietary strategies, from strict frugivory to omnivory, and play a crucial role in diurnal seed dispersal (Kissling et al., 2009). Primates are arboreal, equipped with complex sensory systems and social behaviours, cognitive abilities and manual dexterity, being key seed dispersers in tropical forests (Chapman & Russo, 2006; Fuzessy, Sobral, et al., 2022). These divergent foraging strategies reflect distinct evolutionary constraints and opportunities, offering a natural experiment to disentangle how ecological processes (e.g. trait matching, environmental filtering) and phylogenetic conservatism jointly influence the structure of frugivory networks. By comparing their interactions with plants, we can better understand how phylogenetic and ecological factors shape these networks.

Recent advances in network theory and phylogenetic comparative methods have opened new avenues to investigate whether mutualistic networks are structured by conserved ecological traits or dynamic reciprocal adaptations. In this context, three complementary approaches have emerged as central tools: the Procrustes Approach to Cophylogeny (PACo), network modularity analysis and trait-based approaches. PACo quantifies the degree of phylogenetic congruence between interacting clades by comparing their evolutionary trees, providing insights into the extent to which shared evolutionary history structures species interactions (Balbuena et al., 2013). Although PACo effectively detects cophylogenetic signal—indicating congruent branching patterns between partners—it cannot, on its own, distinguish between coevolution, phylogenetic trait conservatism, or ecological filtering as underlying mechanisms (Perez-Lamarque & Morlon, 2024). Therefore, robust interpretation requires integrating PACo with analyses of network architecture, functional traits and their phylogenetic signal (Figure 1). Although PACo has been applied to various mutualistic systems, its use in frugivory networks, especially across multiple vertebrate groups with distinct ecological and evolutionary traits, remains underexplored (but see Fuzessy, Silveira, et al., 2022).

Modularity analysis, which identifies subgroups of tightly interacting species (Olesen et al., 2007), adds a crucial layer to this framework. In frugivory networks, this organization of species into subgroups with dense internal interactions and sparse connections between groups (Olesen et al., 2007) may arise from ecological specialization, where specific groups of frugivores preferentially interact with particular groups of plants (Mello et al., 2011). This structure can reflect either convergent ecological filtering or historical coevolutionary processes. True coevolutionary dynamics are expected to produce modularity aligned with phylogenetic clustering, as reciprocal adaptations accumulate over evolutionary time within interacting lineages (Agrawal & Zhang, 2021). Conversely, trait-mediated ecological filtering may also generate modularity, but without reciprocal evolutionary change, characteristic of coevolution, often resulting in weaker phylogenetic congruence (Perez-Lamarque & Morlon, 2024). Beyond revealing interaction patterns, modularity has profound implications for the tendency of ecological networks to evolve, as it can buffer disturbances and facilitate local adaptation (Nordbotten et al., 2018).

Importantly, neither PACo nor modularity analysis alone can distinguish between trait-mediated ecological filtering and true coevolution. For instance, if frugivore body size and fruit size both exhibit a strong phylogenetic signal and simultaneously drive modularity by trait conservatism and morphological matching, their combined effects could simulate cophylogenetic patterns without reflecting actual coevolution. Disentangling these alternatives demands an integrative approach that merges cophylogeny, network structure, functional trait data, biogeographic information and phylogenetic signal analysis. This enables a more mechanistic understanding of how mutualistic networks assemble and evolve, shedding light on the eco-evolutionary processes that underpin biodiversity. Despite their potential, these integrative methods remain underexplored in frugivory systems, particularly across taxonomically and ecologically diverse vertebrate groups such as bats, birds and primates (but see Fuzessy, Silveira, et al., 2022).

This study addresses four key objectives: (1) quantifying cophylogenetic signal across frugivory networks using a hierarchical framework (whole-network, frequent interactions, structured modules, and specialized clade levels); (2) testing whether modularity aligns with phylogenetic clusters; (3) evaluating how functional traits of both vertebrates and plants mediate cophylogeny; and (4) assessing phylogenetic conservatism in these traits. By integrating these approaches, we provide a mechanistic understanding of whether frugivory networks are structured by deep evolutionary legacies or contemporary ecological processes—a critical step toward predicting their resilience to anthropogenic change.

2 | METHODS

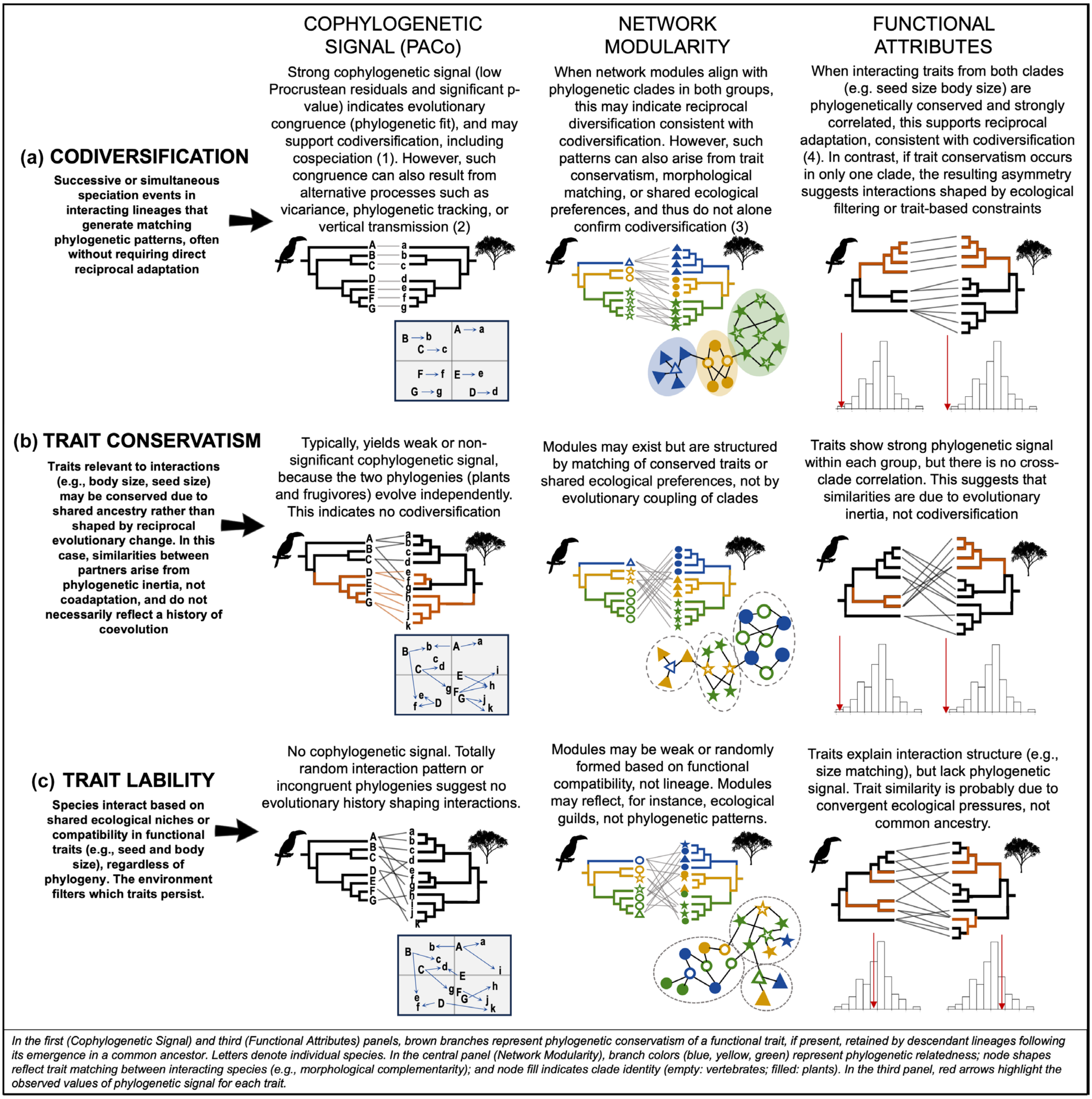
2.1 | Dataset of interactions

We analysed frugivory interactions using the NeoFrugivory database (Fuzessy & Pizo, 2025b), the first comprehensive compilation of frugivory interactions spanning the entire Neotropical realm. This database synthesizes data from 419 studies (1967–2023), documenting 10,175 unique interactions between 2375 plant species and 758 vertebrate species across diverse taxa, including primates, bats, birds, ungulates, reptiles and rodents. NeoFrugivory standardizes interaction records with functional trait data for both plants (e.g. fruit morphology, seed characteristics) and vertebrates (e.g. body mass, diet), enabling robust analyses of ecological networks and evolutionary patterns.

To assess sampling completeness, we estimated sample coverage for the full frugivory network as well as for key vertebrate taxonomic groups (i.e. birds, primates, bats). We relied on presence/absence data, treating each study in the database as an independent sampling unit. For each network (overall and subgroup), we created an incidence frequency matrix in which the first row represented the number of sampling units (i.e. studies), and the second row listed the frequency with which each unique plant–frugivore interaction was recorded across studies. We then generated sample coverage curves to estimate the proportion of interaction diversity captured by the data; these curves are presented in Supporting Material S1.

2.2 | Hierarchical cophylogenetic assessment framework

We implemented a multi-level analytical approach to evaluate cophylogenetic signals across different biological scales: (1) whole-network level, assessing all vertebrate-plant interactions; (2) retaining only interactions with a frequency ≥2 and involving the diet of frugivores; (3) retaining only interactions with a frequency ≥3 and involving the diet of frugivores; (4) modular level, focusing on



COPHYLOGENETIC SIGNAL (PACo)

NETWORK MODULARITY

FUNCTIONAL ATTRIBUTES

(a) CODIVERSIFICATION

Successive or simultaneous speciation events in interacting lineages that generate matching phylogenetic patterns, often without requiring direct reciprocal adaptation

Strong cophylogenetic signal (low Procrustean residuals and significant p-value) indicates evolutionary congruence (phylogenetic fit), and may support codiversification, including cospeciation (1). However, such congruence can also result from alternative processes such as vicariance, phylogenetic tracking, or vertical transmission (2)

When network modules align with phylogenetic clades in both groups, this may indicate reciprocal diversification consistent with codiversification. However, such patterns can also arise from trait conservatism, morphological matching, or shared ecological preferences, and thus do not alone confirm codiversification (3)

When interacting traits from both clades (e.g. seed size body size) are phylogenetically conserved and strongly correlated, this supports reciprocal adaptation, consistent with codiversification (4). In contrast, if trait conservatism occurs in only one clade, the resulting asymmetry suggests interactions shaped by ecological filtering or trait-based constraints

(b) TRAIT CONSERVATISM

Traits relevant to interactions (e.g., body size, seed size) may be conserved due to shared ancestry rather than shaped by reciprocal evolutionary change. In this case, similarities between partners arise from phylogenetic inertia, not coadaptation, and do not necessarily reflect a history of coevolution

Typically, yields weak or non-significant cophylogenetic signal, because the two phylogenies (plants and frugivores) evolve independently. This indicates no codiversification

Modules may exist but are structured by matching of conserved traits or shared ecological preferences, not by evolutionary coupling of clades

Traits show strong phylogenetic signal within each group, but there is no cross-clade correlation. This suggests that similarities are due to evolutionary inertia, not codiversification

(c) TRAIT LABILITY

Species interact based on shared ecological niches or compatibility in functional traits (e.g., seed and body size), regardless of phylogeny. The environment filters which traits persist.

No cophylogenetic signal. Totally random interaction pattern or incongruent phylogenies suggest no evolutionary history shaping interactions.

Modules may be weak or randomly formed based on functional compatibility, not lineage. Modules may reflect, for instance, ecological guilds, not phylogenetic patterns.

Traits explain interaction structure (e.g., size matching), but lack phylogenetic signal. Trait similarity is probably due to convergent ecological pressures, not common ancestry.

In the first (Cophylogenetic Signal) and third (Functional Attributes) panels, brown branches represent phylogenetic conservatism of a functional trait, if present, retained by descendant lineages following its emergence in a common ancestor. Letters denote individual species. In the central panel (Network Modularity), branch colors (blue, yellow, green) represent phylogenetic relatedness; node shapes reflect trait matching between interacting species (e.g., morphological complementarity); and node fill indicates clade identity (empty: vertebrates; filled: plants). In the third panel, red arrows highlight the observed values of phylogenetic signal for each trait.

FIGURE 1 Conceptual framework illustrating how cophylogenetic signal (PACo), network modularity and trait-based approaches can be used in combination to disentangle the ecological and evolutionary processes structuring interaction networks. We depict three scenarios with distinct underlying processes: (a) codiversification, in which successive or simultaneous speciation events generate matching phylogenetic trees; (b) trait conservatism, the tendency of closely related species to retain similar ecological or morphological traits over evolutionary time, which can structure interaction networks and produce phylogenetically correlated patterns; and (c) trait lability, where interactions arise from trait compatibility or shared ecological niches, independent of phylogenetic history. Each scenario is assessed with three common methods: PACo, modularity and trait phylogenetic signal. PACo tests for cophylogenetic signal, quantifying whether the phylogenetic relationships of interacting partners are more similar than expected by chance, based on a Procrustes superimposition of their phylogenetic distance matrices. Modularity defines groups of animals and plants that interact more strongly among themselves. The evolution of functional traits is assessed by comparing the correlation between trait similarity and phylogenetic distance against a null model. Importantly, while individual methods may yield similar outputs across different scenarios, only the integration of all three provides the resolution needed to infer the dominant processes shaping interaction structure. 1. Blasco-Costa et al. (2021); 2. Althoff et al. (2014); 3. Nordbotten et al. (2018); 4. Perez-Lamarque and Morlon (2024).

ecologically significant subgroups (see further explanation below); and (5) specialized clade level, examining plant families with recognized strong relationships with each vertebrate group. To account for rare or opportunistic interactions that deviate from the typical fruit selection behaviour of frugivores (e.g. young or particularly hungry individuals consuming atypical food items out of inexperience or necessity), we progressively increased the interaction frequency threshold ($n > 1$ and above) and assessed how R^2 values responded. When using a threshold >4, R^2 values remained unchanged or even decreased, likely due to reduced sample size.

2.2.1 | Cophylogenetic signal analysis using PACo

To assess the cophylogenetic signal in frugivory interactions between vertebrates (bats, birds and primates) and plants, we employed the PACo (Balbuena et al., 2013). This method evaluates the fit between the phylogenetic trees of two interacting groups by superimposing their phylogenetic distance matrices using a Procrustes rotation. The analysis calculates residuals for each species pair, representing the deviation between observed and expected phylogenetic distances, where low residuals indicate high congruence. We used four key metrics to quantify the cophylogenetic signal: (1) Sum of Squares of Residuals (SS), that measures the total deviation between observed and expected interactions, with lower SS values indicating greater discordance; (2) R^2, that represents the proportion of variance in interactions explained by phylogenetic congruence, with values near 0 suggesting minimal influence of phylogeny and values closer to 1 indicating a strong cophylogenetic signal; (3) *p*-value, that determines the statistical significance of the observed congruence, with a *p*-value <0.05 indicating that the observed signal is unlikely to occur by chance; and (4) individual link contributions, that assess the relative importance of each species pair in the overall model fit.

Residuals from PACo quantify how much each interaction deviates from what would be expected under a perfect phylogenetic matching. These metrics collectively provide a comprehensive understanding of cophylogenetic signal and its implications for the structure of frugivory networks. Vertebrate diet classification was based on EltonTraits (Wilman et al., 2014), which quantifies the proportion of fruit and other dietary components for each species. We defined frugivores as species with ≥50% fruit in their diet, a threshold widely used to distinguish obligate frugivores in ecological studies (e.g. Fleming & Kress, 2013; Kissling et al., 2009). All analyses were performed using the paco package in R, with significance assessed through 1000 permutations.

2.2.2 | Modularity analysis

Ecological interaction networks are often modular, meaning that they consist of subgroups of species that interact more strongly with each other than with species from other modules (Olesen et al., 2007). In modular networks, modules are often composed of phylogenetically related or convergent species (Mello et al., 2019; Schleuning et al., 2014). To evaluate modularity in each vertebrate network, we used the probabilistic Beckett method, which employs Monte Carlo simulations to identify the modular structure of the network. To assess the significance of observed modularity, we generated 1000 randomized networks by permuting the interaction matrix entries while keeping the number of species fixed (i.e. a full matrix shuffle null model). Since modularity is sensitive to network size, we also computed the *z*-score by comparing observed modularity values with those obtained from 1000 randomized networks, allowing for standardized comparisons across groups (Blüthgen et al., 2008; Dormann et al., 2009). This approach ensures that differences in modularity reflect structural properties of the interaction networks rather than variations in network size. Detailed results on the significance of modularity values and the composition of modules are provided in Supporting Material S2.

To identify the most structured modules within the frugivory networks, we selected the best-structured modules for each vertebrate group based on key structural metrics: (1) Network Density, that measures the proportion of existing connections relative to the maximum possible connections within a module. Higher density indicates a more cohesive structure where species are strongly interconnected; (2) Mean Degree, that represents the average number of connections per species within a module. Higher values suggest a more homogeneous distribution of interactions and a central role for the module in the overall network; (3) Mean Betweenness, that quantifies the importance of a node as an intermediary in the flow of interactions between other nodes. Higher values indicate that species within the module act as strategic bridges connecting different parts of the network; and (4) Mean Closeness Centrality, that measures how close, on average, each node is to all others within the module. Higher values reflect greater efficiency in the propagation of interactions and more direct accessibility among species.

To ensure ecological representativeness and structural robustness, we applied specific selection criteria: modules with fewer than three vertebrate or plant species were discarded due to insufficient sample size for meaningful analysis, and modules were ranked based on the normalized sum of the four metrics. The three modules with the highest scores were selected as the most robust for each vertebrate group (bats, birds and primates), ensuring a focus on ecologically significant and well-structured subgroups within the network.

2.2.3 | Taxonomic filtering and specialized interactions

To assess whether the observed patterns are driven by taxonomic biases in the cophylogenetic signal, we filtered interactions to lower taxonomic levels, focusing on plant families with well-documented ecological significance and specialized interactions with their respective dispersers: Piperaceae for bats (e.g. *Carollia* and *Chiroderma* species, which specialize in consuming Piper fruits; Fleming, 1986; Lobova et al., 2009; Thies & Kalko, 2004), Melastomataceae for birds (e.g. Thraupidae species; Loiselle & Blake, 1999), Sapotaceae for primates (e.g. *Ateles* and *Lagothrix* species, which feed on large, fleshy fruits; Chapman & Russo, 2006; Stevenson & Link, 2010).

Importantly, generalist-rich families with high potential for interactions with vertebrates, such as Moraceae, Urticaceae, Solanaceae and Arecaceae, were fully included in all overall analyses. We did not, however, evaluate them as isolated clades in this step, because their broad and non-exclusive interactions with phylogenetically disparate dispersers make them less suitable exemplars of specialization. Including them as focal clades would risk obscuring the specific patterns we aimed to test. Thus, this clade-level filtering should be understood as a complementary analysis designed to highlight cases of stronger ecological specialization, while the generalist families already contributed to the signal in the whole-network and modular analyses. Notably, because such families typically dilute rather than inflate cophylogenetic signal, their inclusion in the overall dataset makes our estimates conservative. The interactions we evaluate at this step (Piperaceae–bats, Melastomataceae–birds, Sapotaceae–primates) likely reflect ecological specialization and, potentially, evolutionary relationships, given their well-documented ecological roles.

2.3 | Functional attributes

2.3.1 | The influence of functional traits on cophylogenetic signal

To explore the influence of functional traits on the shared evolutionary histories of vertebrates and plants, we tested the effects of traits of both vertebrates and plants on the Procrustes residuals, calculated for the complete networks. For morphological traits of plants and vertebrates, and for vertebrate diet, we used the NeoFrugivory database (Fuzessy & Pizo, 2025b).

For vertebrates, we evaluated traits such as diet and body size, and metrics associated with network structure, such as specialization index (*d*'), species strength, and mean phylogenetic distance. Body size reflects ecological and evolutionary adaptations related to resource use, influencing dietary habits, seed dispersal capacity and movement patterns. The specialization index (*d*') quantifies the degree of interaction selectivity, distinguishing between generalist and specialist species based on their deviation from random partner selection (Bascompte et al., 2006). Species strength measures the overall connectivity of each vertebrate within the network (Blüthgen et al., 2006). Mean phylogenetic distance was incorporated to evaluate whether closely related species exhibit similar influences on the cophylogenetic signal.

For plants, we used fruit and seed characteristics known to influence vertebrate consumption, including fruit type, colour, husk presence, number of seeds per fruit, and fruit and seed dimensions (width and length). We used generalized additive models (GAMs) to assess the relationship between these traits and the Procrustes residuals. GAMs were chosen for their flexibility in modelling non-linear relationships. For vertebrates, we fitted separate models for each group (bats, birds and primates) and a hierarchical model that included all groups with taxonomic group as a random effect. For plants, we followed a similar approach, fitting individual models for fruits consumed by each vertebrate group and a hierarchical model integrating all groups.

To better visualize and assess the distribution of plant attributes across vertebrate groups, we conducted a principal coordinates analysis (PCoA), incorporating both continuous and categorical variables. This allowed us to explore how functional traits influence the structure of frugivory networks and their cophylogenetic signals.

2.3.2 | Phylogenetic signal of traits

We assessed phylogenetic conservatism in functional traits using Blomberg's *K*. For each vertebrate group (bats, birds and primates) and for plants, we calculated phylogenetic signal for all continuous traits including body size, specialization index (*d*'), species strength and Procrustean residuals. Trait values were matched to species in the respective phylogenies after removing taxa with missing data. Blomberg's *K* quantifies the extent to which closely related species resemble each other more than expected under a Brownian motion model of trait evolution. Statistical significance was assessed using 1000 random permutations of trait values across the tips of the phylogeny, testing the null hypothesis of no phylogenetic signal ($K = 0$). Although *K* values greater than 1 can indicate stronger phylogenetic conservatism than expected under Brownian motion, our analysis focused on detecting significant deviations from randomness ($K > 0$), rather than testing departures from $K = 1$. This approach helped us identify traits with strong phylogenetic structure and helping interpret patterns observed in our cophylogenetic analyses.

3 | RESULTS

3.1 | Hierarchical cophylogenetic assessment

The PACo analysis revealed a significant, although weak, cophylogenetic signal in frugivory interactions between vertebrates (bats, birds and primates) and plants. Across the complete datasets, the proportion of variance explained by the congruence between the phylogenies of vertebrates and plants (R^2) was low: 4.6% for bats, 1.2% for birds and 1.2% for primates. Despite this, the strongly significant *p*-values ($p = 0$) indicate that the observed patterns did not occur by chance; instead, they reveal a significant cophylogenetic signal between the phylogenies of vertebrates and plants. This suggests that shared evolutionary history played a detectable, albeit limited, role in shaping frugivory interactions in the Neotropics.

When restricting the analysis to interactions with a frequency ≥2 and frugivorous diets, the cophylogenetic signal became more pronounced, with R^2 increasing to 11.6% for bats, 5.1% for birds and 6.4% for primates. Further restricting the analysis to interactions with a frequency ≥3 strengthened the cophylogenetic signal for bats and birds, with R^2 rising to 15.5% and 11.0%, respectively. This demonstrates a slightly greater influence of phylogenetic congruence in shaping these interactions and suggests that more consistent interactions—such as those that are more frequent and involving animals relying more heavily on fruits—are more influenced by the shared evolutionary history between bats, birds and plants. However, for primates, when restricting the analysis to interactions with a frequency ≥3, R^2 decreased to 3.3% and was no longer statistically significant ($p=0.24$), possibly due to the loss of statistical power because of low sample size.

The interaction structure in primates and bats was more compartmentalized than expected by chance, whereas in birds, the observed modularity was lower than expected, reflecting a more diffuse interaction pattern. Modularity values are presented in Table S1a, while module composition is detailed in Figure S1b and Table S1b. The modularity analysis revealed significant differences among the three vertebrate groups. Primates showed the highest *z*-score (20.20), followed by bats (3.10), while birds exhibited a negative *z*-score (−6.43), indicating lower-than-expected modularity under a null model. The PACo analysis within the most structured modules revealed distinct patterns (Table S1c). Among bats, two of the better-structured modules exhibited significant cophylogenetic signals ($p<0.01$), although associated with weak R^2 values (4.7% and 11.3%, respectively). For birds and primates, only one module showed marginally significant cophylogenetic signal ($p=0.03$ for both groups), also associated with a weak R^2 (2.3% and 5.5%, respectively).

When focusing on interactions with plant families known for their specialized relationships with vertebrate groups, the cophylogenetic signal remained weak and non-significant: 5% for bats and Piperaceae ($p=0.91$), 4.5% for birds and Melastomataceae ($p=0.20$), and 8.9% for primates and Sapotaceae ($p=0.12$).

3.2 | Functional attributes

3.2.1 | Influence of functional attributes of vertebrates on cophylogenetic patterns

Functional traits explained cophylogenetic patterns in distinct ways across vertebrate groups. Using GAMs, we found that trait contributions varied markedly between bats, birds and primates when analysed separately, while the hierarchical model combining all groups explained 70.9% of deviance. Group-specific models revealed particularly strong explanatory power for primates (95.7% deviance explained), followed by bats (68.2%) and birds (61.3%), with the hierarchical approach providing additional insights into taxon-specific relationships.

Diet, the only categorical variable evaluated, emerged as a significant factor across all groups, with frugivorous species consistently showing the most negative Procrustes residuals, indicating a higher cophylogenetic signal between phylogenies. In bats, frugivores exhibited the lowest residuals, followed by nectarivores and insectivores (Supporting Material S3; Figure S3e). Similarly, frugivorous birds and primates displayed the strongest signal, with significant differences among dietary categories for both groups (Supporting Material S3; Figure S3e).

Body size was a key driver of cophylogenetic signal, particularly in birds ($p<0.001$). Small birds showed the smallest residuals, meaning that they had the greatest contribution to the cophylogenetic signal, that is, small birds shared a stronger evolutionary history with plants. According to isolated models, the body size of primates also significantly influenced Procrustean residuals ($p<0.001$), with large primates sharing a stronger evolutionary history with plants, though this effect was not significant in the hierarchical model. For bats, body size had no effect, likely due to the smaller variation in bat body size compared to the other two groups of frugivores (Figure 2).

Species strength was significant for birds ($p=0.001$) and bats ($p=0.02$ in the hierarchical model), suggesting that species with higher connectivity in the network contribute more to the cophylogenetic signal. However, this attribute was not significant for primates. Specialization (*d*') was significant only for birds ($p=0.008$), indicating that more specialized species had the greatest contribution to the cophylogenetic signal. In contrast, specialization had no significant effect on bats or primates.

Finally, phylogenetic distance was a significant factor for all groups in the individual models (bats: $p=0.02$; birds: $p=0.008$; primates: $p=0.003$), highlighting the importance of evolutionary proximity in shaping cophylogenetic patterns: closely related species share stronger evolutionary histories with plants (Figure 2). However, in the hierarchical model, phylogenetic distance remained significant only for bats ($p=0.004$) and birds ($p=0.01$), suggesting that its influence is more pronounced when considering group-specific variability (Figure 3). For a complete description of GAM results for vertebrate attributes, please see Supporting Material S3.

3.2.2 | Influence of functional attributes of plants on cophylogenetic patterns

After checking for collinearity among all variables and based on the results of the PCoA contribution plot (Figure 4), we selected fruit length, seed width, number of seeds per fruit, husk presence, colour and fruit type for the models explaining the cophylogenetic patterns. The hierarchical model revealed additional insights, particularly in identifying group-specific patterns. The explanatory power of the individual models was relatively low (bats: $R^2=0.25$, birds: $R^2=0.23$, primates: $R^2=0.08$), but the hierarchical model improved significantly, explaining 57% of the deviance, making it the preferred model for interpretation.

Fruit colour emerged as a significant factor across all groups, indicating that fruit colour is a central trait mediating interactions with vertebrates ($p<0.001$ for all groups). Fruit type also showed significant effects in some cases, particularly for infructescences and

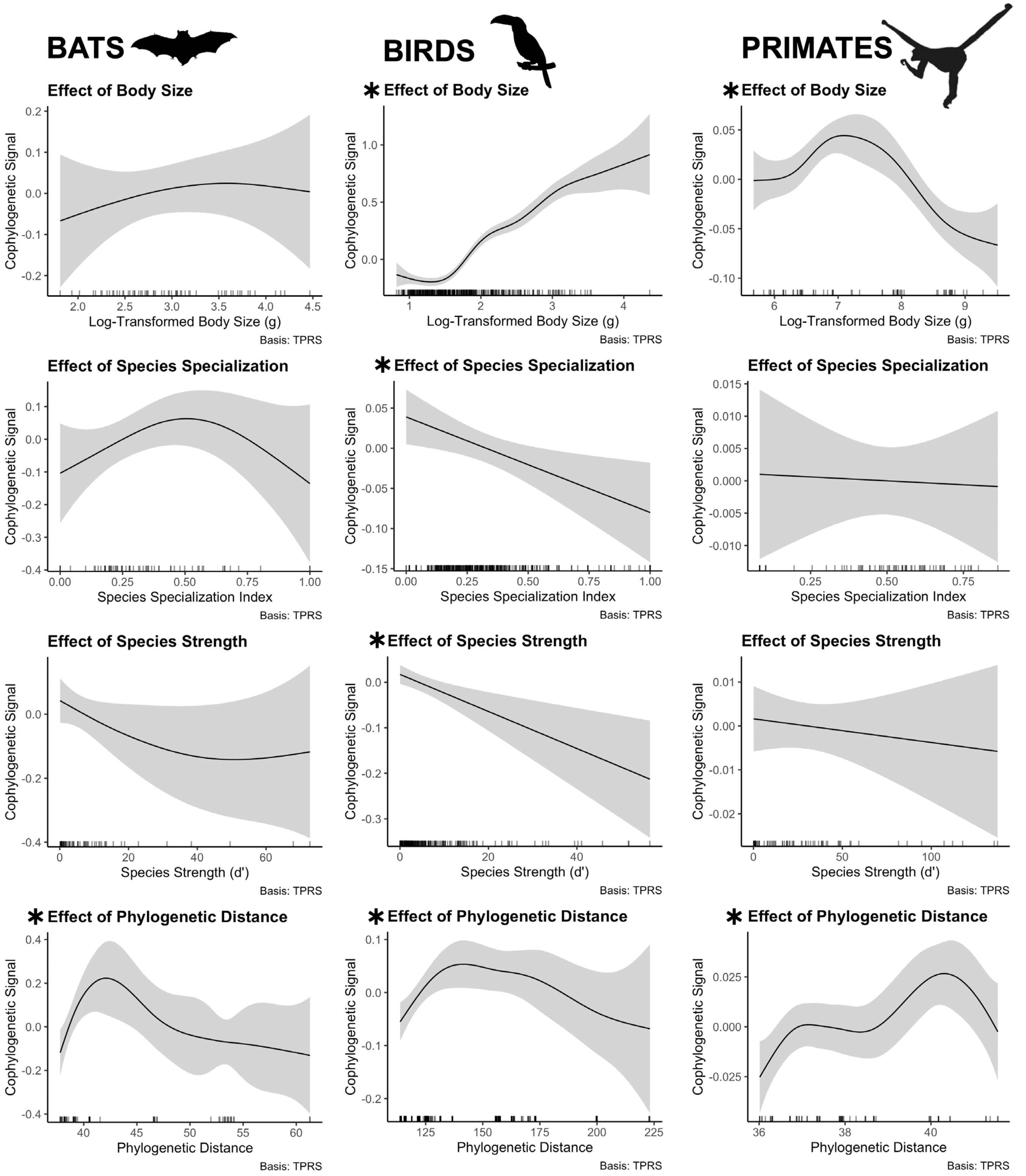


FIGURE 2 Smooth term plots from the individual generalized additive models for vertebrates, showing the relationship between each functional trait and the log-transformed Procrustean residuals (a measure of cophylogenetic signal). Shaded areas represent 95% confidence intervals. The *y*-axis indicates the estimated contribution to the cophylogenetic signal, with lower residuals indicating higher signals. Plots are grouped by vertebrate taxa: bats (left column), birds (centre column) and primates (right column). Significant smooth terms ($p < 0.05$) are highlighted with asterisks (*).

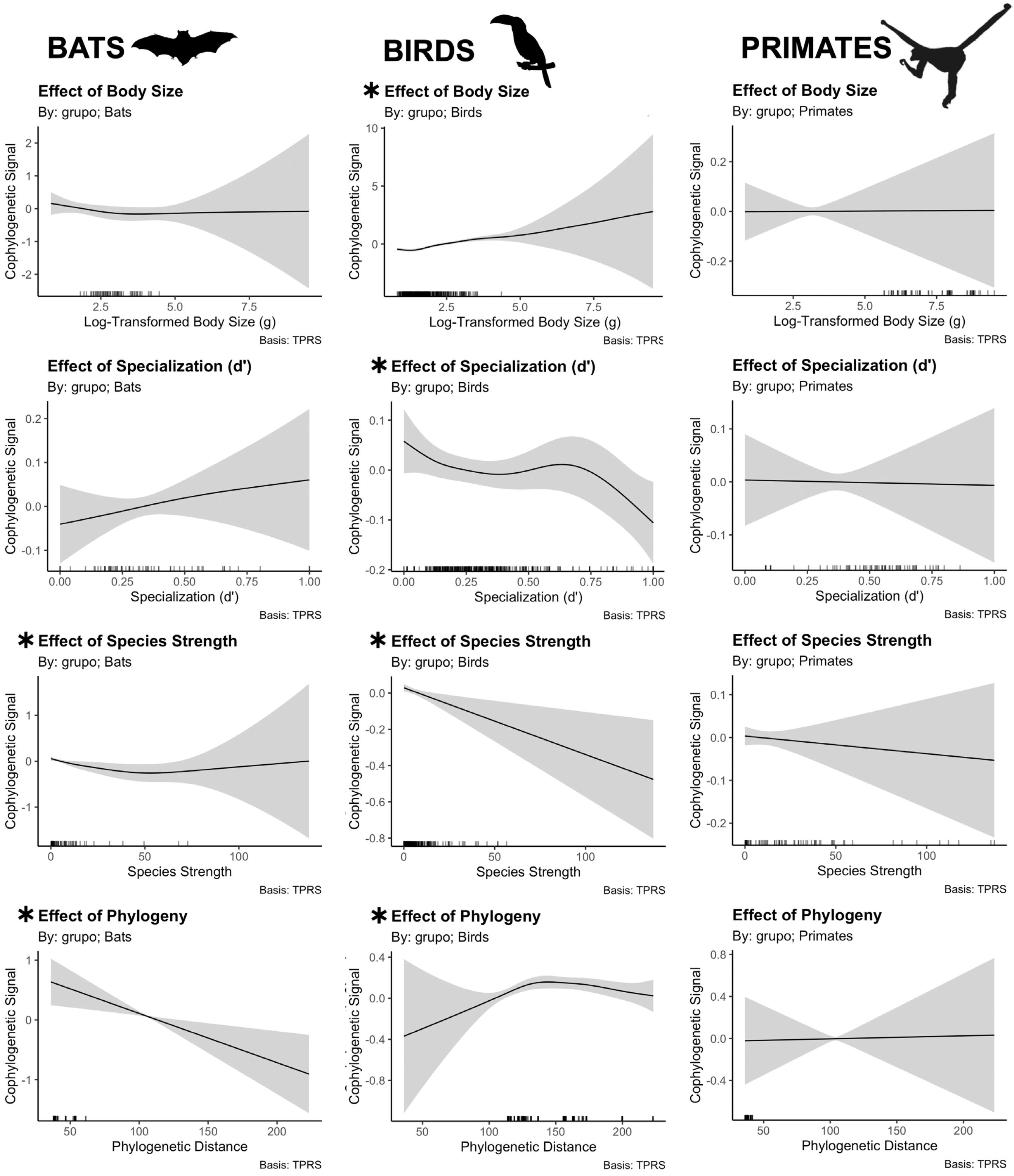


FIGURE 3 Smooth term plots from the hierarchical model for vertebrates, showing the relationship between each functional trait and the log-transformed Procrustean residuals (a measure of cophylogenetic signal). From top to bottom: body size, species strength, specialization (*d*') and phylogenetic distance. Shaded areas represent 95% confidence intervals. The *y*-axis indicates the estimated contribution to the cophylogenetic signal, with lower residuals indicating higher signal. Plots are grouped by vertebrate taxa: bats (left column), birds (centre column) and primates (right column). Significant smooth terms ($p < 0.05$) are highlighted with asterisks (*).

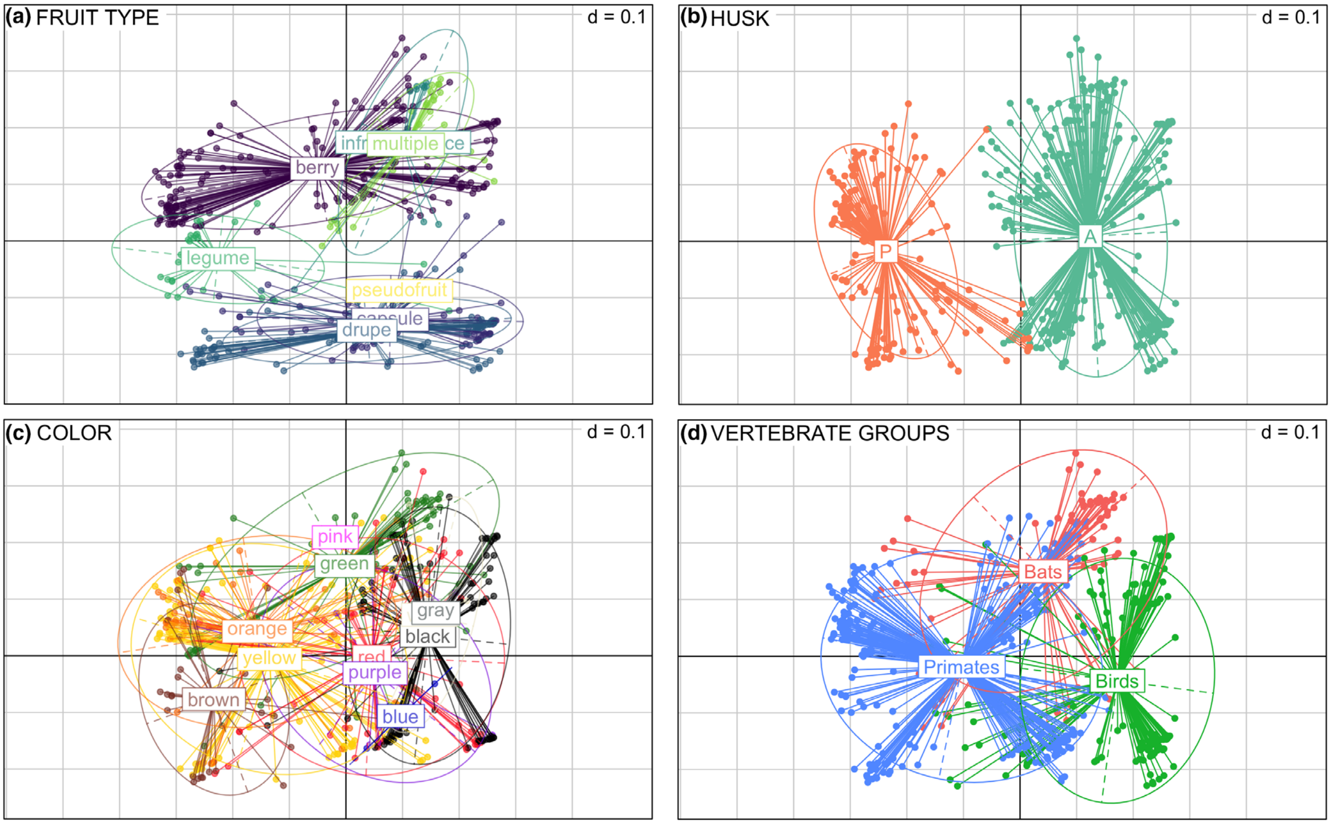


FIGURE 4 Ordination plots showing the distribution of plant species based on fruit attributes: fruit length, seed width, number of seeds per fruit, husk presence, colour and fruit type. The first two axes of the principal coordinates analysis together accounted for 36.63% of the variation (Axis 1: 22.38%, Axis 2: 14.25%). In each plot, species are grouped according to (a) fruit type, (b) husk presence, (c) colour and (d) vertebrate group. For further information, please see the contribution plot and the eigenvalue bar plot in Supporting Material S4b.

multiple fruits ($p < 0.01$), suggesting a minor but relevant influence. The presence of a husk had marginal significance ($p = 0.07$), likely reflecting its importance for mammals (bats and primates), as seen in the individual models (see Supporting Material S4). This is also supported by the PCoA ordination plots, which show clear separation based on fruit traits (Figure 4).

Among continuous traits, fruit length was significant for bats ($p = 0.02$) and birds ($p < 0.001$), but not for primates, indicating that fruit size influences interactions with bats and birds but is less relevant for primates, likely due to their ability to consume a wide range of fruit sizes. The number of seeds per fruit was significant for bats ($p = 0.01$) and birds ($p = 0.005$), with PCoA plots showing a clear separation between fruits with many seeds (e.g. berries, infructescences and multiple fruits) and those with few seeds (e.g. drupes and capsules). Seed width was significant only for birds ($p = 0.01$), suggesting its importance in bird-mediated interactions. Finally, phylogenetic distance was significant for fruits consumed by bats ($p < 0.001$) and birds ($p = 0.03$), indicating that plant phylogeny structures the cophylogenetic signal of interactions within these groups, but not for primates.

In summary, the hierarchical model highlights the importance of fruit colour and, to a lesser extent, fruit type and husk presence in mediating interactions with vertebrates (Figure 5). Continuous traits such as fruit length, seed number and seed width also play significant roles, but their importance varies across vertebrate groups. Phylogenetic distance is relevant for bats and birds, suggesting that evolutionary history shapes their interactions with plants. For primates, other factors not included in the model may be more influential. For a complete description of GAM results for plants, see Supporting Material S4.

3.2.3 | Phylogenetic signal

Our analysis of phylogenetic signal revealed contrasting evolutionary patterns between vertebrate and plant traits. Among vertebrates, body size showed consistent phylogenetic conservatism across all groups, particularly strong in birds and primates (Blomberg's K: birds $= 7.54$, primates $= 1.34$, both $p < 0.001$), confirming that body size is an evolutionarily conserved trait within these clades. Notably, the Procrustean residuals derived from PACo exhibited exceptionally strong phylogenetic signal in all vertebrate groups ($K = 4.32$–72.2, all $p < 0.001$), indicating that cophylogenetic signal between interacting clades is itself a heritable pattern. This finding implies that closely related frugivores tend to deviate from expected interaction patterns in similar ways, potentially reflecting conserved foraging strategies or niche preferences. In contrast, network properties such as species strength showed little to no phylogenetic structure across

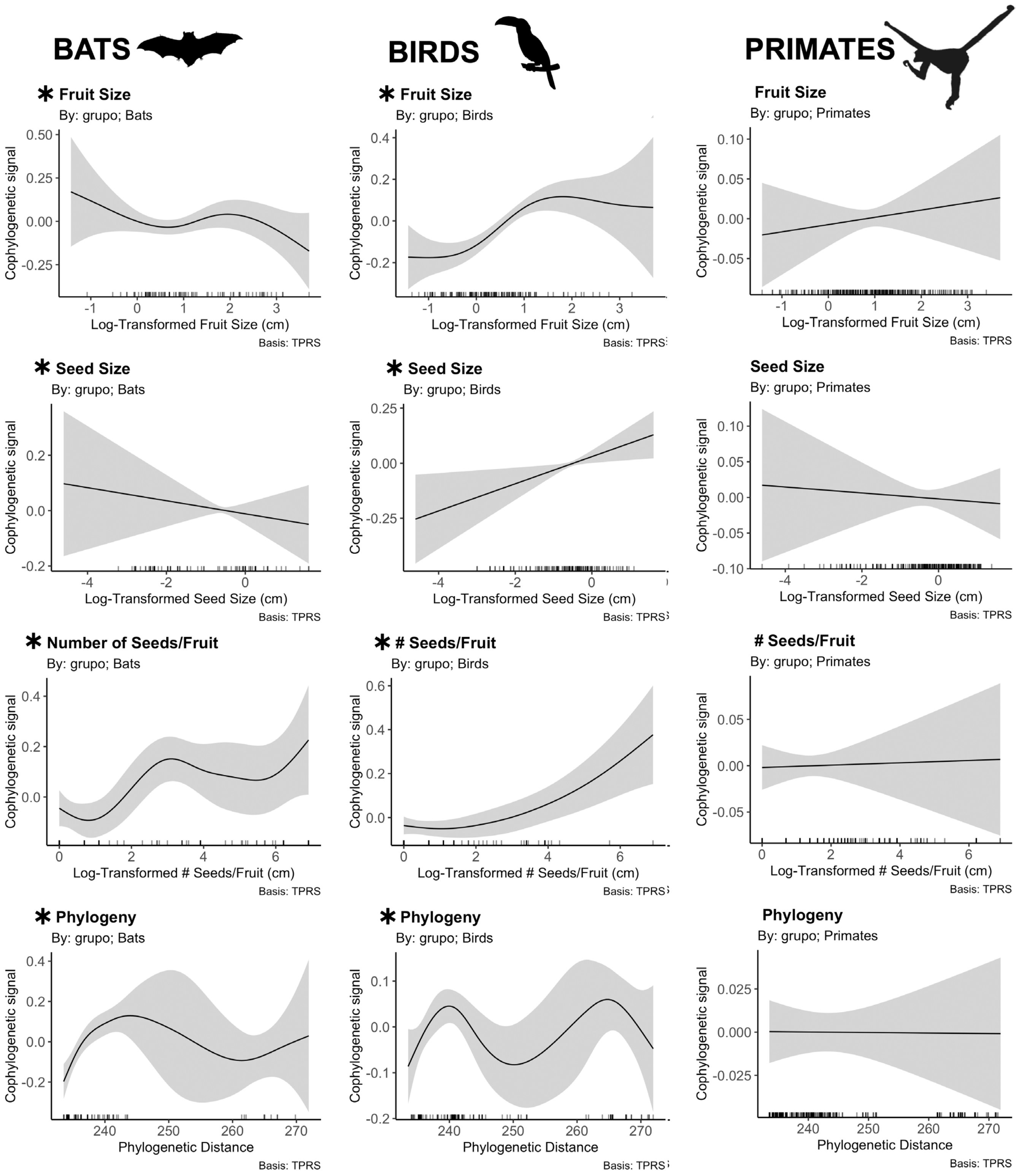


FIGURE 5 Smooth term plots from the hierarchical model for plants, showing the relationship between each attribute and the log-transformed Procrustean residuals (a measure of cophylogenetic signal). From top to bottom: fruit size, seed size, number of seeds per fruit and phylogenetic distance. Shaded areas represent 95% confidence intervals. The y-axis indicates the estimated contribution to the cophylogenetic signal, with lower residuals indicating higher signal. Plots are grouped by vertebrate taxa: bats (left column), birds (centre column) and primates (right column). Significant smooth terms ($p < 0.05$) are highlighted with asterisks (*).

TABLE 1 Phylogenetic signal in vertebrates and plant traits.

Group	Trait	Bloomberg *K*	*p*-value	# species
Bats	Body size	0.35	**0.04***	64
	Procrustean residuals	13.61	**0.00***	67
	Specialization *d'*	0.26	0.12	67
	Species strength	0.21	0.44	67
Birds	Body size	7.54	**0.00***	429
	Procrustean residuals	72.24	**0.00***	429
	Specialization *d'*	0.16	**0.00***	429
	Species strength	0.09	0.36	429
Primates	Body size	1.34	**0.00***	70
	Procrustean residuals	4.32	**0.00***	70
	Specialization *d'*	0.20	**0.00***	70
	Species strength	0.10	0.77	70
Plants	Fruit length	0.01	0.72	1256
	Fruit width	0.00	0.87	1293
	Seed length	0.01	0.71	943
	Seed width	0.00	0.97	1174
	# seeds/fruit	0.07	**0.01***	1184

*Bold values indicate statistical significance.

vertebrate groups ($K=0.09$–0.21, $p>0.05$), suggesting that a species' centrality or influence within the frugivory network evolves independently of lineage. Specialization (*d*') displayed a moderate phylogenetic signal in birds ($K=0.16$, $p<0.001$), but not in bats or primates, pointing to a potentially stronger evolutionary constraint on niche breadth within avian lineages.

Patterns were markedly different for plants. Most morphological traits—fruit and seed length and width—exhibited negligible phylogenetic signal ($K<0.01$, $p>0.7$), suggesting that closely related species are not more similar than expected by chance. This suggests high evolutionary lability and potential ecological convergence in these traits. In contrast, only seed number per fruit exhibited significant phylogenetic signal ($K=0.07$, $p=0.009$), implying some more degree of phylogenetic conservatism, possibly reflecting evolutionary constraints on reproductive allocation strategies. The overall low *K* across plant traits indicates that the observed trait similarity among closely related species is limited, which may result from recent adaptive shifts or convergent trait evolution in response to trait lability (Table 1).

4 | DISCUSSION

Our findings reveal that while a significant cophylogenetic signal exists in frugivory interactions between vertebrates and plants, its overall strength is weak, suggesting limited influence of shared evolutionary history in shaping these networks at large spatial scales. The proportion of variance explained by cophylogenetic signal was generally low across the three vertebrate groups, suggesting that shared evolutionary history plays a limited role in structuring these interactions in the Neotropics. This pattern appears to arise from three key mechanisms: (1) phylogenetic conservatism in vertebrate traits, (2) evolutionary lability in plant traits and (3) network-level effects of generalist species bridging interaction modules. While vertebrate traits like body size and dietary specialization show strong phylogenetic signal (especially in birds and primates), most plant traits mediating interactions (fruit size and seed size) exhibit remarkable evolutionary flexibility. This fundamental asymmetry, where conserved consumers interact with labile resources, generates networks structured more by ecological fitting than by deep evolutionary constraints.

These results align with the growing recognition that shared evolutionary history plays a limited role in structuring mutualistic interactions (Fuzessy, Silveira, et al., 2022; Morlon et al., 2024). Nonetheless, it is important to consider that the strength of phylogenetic signals may vary across spatial scales. At finer scales, historical contingencies, environmental heterogeneity or biogeographic history could exert a stronger influence on partner matching (Dalsgaard et al., 2021). Despite these possibilities, recent evidence suggests that broad-scale patterns can be replicated regionally. For instance, Fuzessy, Silveira, et al. (2022) demonstrated that continental-scale patterns of cophylogenetic signals in primate–plant interactions were replicated across the three major Neotropical rainforests (Amazon, Atlantic Forest and Mesoamerica) indicating that similar eco-evolutionary processes may operate across distinct regional meta-communities regardless of species composition. Even so, we acknowledge that anthropogenic impacts—such as species extinctions, habitat modification and biotic homogenization—may obscure or erode historical interaction patterns, particularly at local scales. Thus, while our results suggest limited phylogenetic structuring overall, it remains possible that more pronounced eco-evolutionary signals may emerge in less disturbed systems or within particular ecological or biogeographic contexts.

Furthermore, while methods such as PACo can detect significant cophylogenetic patterns, these may arise from trait conservatism, morphological matching or biogeographic overlap, rather than strict phylogenetic congruence (Perez-Lamarque & Morlon, 2024). Recent frameworks (e.g. Blasco-Costa et al., 2021) emphasize the importance of distinguishing pattern from mechanism in cophylogenetic studies. In our case, the weak signal at the network level (and its near absence within modules) suggests that evolutionary history leaves a detectable but modest imprint on frugivory networks, likely overridden by ecological factors such as resource availability, trait matching and behavioural flexibility.

Fruits are not consumed randomly, and our modularity results support this interpretation: primates and bats formed well-defined modules, while birds exhibited weaker modularity. Modularity likely raised from trait conservatism and ecological niche breadth, rather than deep phylogenetic legacy. Bats primarily interacted with small-seeded plants, forming structured modules with plants such as *Piper*, *Cecropia* and *Ficus*, likely facilitated by their specialized sensory adaptations (Eiting et al., 2023), whereas large-bodied primates engaged with a broader range of fruit and seed sizes and were uniquely associated with large, single-seeded fruits—patterns indicative of trait-matching processes inherent to frugivory networks (Fuzessy, Sobral, et al., 2022; Schleuning et al., 2015). In contrast, birds displayed more diffuse associations, consistent with generalist foraging strategies and visual detection capacity (Moermond & Denslow, 1985). Although modules may represent fundamental units of eco-evolutionary interactions (Blasco-Costa et al., 2021), their internal structure lacked strong cophylogenetic signals, suggesting that trait lability and trait-matching at intermediate organizational scales were the main factors driving modularity (Donatti et al., 2011; Fuzessy, Sobral, et al., 2022; Schleuning et al., 2014).

When considering more specialized interactions (i.e. recurrent interactions involving the feeding guild of frugivores), the cophylogenetic signal became more pronounced, especially for bats and birds. This pattern suggests that dietary specialization may strengthen the evolutionary coupling between frugivores and their feeding plants. Primates, however, diverged from this trend. Despite their large body size and potential to engage in consistent interactions, they exhibited a weak phylogenetic signal even at higher interaction frequencies. This likely reflects their behavioural flexibility and ecological plasticity in fruit selection, rather than phylogenetic constraints (Russo et al., 2005). Notably, even when analyses were restricted to interactions involving plant families with known tight associations (Piperaceae for bats, Melastomataceae for birds and Sapotaceae for primates), the cophylogenetic signal held weak or non-significant. Although certain plant families are preferentially consumed by specific vertebrate groups, these associations appear to be shaped more by contemporary ecological processes than by deep evolutionary relationships. Thus, although trait lability and specialization are clearly relevant, they may not always translate into detectable cophylogenetic patterns across large clades.

Going further, the contrasting phylogenetic signals between vertebrate and plant traits offer important context for understanding the overall weak cophylogenetic patterns observed. Vertebrate traits such as body size and dietary specialization, particularly in birds and primates, exhibited strong phylogenetic conservatism, whereas most plant traits relevant to frugivory (e.g. fruit and seed sizes) were evolutionarily labile. This asymmetry likely underlies the weak cophylogenetic signal: phylogenetic congruence becomes harder to detect when only one side of the interaction is evolutionarily constrained (Blasco-Costa et al., 2021). Notably, seed number was the only plant trait showing signs of evolutionary constraint, indicating that certain life-history or reproductive traits may preserve subtle phylogenetic imprints even in ecologically structured networks (Barrett, 2013). Despite the evolutionary flexibility of most plant traits, the Procrustean residuals—capturing network-level phylogenetic fit—revealed a strong phylogenetic signal across vertebrate groups (Blomberg's $K=13.6$–72.2). That is, vertebrates tended to maintain lineage-specific interaction patterns, likely due to inherited traits constraining their frugivory niches, while plants exhibit greater evolutionary plasticity in the traits mediating these interactions. Thus, although evolutionary signatures are more apparent on the vertebrate side, the lability of plant traits may enhance the adaptability and resilience of frugivory networks, reinforcing the central role of ecological processes in shaping mutualistic interactions (Acevedo-Quintero et al., 2020; Fuzessy, Sobral, et al., 2022).

Our findings underscore the critical role of vertebrate functional traits in shaping cophylogenetic patterns within frugivory networks. By adopting a trait-based, quantitative approach, we aligned our analyses with emerging cophylogenetic frameworks that move beyond binary interaction matrices to incorporate trait-mediated mechanisms (Blasco-Costa et al., 2021). Among these traits, dietary specialization consistently emerged as the strongest driver: frugivorous lineages across all vertebrate groups exhibited stronger cophylogenetic signals, supporting the idea that narrower diets promote evolutionary congruence with plant partners. These findings are consistent with Fuzessy, Silveira, et al. (2022), who documented a statistically significant yet weak cophylogenetic signals in primate–plant interactions across both continental and regional scales, specially driven by frugivorous lineages. Body size also influenced cophylogenetic patterns, but its effects varied across taxa. In birds, smaller-bodied species showed stronger cophylogenetic signals, likely due to constrained foraging niches and fruit size preferences (Fuzessy, Sobral, et al., 2022), whereas in primates, larger-bodied species were more congruent with plant phylogenies, possibly reflecting reliance on specific clades producing large, energy-rich fruits (Flörchinger et al., 2010; Russo et al., 2005). Hierarchical models integrating all vertebrate groups revealed taxon-specific trait effects. In bats, species strength and phylogenetic distance were the most significant predictors, consistent with their specialized foraging and dependence on particular plant resources. For birds, dietary specialization and body size were more influential, aligning with their visually guided foraging and ecological flexibility. In primates, body size and phylogenetic distance predicted cophylogenetic structure, suggesting that their morphological and behavioural adaptations result in more conserved interactions with certain plant lineages. These contrasts reflect distinct evolutionary and ecological trajectories and highlight the importance of applying group-specific lenses to uncover the drivers of mutualistic network structure (Fuzessy, Silveira, et al., 2022).

Among plant traits, fruit colour emerged as the most influential across all vertebrate groups, reinforcing the importance of visual cues—especially for birds—in attracting frugivores. Fruit type also shaped interaction patterns, with infructescences and multiple-fruit structures favouring consumption by more specialized frugivores. Husk presence, though only marginally significant, may affect fruit accessibility for mammals, especially bats and primates. Continuous traits showed varied effects: fruit length influenced bat and bird interactions, but not primates—likely reflecting their greater manual dexterity. Seed width strongly affected bird interactions, reflecting gape-size limitations, while seed number contributed variably across groups. The prevalence of fleshy fruits in our dataset, notably drupes and berries, likely reflects the high importance of vertebrate dispersers in Neotropical systems. This contrasts with temperate and European assemblages, where dry fruits are commonly consumed by ungulates, granivorous birds and rodents (e.g. Jordano, 1995). Therefore, the observed patterns may not be globally consistent, and caution is warranted when extrapolating these findings to other biomes. Plant phylogenetic distance influenced interactions involving bats and birds, but not primates, suggesting that evolutionary history plays a stronger role in groups reliant on specific fruit traits, whereas primates may forage more opportunistically across diverse plant lineages.

Network-level attributes also played a key role in shaping cophylogenetic signals. Generalist species with high connectivity enhanced network cohesion and contributed significantly to the overall cophylogenetic pattern by linking phylogenetically diverse partners (Donatti et al., 2011; Palacio et al., 2016; Rumeu et al., 2020). The inverse relationship between species strength and Procrustean residuals further supports the idea that highly connected species strengthen the observed cophylogenetic signal. Conversely, specialists—species with narrow interaction breadth—also reinforced cophylogenetic patterns at their node level. This aligns with ecological filtering theory, wherein tight ecological relationships often reflect deeper coevolutionary history (Eriksson, 2016; González-Castro et al., 2015). Importantly, ‘specialization’ must be interpreted with caution. As Carlo et al. (2025) argue, true evolutionary specialization—consistent, constrained resource use over time—differs from context-dependent foraging preferences. While network metrics like *d'* capture interaction breadth, they cannot always distinguish between these scenarios. For example, *Carollia* bats (specialized on *Piper*) or mistletoe birds (specialized on mistletoes) represent true evolutionary specialists, whereas flexible generalists may show strong preferences without long-term evolutionary coupling. This distinction is particularly relevant for primates, whose extreme generalism and behavioural plasticity obscure phylogenetic patterns. Their broad, context-driven diets dilute lineage-specific signals, reinforcing the idea that ecological processes, rather than evolutionary constraints, primarily drive their interactions.

4.1 | Caveats and limitations

Our interaction matrix was assembled from empirically documented frugivory interactions across multiple studies, regions and time periods. While this broad-scale synthesis enabled a comprehensive representation of vertebrate–plant interactions in the Neotropics, it also introduces important limitations. Integrating interactions from disparate spatial and temporal contexts may obscure localized ecological signals, inflate overall connectance, or reduce the detectability of context-dependent patterns such as spatial co-occurrence, phenological synchrony, or dispersal effectiveness. As a result, regional generalizations may mask fine-scale ecological dynamics, and signals of phylogenetic congruence or trait matching may vary, or even intensify, when examined at local scales.

Nonetheless, broad-scale patterns may be spatially replicated in smaller-scale systems. For instance, Fuzessy, Silveira, et al. (2022) demonstrated that strong cophylogenetic signals between primates and plants were consistently observed across three major Neotropical rainforest regions—the Atlantic Forest, Amazon and Mesoamerica—despite differences in species composition. This spatial replication suggests that shared eco-evolutionary dynamics can emerge independently across distinct regional meta-communities, reinforcing the robustness and generality of large-scale interaction patterns. Future studies integrating spatially explicit data with network-level metrics will be crucial to further disentangle how ecological and evolutionary processes operate across scales in shaping mutualistic interactions.

In addition, our sample coverage analyses revealed that while a substantial portion of frugivory interactions has been documented—particularly for primates and bats—the interaction richness continues to exhibit ascending trajectories across all groups. These trends indicate that the available records remain incomplete and likely underestimate the true diversity of frugivory interactions in the Neotropics. Despite these limitations, our synthesis constitutes the most comprehensive compilation of such interactions to date. Thus, although not exhaustive, the dataset provides a robust foundation for investigating large-scale patterns in frugivory networks and their underlying drivers.

5 | CONCLUSION

Overall, frugivory networks emerge from a complex interplay of evolutionary history and ecological filtering, with functional traits—such as diet, body size and interaction frequency—acting as primary drivers of species associations. While some specialized interactions likely reflect coevolutionary history, our results indicate that present-day ecological trait matching largely shapes network structure, producing generally weak cophylogenetic signals. Plant traits such as fruit colour and morphology further highlight the importance of functional compatibility, which may itself be an outcome of past coevolutionary processes. The lability of traits likely enhances network resilience to species loss, as long as key functional traits are maintained—an idea supported by studies of primate-plant interactions where primates act as core seed dispersers (Fuzessy, Sobral, et al., 2022).

Though evolutionary history shapes broader network organization, its influence appears secondary to ecological specialization and structural properties like modularity (Donatti et al., 2011; Schleuning et al., 2014). Therefore, conservation strategies should prioritize the maintenance of functional diversity and species' ecological roles, rather than focusing solely on taxonomic preservation. Future research should integrate ecological, behavioural and genomic data to investigate intraspecific variation and microevolutionary processes underlying interaction patterns (Agrawal & Zhang, 2021). Such approaches will deepen our understanding of the mechanisms sustaining frugivory networks and their essential role in ecosystem functioning.

AUTHOR CONTRIBUTIONS

Lisieux Fuzessy, Miguel Verdú and Marco Aurelio Pizo conceived the ideas and designed the methodology. Lisieux Fuzessy and Marco Aurelio Pizo collected the data. Lisieux Fuzessy analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Author state no conflict of interest.

DATA AVAILABILITY STATEMENT

We analysed frugivory interactions using the NeoFrugivory database (Fuzessy & Pizo, 2025a). This database is publicly available [https://doi.org/10.6084/m9.figshare.28197497.v2]. All data supporting the findings of this study are either included within the manuscript or accessible through the cited database.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Material S1. Sample coverage.

Supporting Material S2. Modularity.

Supporting Material S3. Functional attributes of vertebrates.

Supporting Material S4. Functional attributes of plants.

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