

# Frugivory Specialization in Birds and Fruit Chemistry Structure Mutualistic Networks across the Neotropics

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**ABSTRACT:** The interaction between fruit chemistry and the physiological traits of frugivores is expected to shape the structure of mutualistic seed dispersal networks, but it has been understudied compared with the role of morphological trait matching in structuring interaction patterns. For instance, highly frugivorous birds (i.e., birds that have fruits as the main component of their diets), which characteristically have fast gut passage times, are expected to avoid feeding on lipid-rich fruits because of the long gut retention times associated with lipid digestion. Here, we compiled data from 84 studies conducted in the Neotropics that used focal plant methods to record 35,815 feeding visits made by 317 bird species (155 genera in 28 families) to 165 plant species (82 genera in 48 families). We investigated the relationship between the degree of frugivory of birds (i.e., how much of their diet is composed of fruit) at the genus level and their visits to plant genera that vary in fruit lipid content. We used a hierarchical modeling of species communities approach that accounted for the effects of differences in body size, bird and plant phylogeny, and spatial location of study sites. We found that birds with a low degree of frugivory (e.g., predominantly insectivores) tend to have the highest increase in visitation rates as fruits become more lipid rich, while birds that are more frugivorous tend to increase visits at a lower rate or even decrease visitation rates as lipids increase in fruits. This balance between degree of frugivory and visitation rates to lipid-poor and lipid-rich fruits provides a mechanism to explain specialized dispersal systems and the occurrence of certain physiological nutritional filters, ultimately helping us to understand community-wide interaction patterns between birds and plants.

**Keywords:** animal-plant interactions, mutualistic networks, digestive physiology, seed dispersal, avian ecology, Neotropical plant ecology.

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## Introduction

Understanding the factors that govern the mutualistic interaction between plants and frugivorous animals is a long-held challenge for ecologists. Decades of research show that two types of factors affect bird-plant interactions. First, there are contextual factors defined by the spatial, temporal, and community scenarios in which plant-bird interactions occur. For instance, rates of frugivory are affected by the temporal fluctuations in bird and fruit abundances, as well as by the spatial configuration of fruiting resources per se (Levey et al. 1984; Loiselle and Blake 1991; Carlo et al. 2007). Second, two classes of trait-matching processes between mutualistic partners influence community-wide interactions in a more fundamental manner. First, morphological trait matching such as that between a bird's bill gape and the size of fruits and seeds determines whether a bird species can feed on or disperse the seeds of a fleshy-fruited plant species (Moermond and Denslow 1985). Second, beyond this first morphological trait filter, matching between the gut digestive capacity and the nutritional and chemical traits of pulp takes place (Levey and Martínez del Río 2001). Of these trait-matching processes, morphological trait matching has been amply studied, while the physiological nutritional filter has received comparatively little attention, and its role in structuring mutualistic plant-frugivore communities remains obscure. Studying how matching between frugivore physiology and fruit chemistry structures interactions has proved challenging, as detailed knowledge of fruit chemical composition and the inner workings of frugivores' guts is generally lacking.

Understanding how the digestive physiology of frugivores interacts with fruit chemistry is important because even morphologically similar frugivores can show significant differences in digestive traits (Martínez del Río and Restrepo 1993; Witmer and Van Soest 1998). Differences

in gut digestive capacity can lead to differences in fruit-use patterns between morphologically equivalent bird species (i.e., with similar body mass, bill gape) given the highly variable nutrient profiles of fruits, especially regarding the content of fruit sugars and lipids (Jordano 1995; Witmer and Van Soest 1998). Despite much variation, fleshy fruits can be roughly classified as being either sugar rich and lipid poor (<10% of dry mass in lipids) or lipid rich and sugar poor, with a majority of plant species pertaining to the “sugary” category (Moermond and Denslow 1985; Herrera 1987; Galetti et al. 2011). The hydrophobicity of lipids makes their abundance in pulp negatively correlated with water content while bearing no correlation with protein content (protein at any rate is low in the majority of fleshy fruits; see Jordano 2014). The lipid content of fruits is also phylogenetically conserved, with most variation occurring from genus to upper taxonomic levels (Jordano 1995). Thus, many plant genera and families can characteristically produce lipid-poor and sugar-rich fruits (e.g., *Ficus* in Moraceae, *Miconia* in Melastomataceae) or lipid-rich and sugar-poor fruits (e.g., *Ocotea* in Lauraceae, *Trichilia* in Meliaceae; Moermond and Denslow 1985; Jordano 2014).

Balancing fruit choices based on the relative content of sugars and lipids of the fruits in a community can be important because divergent physiological strategies are required for the digestion and assimilation of each kind of nutrient (Martinez del Rio et al. 1989; Stiles 1993; Witmer and Van Soest 1998). For instance, while sugars are fast to absorb, lipids require much longer gut retention times to break down metabolically because of their large size and complexity relative to sugars (Karasov and Martínez del Río 2007). Thus, it should be expected that bird species that eat foods requiring longer gut passage times, such as omnivores and insectivores that constantly mix fruit with animal matter (Herrera 1984), will be able to readily use both sugar-rich and lipid-rich fruits. Conversely, as a result of relatively fast gut transit times of digesta, frugivorous birds specializing on sugar-rich fruits would be unable to properly absorb nutrients from lipid-rich fruits (Witmer and Van Soest 1998). Birds with fast gut passage times should therefore avoid lipid-rich fruits, although such fruits will always be more energetically profitable. This leads us to predict that lipid-rich fruits should be consumed and dispersed more frequently by insectivorous and omnivorous birds that have guts better equipped to deal with lipids than the more heavily frugivorous species that specialize on sugary fruits (Levey and Martinez del Rio 2001). In fact, many field studies have reported and highlighted the observation that insectivores and omnivores feed on lipid-rich fruits and disperse their seeds often at higher rates than predominantly frugivorous birds (e.g., Howe and Vande Kerckhove 1979; Carlo et al. 2003; Pizo

and Santos 2011; Carlo and Morales 2016). Still, a formal test of such interaction patterns has never been conducted despite the potential ecological and evolutionary implications for mutualistic plant-frugivore communities if this indeed is a general phenomenon.

Here, we investigated the relationship between the frugivory degree of birds (i.e., how much of their diet is composed of fruit) and their relative importance as visitors to plants that vary in fruit lipid content. We hypothesized that the relative contribution of visits by predominantly nonfrugivorous birds would increase with the lipid content of fruits. Our analyses rely on the largest compilation of bird visitation records to focal plant species across the Neotropics, and the results challenge the notion that the functional role of birds in seed dispersal can be approximated by simple dietary categorizations such as “frugivore” and “insectivore.”

## Methods

### *Data Compilation*

We searched the literature (i.e., papers in peer-reviewed, indexed journals as well as dissertations and theses) for studies that reported quantitative measures of feeding visits by birds to focal fruiting plants. We searched the databases Google Scholar, Scopus, and Web of Science using the terms “bird,” “avian,” “frugivory,” and “seed dispersal” and their Portuguese and Spanish equivalents. We found 84 studies conducted in five Neotropical countries between 1971 and 2015 that included a variety of regions, biomes, and habitats (table S1; tables S1–S10 are available online). Some studies were conducted on the same site and were combined to yield 70 distinct localities. These studies share a common focal plant methodology that entailed observing a plant for a fixed period of time to record all bird visitors, and they are largely representative of species from the most common and widespread plant and bird genera of the Neotropics (tables S2, S5).

### *Bird and Plant Traits*

Our combined focal plant visitation data set has 165 plant species in 82 genera and 48 families and 317 bird species in 155 genera and 28 families (tables S2, S3, S5). Estimates for bird functional traits, namely their body mass and frugivory degree, were obtained for all visiting bird species from the EltonTraits 1.0 database (Wilman et al. 2014). However, estimates for the percentage of lipid content of fruit pulp were found for only 60 plant species. For the additional 105 plant species, the percentage of lipid content of fruits was available from only one or more congeneric species (table S2; data are available

in GitHub [<https://github.com/jmmorales/lipids/tree/v01>; Pizo et al. 2020]). Given that the majority of plant species lacked species-level data on the percentage of lipid content, we opted to conduct analyses at the genus level to have a wider representation of taxa and study areas. Despite the existence of significant interspecific variation, fruit nutrient profiles tend to be conserved at the genus and family levels (Jordano 1995). The same holds true for the diet and body mass of birds (Böhning-Gaese and Oberrath 1999).

A total of 94 bird genera (60.6%) were represented by only one species, and 61 genera (39.4%) were represented by 2–12 species. We used the species-level trait values for those genera with only one bird species in the data set. For those with two or more, we used the average trait value across the recorded species. Psittaciformes were excluded, since they feed mostly on seeds rather than on pulp (Galetti and Rodrigues 1992). Of the 82 plant genera, 40 (48.78%) were represented by one species, and the rest were represented by a range of 2–22 species. For the 42 plant genera with two or more species in the data set, the fruit lipid content among the species for which we had data was usually not very variable, although there are a few exceptions (fig. S1; figs. S1–S5 are available online). Overall, there were 29 genera represented by only a single plant species for which the fruit lipid content value belonged to that same species. Thus, 35.4% of genus-level data for the plant trait is effectively species-level data. Fruit lipid values used for the rest of the plant genera were averaged across the available data from congeners (i.e., including a portion of the focal plant species depending on availability of fruit lipid data).

Given that this approach can miss important intra-generic variation, we examined how fruit and bird trait variance was partitioned among genera and families. For this, we used linear models where trait values (percentage of lipid content, bird frugivory degree, and body mass) were a function of family and genus, with genus nested within family. The results of this nested analysis mirror findings of previous studies (e.g., Jordano 1995; Böhning-Gaese and Oberrath 1999) and show that most of the trait variance occurs at the family level for both fruit lipids (62.8%) and bird traits (46.2% for frugivory degree and 74.6% for body mass), while variance within genera accounts for small fractions of the total variance (6.0%–20.7%; table S4; fig. S1). Residual variance (among-species variation and measurement error) was 25.76% for lipids in fruits, 13% for degree of frugivory, and 34% for body mass.

#### *Visitation Data Analysis*

We analyzed the data following the Bayesian hierarchical modeling of species communities (HMSC) approach

of Ovaskainen et al. (2017), which belongs to the class of joint species distribution models. In these analyses, we modeled the number of visits from different bird genera to the focal plant genera at each site using a negative binomial distribution, where the expected number of visits was a linear function of the lipid content of the fruits from each plant genus (log link). We allowed each bird genus to have its own intercept and a slope for the regression on the fruit lipid values of focal plant genera. We modeled these intercepts and slopes as linear functions of the two bird traits: degree of frugivory and log-transformed body size. Both variables were centered and standardized before the regression. To account for phylogenetic relationship in the responses of birds to lipid content, we modeled the residual covariation among the intercepts and slopes as a function of phylogenetic relationships among the bird genera.

The idea behind our approach is to relate, in a single model, the way birds react to the lipid content of fruits to their degree of frugivory and their body size. In our model, the number of visits that birds make to a plant depends on the lipid content of the plant's fruits. This relationship is captured by the slope of a negative binomial regression between fruit lipid content and visits, while the intercept gives the expected number of visits to a plant with average lipid content (because we centered the variables, the average lipid content equals the intercept). Both the intercept and slope are, however, allowed to vary by bird genus as a linear function of (log) body size and degree of frugivory. Thus, if the degree of frugivory of different birds affects how they respond to lipids in fruits, we should find that the coefficient relating degree of frugivory to the slope of the negative binomial regression is different from zero.

We included the site and the plant genera as random effects. The noise structure assumed for both of these levels was Gaussian decaying covariance functions, where the distance matrix for sites was based on Euclidian distance and the distance matrix for plants was based on phylogenetic distance. The overdispersion parameter of the negative binomial was estimated as a free parameter. We obtained consensus trees for the bird and plant genera phylogenies from <https://birdtree.org> (Jetz et al. 2012) and Phylomatic version 3 (Webb and Donoghue 2005), respectively (figs. S2, S3). Further details on model structure and priors for all parameters can be found in the supplemental PDF (available online). In general, we used weakly informative priors, but for parameter  $\rho$  that relates bird phylogenetic correlations to the covariance among regression parameters, we used a mixture of two beta distributions: one with mass concentrated near zero, and hence allowing for the possibility of no phylogenetic signal (Beta(1, 100)), and one uniform between zero and one

(Beta(1, 1)). The proportion in the prior mix was 0.5 for both distributions.

We fitted the model using Stan through R (Carpenter et al. 2017; Stan Development Team 2018). We ran each of four Markov chain Monte Carlo analyses for 100,000 iterations, of which we discarded the first 50,000 iterations as warm-up and thinned the remaining by 50, yielding 1,000 samples of the posterior distribution per chain and thus 4,000 samples in total. We examined convergence through distributions of effective sample size potential scale reduction factors (Carpenter et al. 2017). In addition to the genus-level analyses and to verify the generality of results using genus-level data, we ran a species-level analysis using the exact same framework on a data subset of 60 plant species (in 47 of the 70 sites) for which both percentage of lipid content and phylogenetic data were available. The code used to analyze the data is available in GitHub (<https://github.com/jmmorales/lipids/tree/v01>; Pizo et al. 2020).

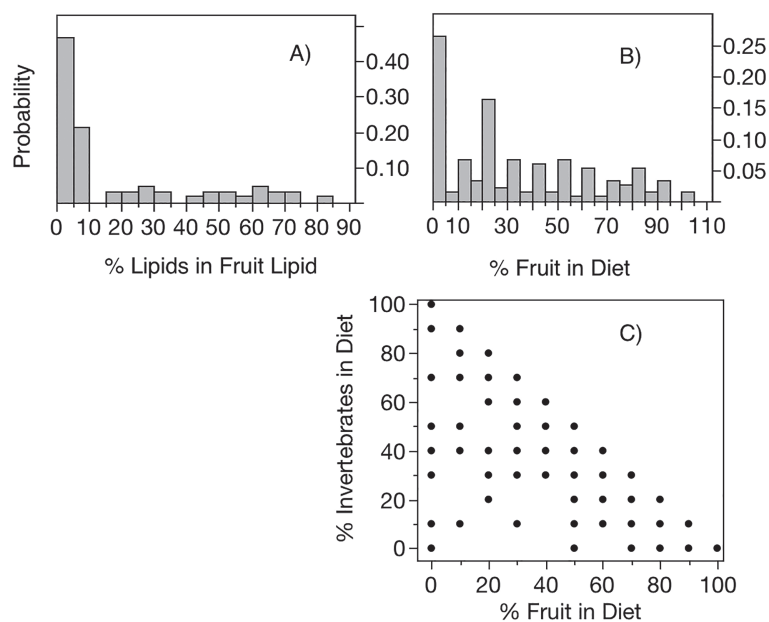
We used the *igraph* package (ver. 1.2.4.1; Csardi and Nepusz 2006) to visualize the relative contribution (i.e., with weighted edges) of bird visits from different diet categories to lipid-rich and lipid-poor plants. For this, we used 12 studies that included the focal observation of at least four plant species at the same location and at least one plant with high lipid content and one with low lipid content. In each graph, we color-coded plants vertices as

high (>33%), medium (10%–33%), and low (0%–10%) lipid content. We color-coded bird vertices by fruit diet: primarily insectivorous (degree of frugivory: 0%–33%), omnivorous (34%–66%), and primarily frugivorous (>67%).

## Results

The mean lipid content of fruits for the 82 plant genera in the data set ranged from 0.04% to 83.3% in a dry mass basis, but more than half of the genera were lipid poor, with less than 10% lipid content (fig. 1A; table S2). Birds with predominantly insectivorous and omnivorous diets comprised 129 of the 155 registered bird genera and were the most frequent visitors (44.3% and 33.9% of all visits, respectively). Bird genera with fruit-dominated diets accounted for 21.8% of all visits (fig. 1B). The frequency of fruit items in the diets of all bird genera had an inverse relationship with the fraction of invertebrates (mostly insects) in their diets (fig. 1C). Thus, although alternate food types may be used (e.g., nectar, seeds), increasing the degree of frugivory generally implies a decrease of insectivory.

All Markov chains of the HMSC model converged (maximum  $\hat{R}$ : 1.002) and obtained a good number of effective posterior samples (minimum: 2,121; median: 3,872). Results show that most birds (78.84%) responded positively to fruit lipid content but also that lipids had a



**Figure 1:** Frequency distribution of the percentage of lipids in fruit pulp (on a dry mass basis; A) and percentage of fruit in bird diets (B) in a sample of 82 plant genera and 155 bird genera reported in 84 studies conducted in the Neotropics. Note that most plants are lipid poor, with <10% lipid content, and that most birds visiting plants to eat fruit have diets dominated by nonfruit items (mostly invertebrates). In general, a lower frugivory degree implies that birds are more insectivorous (C).



selective effect on bird visitors (table 1). Both the baseline rate at which birds visited plants and the dependency of the visitation rate on fruit lipid content depended on the degree of frugivory and body mass of birds (fig. 2A–2C). The baseline visitation rate was highest for frugivorous birds, but this was associated with the greatest decrease in visitation rate as a function of fruit lipid content (fig. 2E). That is, birds with a low degree of frugivory (omnivores and insectivores) tend to have the highest increase in visitation rates as fruits become more lipid rich, while birds that are more frugivorous tend to increase visits at a lower rate or even decrease visitation rates as lipids increase in fruits (fig. 2B). Also, the visitation rate of small birds was higher than that of large birds, but there was no clear relationship between body size and dependency of visitation rate on lipid contents (fig. 2C, 2D). The predicted visitation rate for a bird with an average body size illustrates the interaction between degree of frugivory and fruit lipids: insectivores and omnivores respond positively to fruit lipids but highly frugivorous birds respond negatively (fig. 2E). Note that this interaction is not estimated as a parameter but rather arises because both the intercept and the slope of the regression between lipid in fruit and number of visits are a function of bird degree of frugivory (and body mass). The same general patterns are obtained when we run the model using a subset with the available species-level data only, but results are weaker (posteriors include zero), possibly because many bird and plant taxa are missing with this approach (fig. S4E; tables S6–S8).

The data were not very informative about a phylogenetic signal in bird responses. The posterior mean for  $\rho$  was 0.19, with 95% credible interval of 0.00–0.62 (table S9). Site random effects were relatively large compared with plant random effects. Random effects did not depend strongly on distance among sites or cophenetic distance among plants (table S10; fig. S5).

The partitioning of species interactions according to bird diet traits and lipid content was evident when repre-

senting local community interactions as networks (fig. 3). Within sites, lipid-rich plants were visited mostly by fruit-eating insectivores, while primarily frugivorous genera mainly visited low-lipid fruiting plants (fig. 3).

The lipid by fruit diet interaction was also patent at the scale of bird and plant families (fig. 4). Primarily insectivorous Tyrannidae accounted for most visits to lipid-rich plant families, such as Meliaceae, Salicaceae, Sapindaceae, and Loranthaceae, while the primarily frugivorous Thraupidae were more frequent visitors to lipid-poor (and sugar-rich) Melastomataceae and Moraceae (fig. 4). This is consistent with the moderate phylogenetic effect revealed by the HMSC model in the pattern of bird responses to fruit lipid content (table S5). The bird genera in these two passerine families and Turdidae accounted for most visits (73.6%) to focal plants, the most frequent being the tanager family Thraupidae (32.3%), followed by flycatchers in Tyrannidae (23.9%) and thrushes in Turdidae (17.3%). Covariance in visitation rates decreased relatively quickly with distance among sites or with cophenetic distance among plants (table S10).

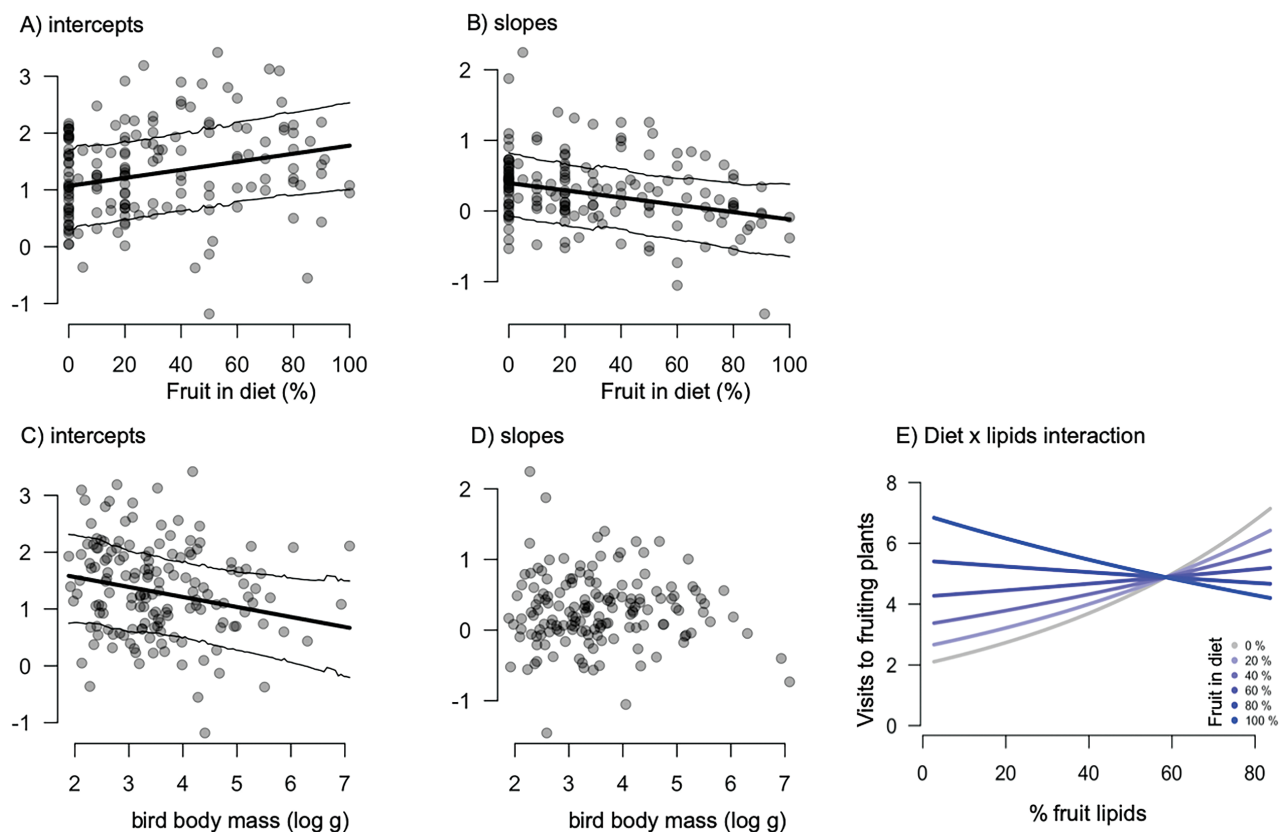
## Discussion

Our study shows a balance between the degree of frugivory of birds and their visitation rates to lipid-poor and lipid-rich plant genera. Lipid-poor plants are visited more often by birds that are more specialized in eating fruit, while plants that are rich in lipids interact more often with birds that have predominantly insectivorous diets (i.e., lower frugivory degrees; figs. 3, 4). This happens even though frugivorous birds make more visits to fruiting plants (fig. 2). These results overturn a long-held hypothesis that increased lipid concentration in pulp makes fruits more attractive to frugivores (Stiles 1993), as not all bird genera respond positively to increases in fruit lipid content. Fruit specialization appears to be constrained by the dominant types of nutrients in fruit, at least in some groups of common Neotropical passerines.

**Table 1:** Parameter estimates for the effects of bird traits on the regression between bird visits and fruit lipid content

	Mean	2.50%	97.50%	$n_{\text{eff}}$	$\hat{R}$
Expected intercept	1.291	.569	1.952	2,829.674	1.001
Expected slope on lipid content	.234	-.251	.620	4,160.145	.999
Frugivory effect on intercept	.207	.041	.379	3,822.215	1.000
Frugivory effect on slope	-.150	-.283	-.021	4,042.242	1.000
Body mass effect on intercept	-.187	-.379	-.007	3,970.170	1.000
Body mass effect on slope	.031	-.111	.180	4,107.339	1.000

Note: The expected intercept corresponds to the average (log) proportion of visits by birds with average degree of frugivory and average (log) body mass to a plant with average lipid content. The degree of frugivory increased this baseline, while body mass decreased it. The expected slope of visits with fruit lipid content was positive and decreased with increasing frugivory degree. Posterior mean, quantiles, effective sample size of posteriors ( $n_{\text{eff}}$ ), and convergence diagnostics ( $\hat{R}$ ) are reported.

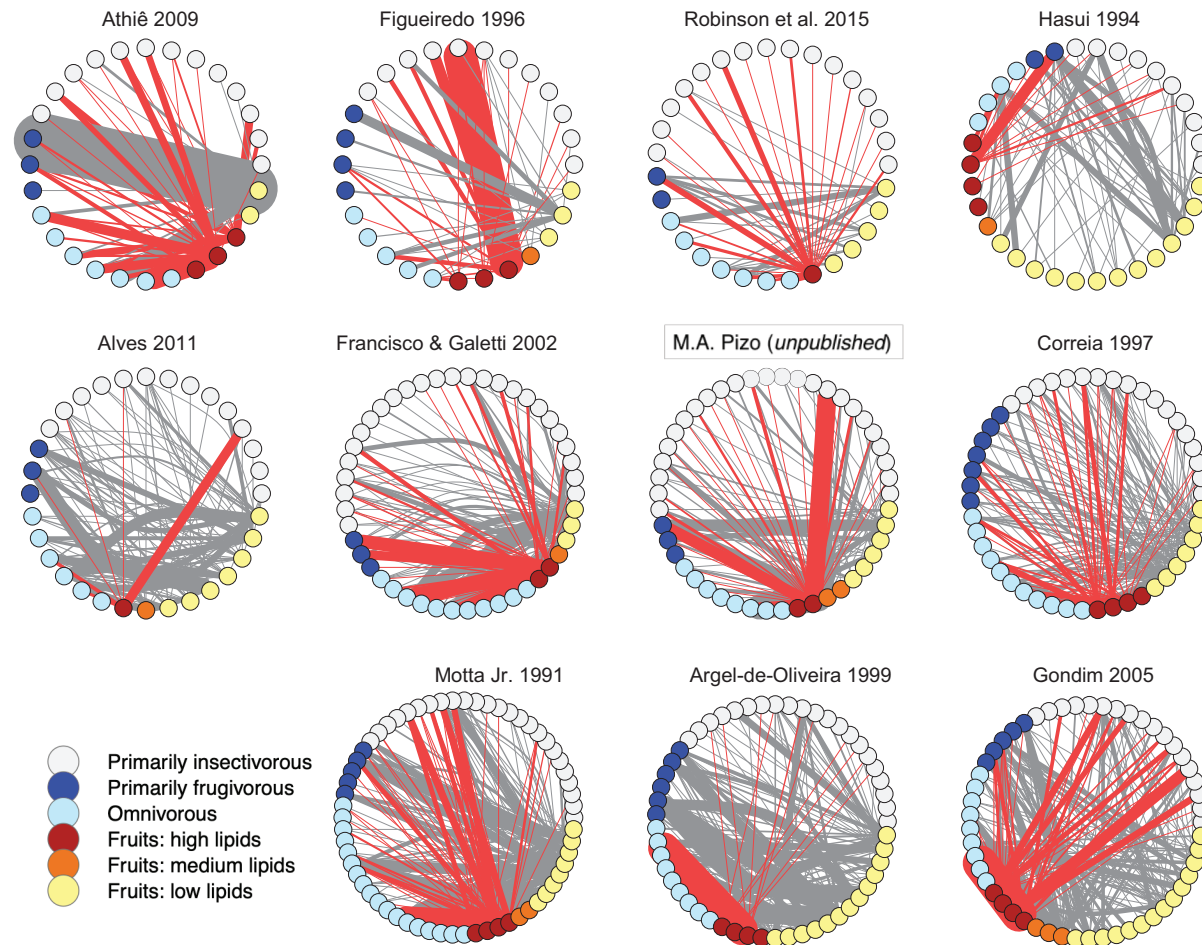


**Figure 2:** Percentage of fruit in diet (frugivory degree) and body mass affect the response of birds to the lipid content of fruits. *A* shows the intercept of the regression between the expected number of visits (log link) and fruit lipid content against the degree of frugivory (percentage of fruit in their diet) of each bird genus. *B* shows how the slope of the relationship between fruit lipids and visits (log link) changes with the bird's degree of frugivory. *C* and *D* show intercepts and slopes in relation to body size, respectively. The thick lines show the modeled linear relationships between intercepts and slopes and the degree of frugivory. The thin lines show 95% credible intervals. There is no line in *D*, as we did not find a clear relationship between slopes and body mass. In *E*, by combining the estimated intercepts and slopes as functions of frugivory degree for average body mass and transforming the log link to number of visits, we can see that birds that usually consume low amounts of fruit according to EltonTraits (Wilman et al. 2014) respond more strongly to lipid-rich fruits, while frugivorous birds decrease the number of visits when fruit lipid content increases.

The underlying mechanism for these patterns is likely to be driven by the covariance between birds' dietary specialization in fruit and the capacity of some avian guts to digest disparate nutrient types, such as lipids and sugars (Levey and Karasov 1989; Martínez del Río 1990; Fuentes 1994; Levey and Martínez del Río 2001). For example, fruits poor in lipids are typically rich in water and sugars that are rapidly absorbed by bird guts via active and passive transport (Jordano 1995; Karasov and Martínez del Río 2007). Conversely, absorption of lipids is a longer multistep process that involves emulsification and hydrolysis of larger molecules (Karasov and Martínez del Río 2007). Thus, it is difficult for predominantly frugivorous birds with fast gut transit times optimized for sugar absorption to process lipid-rich fruits (Herrera 1984; Martínez del Río et al. 1988; Martínez del Río 1990). Predom-

inantly insectivorous birds have slower gut transit times than heavily frugivorous birds and digestive machinery adapted to digest lipids found more abundantly in animal prey, as they are predisposed to readily feed on oily fruits (Martínez del Río et al. 1988; Fuentes 1994).

Another factor that could contribute to the balance between frugivory degree and visitation to lipid-poor and lipid-rich plants is the level of chemical defenses in fruit. For example, the defense trade-off hypothesis (Cipollini and Levey 1997) predicts a negative relationship between some nutrient types and the amounts of secondary metabolites in fruit pulp. Fruit removal rates of lipid-poor fruits are on average slower than those of lipid-rich fruits (Cazetta et al. 2007). Slow removal times can thus increase the susceptibility of lipid-poor fruits to microbial pathogens, promoting selection for the chemical defense



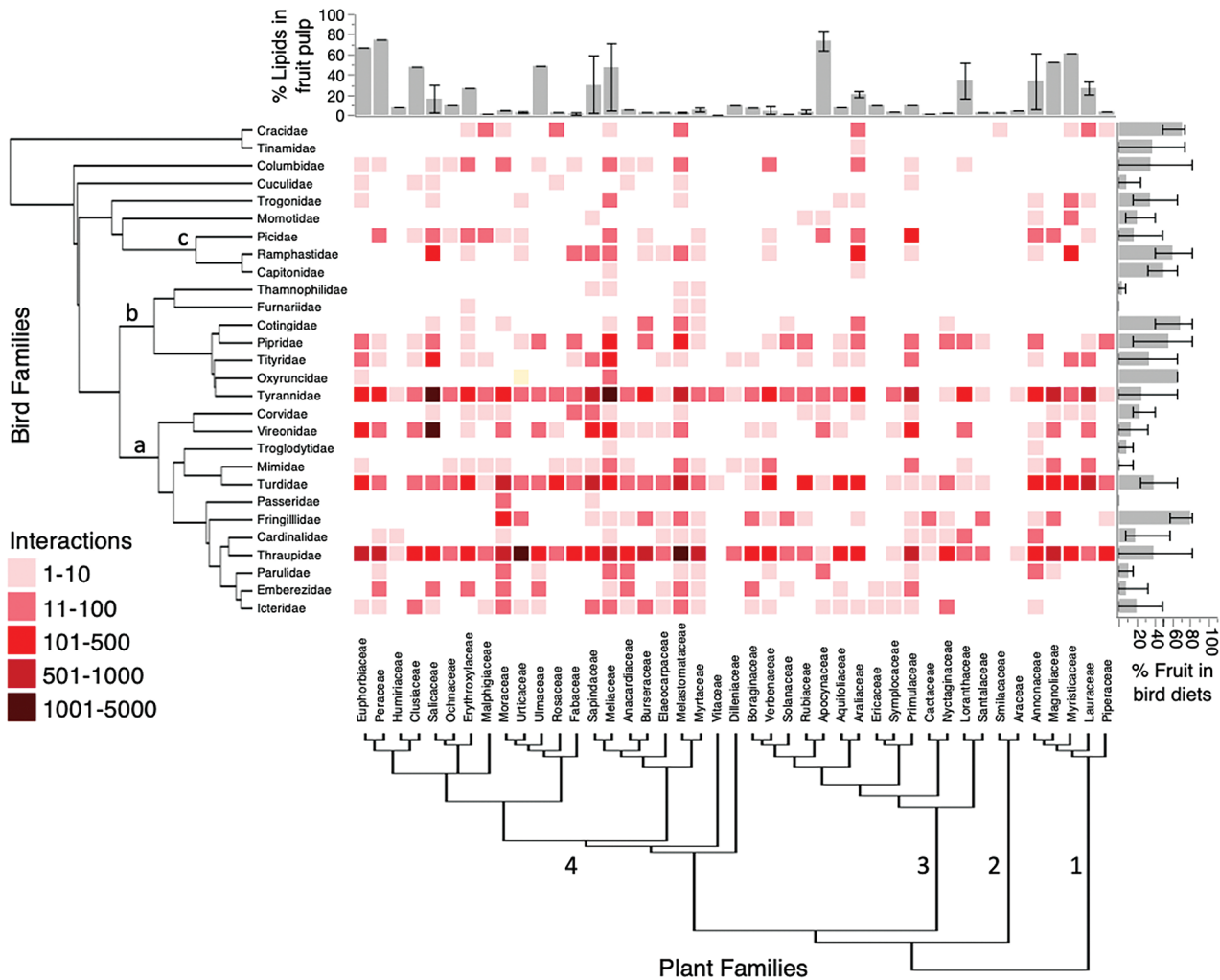
**Figure 3:** Circular network graphs from 11 Neotropical studies that recorded bird visits to five or more plant species in a community, including plants with different lipid content in fruits (high: >33%; medium: 10%–33%; low: <10%). Bird genera were grouped by fruit diet (frugivorous: >67% fruit diet; omnivorous: 33%–67% fruit diet; insectivorous: <33% fruit diet). Edges are weighted by the number of visits, and the interactions involving lipid-rich fruits are highlighted in red. Note that in most sites, lipid-rich fruits (red vertices) interact primarily with insectivores (gray vertices) or omnivores (light blue vertices). Conversely, highly frugivorous birds (blue vertices) interact primarily with lipid-poor (sugar-rich) plants (yellow vertices). Data sources are indicated on top of each graph (see the supplemental PDF, available online, for more details and complete references).

of their pulp (Cipollini and Levey 1997). Accordingly, heavily frugivorous birds have superior detoxifying capacities than predominantly insectivorous birds (Herrera 1984), which could further accentuate differences in the dietary guilds of birds visiting lipid-rich and lipid-poor plants.

#### *Ecological and Evolutionary Implications*

*Lipids and Diet Specialization of Frugivorous Birds.* Our results show that birds previously portrayed as “opportunistic” frugivores for having diets dominated by insects contribute the majority of community-level frugivory interactions for plants with oily fruits (figs. 3, 4). Consistent

with our findings, a recent study on *Bursera* tree species in the dry forests of southwestern Mexico finds *Myarchus* flycatchers (Tyrannidae) to be the primary seed dispersers (Almazán-Núñez et al. 2016). In fact, our analysis shows that tyrant flycatchers are, after tanagers and allies (Thraupidae), the second-most frequent Neotropical frugivores, cumulatively contributing more visits to focal plants than the better-known thrushes (Turdidae; fig. 4). It is puzzling that the role of this key Neotropical family, which happens to also be the most species rich of the hemisphere, has been so neglected by frugivory studies (e.g., Fleming and Kress 2013). In fact, the contribution of tyrant flycatchers (Tyrannidae, chiefly insectivorous) to frugivory of plant families with oily fruit (e.g., Meliaceae, Flacourtiaceae) is



**Figure 4:** Heat map showing visits by fruit-eating birds to focal fruiting plants from the pooled data of 84 Neotropical studies. The average fruit diet ( $\pm$ data range, bars on right) and the average percentage of fruit lipid content ( $\pm$ data range, bars on top) are shown for the genera in each bird and plant family present in the sample. Note that the heavy concentration of interactions in the lower left corner of the graph is indicative of phylogenetic structuring of the interactions for both bird and plant families. Plant clades: 1 = asterids; 2 = monocots; 3 = magnolids; 4 = rosids. Bird clades: a = Passeriformes (oscines); b = Passeriformes (suboscines); c = Piciformes.

remarkable across all Neotropical studies, noting that their frugivory services extend beyond oily fruits to virtually all plant families (fig. 4).

Although the specialization of highly frugivorous birds on sugary fruits is well established (Martínez del Río et al. 1992; Witmer 1998), the specialization of insectivorous birds on lipid-rich fruit is unclear. Studies report that some bird species with diets dominated by insects (e.g., starlings) prefer lipid-rich fruits and lack enzymes to digest certain sugars, pointing to fruit nutrient specialization (Martínez del Río et al. 1988; Fuentes 1994). However, laboratory and field studies show that many insectivorous birds commonly feed on and effectively disperse seeds of lipid-poor fruits (e.g., Borowicz 1988; Carlo 2005; González-Castro

et al. 2015). Conversely, reports of highly frugivorous bird genera, such as *Tangara*, *Spindalis*, *Euphonia*, and *Chlorophonia*, feeding on lipid-rich fruits are rare or nonexistent. This suggests that specialization on sugary fruits may limit interactions with plants with oily fruits, but not vice versa.

Our findings illustrate another way in which plants select among agents of seed dispersal. Because fruits can interact with both mutualistic and antagonistic organisms, it is intriguing how plants filter the antagonistic interactions in favor of the mutualistic ones. Selection can be achieved by several strategies that include mechanical barriers, such as the size and accessibility of fruits (Guimarães et al. 2008), and secondary metabolites that deter some frugivores but not others (Tewksbury and Nabhan 2001). But what are



the benefits for plants, if any, of incurring such evolutionary choices? Some evidence suggests that oil-rich fruits have, on average, larger seeds and higher seed-to-pulp mass ratios than fruits with low lipid content (Cazetta et al. 2007). Thus, the evolution of lipid-rich fruits may allow plants to pack larger seeds into less pulp and attract predominantly insectivorous birds while discouraging small frugivore specialists.

From a plant's perspective, insectivores can present differences or even advantages for seed dispersal compared with some of the highly frugivorous Neotropical birds. Many insectivores have little mandibulation ability and have no choice but to swallow entire fruits and seeds (Moermond and Denslow 1985). Species with less frugivorous diets may also generate broader seed shadows and disperse seeds to longer distances because they spend less time feeding on plants (Pratt and Stiles 1983) and move more frequently across habitats in heterogeneous landscapes (Pizo and Santos 2011; Carlo and Morales 2016; González-Varo et al. 2017; Camargo et al. 2020). In contrast, the longer residence times of specialized frugivores on fruiting plants leads to shorter dispersal distances and highly aggregated seed shadows (Aukema 2004). Many specialized frugivores (e.g., tanagers) are skillful in handling fruit to separate seeds from pulp of many fruits, particularly those with larger seeds, which reduces the effectiveness of seed dispersal, particularly for fruits with large seeds and higher seed-to-pulp mass ratios (Moermond and Denslow 1985; Levey 1987; Carlo et al. 2003; Schupp et al. 2010).

*Fruit Lipids and the Structure of Plant-Frugivore Interaction Networks.* The patterning of bird-plant interactions by fruit nutrients offers another mechanism structuring mutualistic seed dispersal networks. Our analyses show that fruit lipid content could explain why some of the possible community interactions are infrequent or never recorded. Thus, fruit lipid content can contribute to so-called forbidden interactions and promote modularity (sensu Olesen et al. 2011; Bascompte and Jordano 2014). Our results also help explain the apparent paradox of studies that report plants with lipid-rich fruits being dispersed chiefly by predominantly insectivorous birds, such as tyrant flycatchers (Tyrannidae; Restrepo et al. 2002; Guerra and Pizo 2014; Almazán-Núñez et al. 2016) and vireos (Vireonidae; Howe and Vande Kerckhove 1979; Pizo 1997; Carlo et al. 2003), in communities with no shortage of highly frugivorous birds.

*Perspectives for Future Research.* More than 25 years ago, Martínez del Río and Restrepo (1993) suggested that an in-depth study of the diversity of digestive characteristics of frugivores hand in hand with advances in fruit nutrient

analysis would reveal a much richer picture of the mutualistic interactions of frugivores and plants. The data we compiled and analyzed here are a step toward understanding the effects of lipids on frugivore-plant community interactions, but much remains to be investigated. Do fruit lipids have similar effects outside the Neotropics? We believe so, but studies designed to test the generality of our results are needed. Some evidence has been found in other regions, including the Mediterranean, where insectivores (*Ficedula hypoleuca* and *Parus caeruleus*) are the primary frugivores of the most lipid-rich fruits (i.e., *Cornus sanguinea* and *Pistacia terebinthus*; Fuentes 1994). In North America, warblers and other bird insectivores are the primary frugivores of lipid-rich fruits of *Myrica* spp. (Place and Stiles 1992).

It will be important to assess whether the interaction between frugivore diet specialization and plant nutrient profiles affect the evolution of plant-frugivore communication through color and scent trait “branding” of fruits (Stournaras et al. 2015; Nevo et al. 2019). For instance, fruits rich in sugars can have distinctive color and scent trait spaces that set them apart as a group and thus serve as honest advertisement for their nutrient content. But lipid-rich fruits seem to lack such nutrient-branding distinctiveness, at least in terms of color trait spaces (Stournaras et al. 2015). Differences in the branding and honesty of signaling in fruits with contrasting nutrient profiles are intriguing and should be further investigated, especially because of correlations that exist between fruit nutrient and morphological traits (Cazetta et al. 2012) and their influence on the frugivore species attracted and the associated seed dispersal effectiveness (sensu Schupp et al. 2010). Ultimately, future research on these topics will improve our understanding of the ecological and evolutionary drivers of plant-animal communities and their mutualistic networks of interaction (Stouffer and Bascompte 2011; Guimarães et al. 2017).

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### Statement of Authorship

M.A.P. collected the data and, together with T.A.C., conceived the study. J.M.M., O.O., and T.A.C. analyzed the data. All authors wrote the manuscript.

### Data and Code Availability

R and Stan code for the analyses are available at the data repository in GitHub (<https://github.com/jmmorales/lipids/tree/v01>; <https://doi.org/10.5281/zenodo.4051127>; Pizo et al. 2020).

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Left, a Puerto Rican spindalis, *Spindalis portoricensis* (Thraupidae), endemic to the island of Puerto Rico, eating the infructescences of *Cecropia schreberiana* (Urticaceae). Photo: Tomás A. Carlo. Above right, a red-breasted toucan, *Ramphastos dicolorus* (Ramphastidae), eating the fruits of the palm *Euterpe edulis* in the Brazilian Atlantic Forest. Below right, a brassy-breasted tanager, *Tangara desmaresti* (Thraupidae), eating fruits in the Brazilian Atlantic Forest. Photos: Mathias Pires.