

Phylogenetic congruence between Neotropical primates and plants is driven by frugivory

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Abstract

Seed dispersal, by entailing multiple benefits to plants and frugivores, potential drives trait evolution and species diversification. Frugivory and seed dispersal shaped the coevolution of interacting clades, with consequences to speciation and diversification evidenced for e.g., primates. Evidences for macro-coevolutionary patterns in multi-specific, plant-animal mutualisms are scarce, and the mechanisms driven them remain unexplored. We tested for phylogenetic congruences in primate-plant interactions in Neotropics and show that both primates and plants share evolutionary history. Phylogenetic congruence between Platyrrhini and Angiosperms was asymmetrically driven by the most generalist primates interacting with a wide-range of specialist Angiosperms. Consistently similar eco-evolutionary dynamics seem to be operating irrespective of local assemblages, since the signal emerged independently across three Neotropical regions. Our analysis supports the idea that macroevolutionary, coevolved patterns among interacting mutualistic partners are driven by super-generalist taxa. Trait convergence among multiple partners within multi-specific assemblages appears as a mechanism favouring these coevolved outcomes.

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Abstract

Seed dispersal, by entailing multiple benefits to plants and frugivores, potential drives trait evolution and species diversification. Frugivory and seed dispersal shaped the coevolution of interacting clades, with consequences to speciation and diversification evidenced for e.g., primates. Evidences for macro-coevolutionary patterns in multi-specific, plant-animal mutualisms are scarce, and the mechanisms driven them remain unexplored. We tested for phylogenetic congruences in primate-plant interactions in Neotropics and show that both primates and plants share evolutionary history. Phylogenetic congruence between Platyrrhini and Angiosperms was asymmetrically driven by the most generalist primates interacting with a wide-range of specialist Angiosperms. Consistently similar eco-evolutionary dynamics seem to be operating irrespective of local assemblages, since the signal emerged independently across three Neotropical regions. Our analysis supports the idea that macroevolutionary, coevolved patterns among interacting mutualistic partners are driven by super-generalist taxa. Trait convergence among multiple partners within multi-specific assemblages appears as a mechanism favouring these coevolved outcomes.

Introduction

Seed dispersal, a mutualistic interaction resulting from fruit consumption, shapes evolutionary patterns (Burin et al. 2021), and is a major engine for trait diversification in both plants and frugivores (Guimarães et al 2011, Lengyel et al 2010, Gomez & Verdu 2012, Rojas et al. 2012, but see Scott 2019). Mutual gains set the odds of interactions, and are reciprocally crucial: fruits are key resources for many vertebrates, whereas most tropical forest trees rely on fruit-eating vertebrates as dispersal vectors (Howe 2014). Frugivory has evolved independently numerous times along the evolutionary history of vertebrates. This is also true for Neotropical primates (Hawes and Peres 2014), a major order of fruit-eating vertebrates (Fleming & Kress 2011). Fruit intake is clearly related to dispersal potential, and all Platyrrhini primates routinely eat fruits (Hawes and Peres 2014). The amount of fruit in diet has significant consequences for primate seed dispersal effectiveness (Fuzessy et al 2016, 2017). Yet, the extent to which variation in the degree of frugivory explains the evolutionary history of primates shared with Angiosperms remains largely unexplored (but see Gomez and Verdú 2012).

A key knowledge gap preventing a better assessment of the role of frugivory in shaping the evolution of primates and plants lies in the difficulties in understanding the consequences of seed dispersal to the concurrent diversification of both interacting clades (DeCasien et al 2017, Scott 2019). Seed dispersal is characterized by low degrees of specialization (Stiles & Rosselli 1993, Donatti et al 2011), and most primates have generalist feeding habits (Hawes and Peres 2014). Thus, the potential of the mutual gains to promote plant-primate codiversification (correlation in speciation events) and/or coevolution (reciprocal evolutionary changes in traits) remains challenging to assess.

Considerable effort has been dedicated to uncover how Primates have diversified and to what extent behavioral, ecological and morphological traits have contributed to both speciation and extinction rates (Gittleman & Purvis, 1998; Gomez & Verdu, 2012; Harcourt, Coppeto & Parks, 2002; Isaac et al. 2005; Matthews et al. 2011; Nunn et al., 2004). Primates are socially and ecologically complex (Lefebvre et al. 2004, Dunbar and

MacDonald 2013, Tran 2014), but unequivocal evidence supporting the role of frugivory and seed dispersal in primate diversification is lacking. The capacity to efficiently detect and consume fruits and disperse seeds is linked to larger range size, and higher diversification rates (Gomez & Verdu 2012, Valenta et al. 2018) and cognitive complexity (DeCasien et al. 2017). However, activity pattern, but not frugivory, is the only parameter correlated with primate diversification, with higher rates observed in diurnal primates compared to nocturnal species (Scott 2019). Considering that a diurnal habit is tightly related to primate color vision, the emerging pattern may also underscore a relationship between foraging behavior and the capacity to visually detect fruits (Kawamura 2016). For example, the evolution of trichromatic colour vision by the majority of anthropoid primates has been linked to the efficient detection and selection of food, particularly ripe fruits among leaves in dappled light (Smith et al. 2003).

The evolutionary consequences of seed dispersal also remain unclear from the plant perspective. The intimate relation with certain groups of vertebrates is hypothesized to promote the evolution of dispersal syndromes, i.e., the nonrandom association of plant traits with specific disperser groups (Gautier-Hion et al 1985). For instance, many studies attempted to distinguish bird-dispersed from primate-dispersed fruits (Janson 1983; Gautier-Hion et al 1985; Voigt et al 2004; Lomáscolo et al 2008), although the specificity of such syndromes remains a contentious issue (Valenta et al. 2018).

Theoretical studies on mutualistic networks suggest that the establishment of a link between two partners occurs when an interaction evolves successfully, and more species can be attached by evolutionary trait convergence (Guimarães et al 2011). Although we are still unable to draw strong evidence of the potential of seed dispersal in promoting reciprocal selective responses between closely linked primates and plants (but see Guimarães et al. 2017), recent eco-phylogenetic tools allow to assess both the shared evolutionary histories and the contribution of a particular clade to the coevolutionary dynamics (Hutchinson et al. 2017). In particular, eco-phylogenetic analysis allows the detection of a non-random shared pattern or signal in the evolutionary trajectories of unrelated species groups that interact in some way (e.g., frugivores and plants, hosts and parasites, etc.).

By estimating the cophylogenetic signals ('CS') in plant-primate interactions we can quantify the degree at which the topology and chronology of the phylogenies of interacting clades are congruent, and whether interaction between evolutionarily coupled taxa still occurs. Thus, CS allows more precise inferences on how ecological interactions shape diversification patterns (Balbuena et al. 2013, Aizen et al. 2016, Hutchinson et al. 2017).

Here we tested for a phylogenetic congruence in primates and plants both at continental and regional scales in the Neotropics, the most biodiverse region of the planet (Raven et al. 2020). Under a strong CS, we expect a low overlap in fruit consumption among primates and other fruit-eating vertebrates, since strong associations involve strong shared selection pressures. We further assessed whether the magnitude of CS can be explained by primate feeding guild and frugivory degree, and fruit traits known to shape seed dispersal abilities (fruit length and seed diameter). We hypothesize that CS will particularly arise in the most frugivore lineages, whereas clades with the lowest frugivory degree will contribute less to define the past history shared among Neotropical primates and Angiosperms. As for fruit traits, we expect larger fruits and seeds sizes to contribute more to CS than smaller fruits and seeds, since the former are associated to plants exclusively or primarily dispersed by primates (Jordano 1995, Valenta et al. 2018).

Material and Methods

Database

We performed a comprehensive literature search on plant species potentially dispersed by Neotropical primates, using both Web of Science and Google Scholar. Search details and the complete list of studies are available in Supplementary Material S1.

To evaluate the overlap in fruit consumption between primates with other vertebrates, based on the list for primates, we searched for other vertebrates also interacting with the fruits. We obtained records of frugivore-

plant interactions whenever details of fruit handling, swallowing, consumption and delivery of seeds were provided by the authors. We obtained data by birds, bats, small mammals and ungulates (Supplementary Material S2).

Phylogenetic reconstruction

We reconstructed the primate species-level phylogeny and the plant genus-level phylogeny, aiming to optimize the number of observed interactions and reduce phylogeny resolution issues. Further details on phylogenetic reconstructions are available in Supplementary Material S4.

Cophylogenetic signal (CS)

To conduct a direct assessment of CS between Angiosperms and primates, we implemented a Procrustean Approach to Cophylogeny (PACo; Balbuena et al. 2013). The PACo approach addresses cophylogeny by optimizing the phylogeny fit using interaction graphs of a given matrix. The cophylogenetic signal of each individual interaction is given by the squared residual distance, r , between the two corresponding points in the phylogenetic trees. PACo thus returns a quantification of the global fit of the phylogenetic objects based on observed interactions as the sum of squared residual distances ($R = \sum r^2$) between phylogenetic-interaction graphs (Balbuena et al. 2013). As in any regression analysis, the smaller the residual distances, the better the fit of the two phylogenies to each other and the more support for a hypothesis of CS as reflected by the extant interactions (Hutchinson et al. 2017).

A high CS illustrates a strong congruency of the phylogenies of the two partner groups. Procrustean residuals measure the variation in interactions that is not explained by the co-phylogenetic structure of the interaction matrix, so that interactions with small Procrustean residuals contribute the most to CS, while those deviating more from the expectation derived from the shared phylogenetic history contribute the less to CS. CS was considered to be significant when it was smaller than 95% of the values obtained from 1,000 randomizations of the aggregated interaction dataset. Further details are available in Supplementary Material S5.

To ensure that the cophylogenetic pattern at the continental scale in the whole Neotropics was not due to distinct geographical subsets of primate species and plant genera coexisting in different regions, we split our dataset into the following Neotropical biogeographic forests (Morrone 2014): Atlantic forest, Amazon forest and Mesoamerican tropical forest. We then filtered our dataset and obtained, for each region, specific phylogenies of plants and primates, and their respective seed dispersal interactions. We then measured the CS and tested for its significance following the same statistical approach as for the continent-wide assessment.

The influence of functional traits on CS

We obtained data on primate (body size; degree of frugivory and dietary guild) and plant (fruit length and seed diameter) (Table S2) to test whether they affect the magnitude of the CS, by characterizing each interaction by its Procrustean residual. We accounted for the possible influence of the sample size to control for sampling bias (Supplementary Material S3).

Fruit length and seed diameter are traits that tend to be conserved along the phylogenetic tree (Jordano 1995, Moles et al. 2005), thus we used average values obtained for each plant genera as measures. We tested the model for multicollinearity of the variables by using the variance inflation factor (VIF). Multicollinearity occurs when two or more predictors are correlated and provide redundant information about the response. VIF values for body size was found to be high (VIF=8.39, tolerance = 0.08), which were also correlated with model intercept (0.9). Facing the likely confounding property of body size added to the collinearity produced, we decided to suppress it from our model (see explanation in Supplementary Material S3).

We fitted our final model with variables describing primate biology in terms of the amount of fruit intake and functional role played according to dietary category, such as the frugivory degree (percentage of the diet that corresponds to fruit pulp, excluding seed predatory interactions) and dietary guild (percentage of each food item in the diet). The former adds information on the real amount of fruit pulp in diet, whereas the latter informs about the effects of morphological variation resulting from adaptations of the digestive

tract (Hawes and Peres 2014), with relevant consequences for the ability of seeds to germinate after being defecated (Fuzessy et al. 2016). Our GLMM included then Procrustean residuals as a response variable, primate species and plant genera as random effects, and functional traits (frugivory degree and dietary guilds for primates; fruit length and seed diameter for plants) as fixed effects, using the ‘lmerTest’ package (Kuznetsova et al. 2017).

Results

We gathered information on 1,614 interactions between 34 primate species, in six subfamilies and three families, and 960 plant species in 311 genera and 98 families across Neotropical rainforests. Primates were the exclusive seed dispersers of 627 (65%) species (in 233 genera) (Fig. 1). Birds overlapped 147 plant species with primates (in 80 genera), bats 48 (in 32 genera), ungulates 17 (in 16 genera), and small mammals 9 (in nine genera). Finally, 112 plant species (in 68 genera) were found to be dispersed by more than one vertebrate group plus primates. The most exclusively primate-dispersed family was Sapotaceae (70 species, or 5.5% of the total 1,273 species), followed by Menispermaceae (22 species, or 5% of the 440 species), and Moraceae (44 species, or 3.7% of the 1,180 species) (Figure S6).

We detected a strong evidence of a coupled evolutionary history among primates and plants based on seed dispersal interactions ($R = 0.99$, $p < 0.001$). The residual contribution to the overall magnitude of the signal varied among interacting species.

Specialization or generalization of each plant and primate species (quantified by the number of interaction partners) predicted the CS of their interactions: the most interacting primates (those presenting highest degrees) had the shortest residual distances, thus contributing more to the CS ($t = -8.76$, $p < 0.001$). In turn, the most interacting plants were those with the largest residual distances, contributing less to the CS ($t = 2.5$, $p = 0.01$, Figure S7). Primate functional traits (degree of frugivory: $F = 4.65$, $p = 0.03$; feeding guild: $F = 7405.30$, $p < 0.001$), but not plant traits (fruit length: $F = 0.21$, $p = 0.65$; seed diameter: $F = 0.13$, $p = 0.72$), determined the magnitude of the influence of the interaction on the overall CS.

At the continental scale, major frugivore primates (*Ateles*, *Lagothrix* and *Brachyteles*) and the frugivore-folivores (*Alouatta*) contributed more to the strength of the CS, followed by the omnivores (*Cebus* and *Sapajus*) and frugivore-insectivores (*Leontopithecus* and *Saguinus*). On the other hand, mostly seed predators (*Cacajao*, *Chiropotes* and *Callicebus* species) showed the largest Procrustean residual values, with the smallest contribution to the signal as expected (Fig. 2, Table S8.a and Figure S8.a, Tables S9).

The continental pattern was consistent when broken-down at the regional/biome scale. We found a strong CS on primate-fruit interactions in the Atlantic forest ($R = 0.98$, $p < 0.001$), the Amazon forest ($R = 0.99$, $p = 0.014$), and in Mesoamerican forests ($R = 0.98$, $p = 0.008$). The contribution by each primate feeding guild in Amazon followed the continental pattern, while in the Atlantic Forest folivores contributed slightly more than frugivores, and in the Mesoamerica omnivores had the greatest contribution to CS (Fig. 3, Tables S8.b and Figure S8.b).

Discussion

Understanding the eco-evolutionary dynamics of species interactions remains challenging due to intrinsic complexities involved in mutualisms, especially in species-rich communities (Hall et al. 2020). Complexities arise from the multi-specific, mega-diversified nature of most mutualisms among free-living species, but also from difficulties to infer process from the simple co-phylogenetic patterns (Poisot 2015). Seed dispersal has been hypothesized to drive coevolution between plants and frugivores, shaping the present-day patterns of interactions and the evolution of fruit traits (Guimaraes et al 2011, 2017, Lengyel et al 2010, Rojas et al. 2012, Eriksson 2016), but empirical evidence remains elusive both for pattern and process. We show a significant cophylogenetic signal (CS) which is strong evidence that phylogenies of interacting Platyrrhini primates and fleshy-fruited Angiosperms are congruent across the Neotropics, supporting long-standing claims that interactions between Angiosperms and primates are shaped by coevolution (Sussman 1991, 1995; Eriksson 2016). CS emerged independently in three tropical rainforests (Mesoamerica, Amazonia and Atlantic Forest),

asymmetrically driven by generalist primates dispersing specialist angiosperms. Interestingly, the consistency between the continental and local scales evidence spatial replication of the process, and support the idea of similar eco-evolutionary dynamics operating irrespective of species composition in regional/biome meta-communities.

Recent estimates suggest primate origins from 55.8 to 50.3 Mya, in the early Eocene (O’Leary et al. 2013), consistent with the rise and dominance of modern tropical rainforests (Sussman 2017). During primate diversification, adaptive locomotion, reproductive biology, skull morphology, dentition and feeding niches have possibly arisen as a coevolutionary response to fruiting plants (Sussman et al. 2013). In the specific case of the New World primates, the divergence times in the modern Platyrrhini is estimated to be 20.1 Mya, during the Oligocene-Miocene boundary (Schrägo 2007). This was nearly the time of diversification of many extant lineages of fleshy-fruited Angiosperms. Even though many families seem to have conserved fruit traits ever since the Eocene (Eriksson et al. 2000), drupes and berries, the most consumed fleshy-fruits by primates, have evolved much more recently. For instance, Bolmgren & Eriksson (2005) found that almost half of fleshy-fruited clades are younger than 40 Mya, and Eriksson (2016) provides many examples in Arecaceae, Rubiaceae and Solanaceae with a drastic increase in diversification between 40 to 18 Mya. This time-scale overlap in diversification of both Neotropical primates and fleshy-fruited plants is consistent with our idea that seed dispersal somehow coupled their evolutionary history.

The congruence in phylogenies was clearly driven by seed dispersal, as evidenced from strong effects of the primate frugivory-related variables. Chronological evidence supports the origin of primate frugivory at the end of the first stage of Angiosperm diversification (Eriksson 2016). As expected, the cophylogenetic relation among plants and primates was shaped mainly by the most frugivorous taxa, although specific plant traits were not pivotal in driving such a signal. At the continental scale, mainly frugivores and frugivore-folivores, the major seed dispersers (Fuzessy et al. 2016), were the feeding guilds contributing most to the signal, whereas, not surprisingly, seed predators had the least contribution. Seed predators (Pitheciidae) are absent in Mesoamerican forests (Estrada et al. 2005), where frugivore-insectivores were found to contribute the least, while omnivores were followed by the frugivores and frugivore-folivores as those with the highest contribution. This variation may be a consequence of the relative importance in terms of number of species in each guild inhabiting different regions, added to their conservation status, and therefore the number of interactions performed. For instance, in the Atlantic Forest, the only mainly frugivores are the *Brachyteles*, with only two species threatened by extinction. On the other hand, in the Amazon, *Ateles* and the *Lagothrix* play the most important role as frugivores, and are much better represented.

Recent studies on the visual adaptations of primates support intrinsic relationships between primate diversification and the capacity to detect plant resources (Valenta et al. 2018, Onstein et al. 2020, but see Heymann & Fuzessy 2021). The evolution of modern primates, therefore, may be directly related to improved means of efficiently exploiting fleshy-fruit food resources (Sussman 2017), although in some cases evidence is limited to particular clades and recent times (e.g., Onstein et al. 2020). Our analysis reveals a CS at the whole phylogenetic tree, although some clades (e.g., Atelidae) had larger contributions to the signal. These findings, together with the evidence of an early frugivorous habit over primate diversification (Sussman et al. 2013), supports the prominent phylogenetic congruence in Neotropical primate-fruit interactions driven by primate frugivore-related, functional traits. It also provides clues that diversification is an ongoing process, given the large contribution from recent Platyrrhini clades.

Reconstructing the evolutionary history of plants based on fruit traits as a response to selective pressures generated by interacting primates is still challenging. In this case, the phenotypic responses may be more strongly subjected to phylogenetic constraints, i.e., reflect inherited ancestral characteristics rather than traits adapted to an ecological niche (Jordano 1995, Valenta and Nevo 2020). Our results show that diaspore size, key morphological constraint to the establishment of mutualistic interactions (Dehling et al. 2014), was not an important driver of the CS. Most studies evaluating plant adaptive responses to mutualisms with primates based on current empirical data have found weak evidences of phylogenetic signals (Valenta et al. 2016, Valenta et al. 2018 - fruit color; Nevo et al. 2018, Nevo et al. 2020 - fruit scent; Valenta et al. 2016 -

size, mass and hardness), a likely consequence of the low specificity found in extant interactions.

Frugivorous birds and mammals are the major seed dispersers in the tropics (Fleming and Kress 2011). Considering the primate-centered basis of our dataset, and despite the low overlap in fruit consumption among primates and other fruit-eating vertebrates, our results reflect the trend of plants to share multiple dispersers. This is not only true for recent times, so it is important to consider that, throughout evolutionary history, primates were not the only interacting taxa with the radiating fruiting plants.

At the time of Angiosperm radiation, the diversification of the earliest modern-looking primates in parallel with that of other mammals and fruit-eating birds, propelled the beginning of a shared evolutionary relationship (Sussman 2017). It helps us to explain how such low specificity prevents a detection of strong phylogenetic patterns. However, the CS appears even in a suprageneralist system where other frugivorous groups may be also shaping plant diversification. We also observed an asymmetry in terms of the number of interactions performed by each plant genera and primate species, which explained the influence on the CS in an opposite direction: primates dispersing the greater diversity of plants (i.e., generalists), and plants dispersed by fewer primates (i.e., specialists), contributed the most to CS strength. Interestingly, asymmetry is an inherent property of coevolutionary networks that allows the long-term coexistence of the interacting species (Bascompte et al 2006).

Besides fruits, Platyrrhini primates also include leaves, flowers, seeds, nuts, nectar, and animal preys as feeding resource (Hawes and Peres 2014). Distinct amounts of each item vary across taxa (Hawes and Peres 2014), thus less frugivorous primates and other coexisting frugivorous clades, may be acting together favoring a process known as diffuse coevolution (Erikson 2016). It is unlikely that frugivores and plants share a very tight coevolutionary history (Valenta and Nevo 2020), such as those observed in host-parasite interactions (Brooks 1988, Gandon 2002), or plant-pollinator interactions (Herrera 2019). Instead, spatio-temporal asymmetries, disruptions in relationships between patterns, and shifts between periods of coevolution among coexisting clades should lead to reciprocal adaptive changes, ultimately resulting in a weak process (Erikson 2016), as shown here. Primate evolution seem to have somehow “tracked” plant radiations, resulting in a coevolutionary history with asymmetric influences.

The multi-specific character of the process delineating the CS does not mean that primates and plants have not coevolved or that coevolution has necessarily been the primary force fueling diversification (see e.g., Althoff et al. 2014, Poisot 2015). Instead, it seems to occur in a much more complex framework, including both direct and indirect effects underlined by three non-exclusive main processes (Guimaraes et al 2011, 2017). First, selection regimes imposed by generalized multiple-partner interactions, such as seed dispersal, are the outcome of a complex interplay among selection pressures operating through multiple pathways, leading to slow, but continuous, coevolution. Coevolution repeatedly reshapes selection regimes and species traits by speeding up the overall diversification rate in interacting clades. Second, coevolution results in higher trait complementarity among interacting partners (reduced mismatch and increased trait convergence), and the level of integration may provide a mechanism for the emergence of community-level trait patterns. Finally, convergence tends to be higher in the presence of super-generalists, here represented by the most frugivorous primates, responsible to interact with a wide-range of plant species and thus establishing the magnitude of the observed CS. Our results evidence and indicate a strong non-random pattern in the diversification of primarily primate-dispersed neotropical genera and their primate disperser partners, reinforced by the replicated consistency found in three major neotropical biomes. While the processes involved in such high-level macroevolutionary patterns remain obscure, our approach highlights replicated consistence over large biogeographic extents and evidences the strong potential of highly-diversified mutualisms among free-living species in macroevolution.

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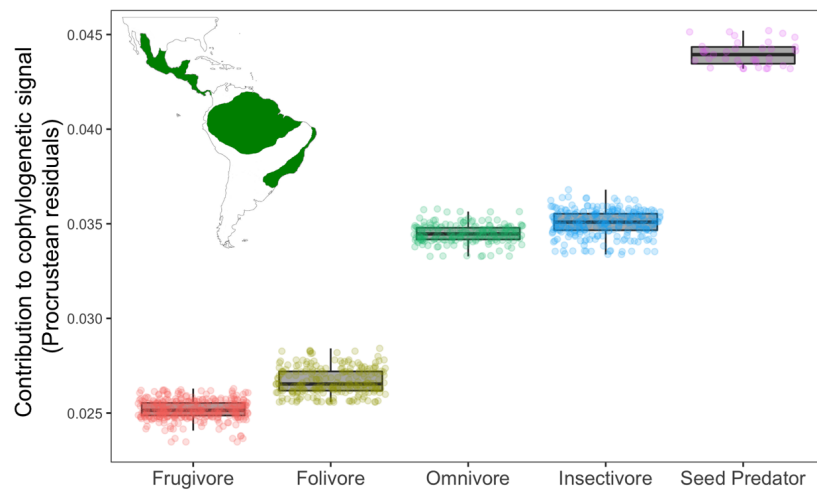


Figure 2

Figure 3

