






## LETTER

# Global Trends of Trait Matching in Avian Frugivory and Its Consequences for the Complementarity and Irreplaceability of Birds

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## ABSTRACT

It is generally accepted that small birds cannot eat large fruits and that highly frugivorous species prefer lipid-poor ones (morphological and nutritional trait-matching). Yet, it is unclear if these rules operate globally and if their strength varies with latitude and on islands. This could have important functional implications for the degree of complementarity and irreplaceability of birds. We analyse avian frugivory in 59 communities across the globe and show that trait-matching is widespread. The strength of morphological trait-matching increased with latitude, and especially on islands, leading to high complementarity between large and small birds. However, whether this resulted in irreplaceability depended on the range of fruit sizes available in the community. Nutritional trait-matching was also common, but did not lead to complementarity or irreplaceability because birds with contrasting diets did not show opposite responses to lipid-poor fruits. We show that trait-matching is pervasive, but its functional consequences are complex.

## 1 | Introduction

Understanding animal foraging rules will help us to better predict trophic interactions within communities and their functional consequences (Schleuning, García, and Tobias 2023; Valdovinos 2019). In particular, interactions involved in plant–animal mutualisms sustain important ecological functions like pollination and seed dispersal (Schleuning, Fründ, and García 2015). In this context, three main interaction rules have been proposed—(i) partners must co-occur in space and time; (ii) more abundant species have a higher encounter probability; and (iii) traits that make interactions possible

(or more likely) should match between partners (Vázquez et al. 2009). The first two determine the possibility and rate of plant–animal encounters. The latter reflects how animal traits affect their ability to manipulate and process the food offered by plants. In the case of frugivorous birds that disperse the seeds of fleshy-fruited plants, two main trait-matching rules have been described. First, there are size-driven constraints in the ability of birds to manipulate fruits (Wheelwright 1985), and hence, small-beaked species tend to preferentially consume small fruits (Dehling et al. 2014) (morphological trait-matching, hereafter). Second, highly frugivorous birds cannot efficiently absorb lipids due to their short transit times (Levey

and Martínez del Río 2001). Thus, these species tend to consume sugar-rich fruits, while insectivorous birds prefer lipidic ones (Pizo et al. 2021, nutritional trait-matching, hereafter). Evidence of these trait-matching rules has been reported in local communities and at regional scales (e.g., Bender et al. 2018; Dehling et al. 2014; McFadden et al. 2022; Pizo et al. 2021), but to what extent they apply globally remains to be tested.

Since trait-matching is tightly linked to the ability of frugivores to consume fruits and absorb their nutrients, these rules should remain similar across communities (e.g., small-beaked birds will preferentially consume small fruits). However, the strength of trait-matching (i.e., how much frugivores' traits affect their response to fruit traits) may vary according to the characteristics of fruit and frugivore assemblages. For instance, if fruits are similar with respect to a given trait (low interspecific variability), trait-matching will have a minor effect on frugivores' foraging choices. Accordingly, strong morphological matching between partners has been found in communities with large variation in fruit and bird sizes (Bender et al. 2018; Dehling et al. 2014), while a weak effect of traits on interaction frequencies has been reported in communities with similar species (Pizo et al. 2022). In addition, the strength of trait-matching may depend on the average trait values within communities. For example, if all fruits are relatively small (or all birds large-beaked), size-driven constraints may not matter much, weakening morphological trait-matching between partners. Both characteristics of communities (average trait values and their variability) can differ due to changes in species composition and richness, distinct evolutionary histories, colonisation rates or environmental filters (Hampe 2003; McFadden et al. 2022; Sinnott-Armstrong et al. 2018). At macroscales, latitude and islands represent two of the most important factors driving differences in such processes (Gillison 2018; Schrader et al. 2021), and hence, are likely to affect trait-matching strength between fruits and frugivores.

In principle, trait-matching should be strong near the tropics because communities are diverse and harbour birds and fruits of contrasting traits (Crouch and Jablonski 2023; Sinnott-Armstrong et al. 2018). In addition, fruits represent important food resources for birds (Kissling, Böhning-Gaese, and Jetz 2009), are abundant (Jordano 2000) and available for long periods of time (Ting, Hartley, and Burns 2008). Under such circumstances, more specialised interactions and a strong trait-matching between partners are expected (McFadden et al. 2022; Brimacombe et al. 2022). If trait-matching is strong, dissimilar frugivores will forage on different sets of fruits (Bender et al. 2018; Dehling et al. 2014; Pizo et al. 2021) and will complementarily contribute to community-level seed dispersal (Schleuning, Fründ, and García 2015). If frugivores play complementary roles, they may be irreplaceable within communities because their loss can compromise the dispersal of certain plant species (Morán-López et al. 2020). The remaining species may not (or scarcely) consume the fruits previously dispersed by missing birds because they have trouble handling or digesting them (Galetti et al. 2013; González-Castro et al. 2022). For instance, in tropical ecosystems, the dispersal of large-fruited plants can decline after the loss

of large birds (e.g., Bello et al. 2024; Kurten 2013; Terborgh et al. 2008). Less attention has been paid to the functional complementarity of frugivorous birds in temperate areas (Rogers et al. 2021, but see García, Donoso, and Rodríguez-Pérez 2018; González-Varo et al. 2023). Probably because temperate birds have mixed diets (Levey and Karasov 1989), fruits tend to be small (Sinnott-Armstrong et al. 2018) and there is comparatively less interspecific variability within communities than in the tropics (Crouch and Jablonski 2023; Sinnott-Armstrong et al. 2018). However, studies based on network metrics have found an increase in modularity and specialisation in frugivory interactions with increasing latitude (Dalsgaard et al. 2017; Schleuning et al. 2012, 2014). These patterns suggest a strong trait-matching, and hence, a high degree of complementarity and irreplaceability of birds at high latitudes.

Whether trait-matching should be strong or weak on islands compared to the mainland is also controversial. Low richness and colonisation filters can lead to more homogeneous assemblages than on the mainland facilitating more generalised interactions between birds and fruits (Kaiser-Bunbury, Traveset, and Hansen 2010; Naniwadekar et al. 2019; Traveset and Navarro 2018). On the other hand, the stochastic arrival of species and speciation processes can increase trait variability (Barajas Barbosa et al. 2023) facilitating specialised interactions (González-Castro, Traveset, and Nogales, 2012). These different processes may have important implications for the conservation of island frugivory. Generalised interactions would facilitate the dispersal of exotic fleshy-fruited species (Zhu et al. 2024), whereas a strong trait-matching would enhance the vulnerability of plant communities to species loss (Case and Tarwater 2020). Both processes (i.e., biological invasions and defaunation) indeed represent important threats to island biodiversity (Nogales et al. 2024). In sum, even though we expect the strength of trait-matching to vary with latitude and on islands, the direction of such changes remains untested for plant–frugivore interactions. Changes in the strength of trait-matching may have important consequences for the complementarity and irreplaceability of birds with respect to their seed-dispersal functions.

We conducted the first global study of trait-matching in plant–frugivore interactions by gathering information on avian frugivory in 59 plant and bird communities located at a wide range of latitudes and in mainland and island areas. Using bird and plant traits, we built a joint species frugivory model in which the probability that a bird interacts with a plant species depends on the abundance of both and on bird responses to the size and lipid content of fruits. According to trait-matching rules, bird responses to fruit traits are a function of their beak width and their degree of frugivory. With model estimates of trait-matching, we evaluated if it is a generalisable rule in frugivory and tested if its strength varies with latitude and on islands. To explore the functional consequences of trait-matching, we simulated frugivory within communities based on model estimates of interaction probabilities and quantified complementarity and irreplaceability of birds with distinctive traits. We found that morphological and nutritional trait-matching affected frugivory across the globe. Morphological trait-matching was stronger in temperate communities, especially on islands, leading to a greater functional

complementarity between small and large birds. Yet, latitudinal trends in the irreplaceability of birds were more complex. Our work provides new insights about the degree of generalisation of trait-matching in avian frugivory and its functional consequences at a global scale.

## 2 | Methods

### 2.1 | Data Compilation

We gathered a dataset containing information on plant–frugivore interactions recorded in 59 communities located across a wide range of latitudes (from 0.23° to 53°) and in mainland and island areas (42 and 17 communities, respectively) (Appendix SC, Figure SC1,2). Communities were not homogeneously distributed across realms. Most communities belonged to the Neotropical realm followed by the Palearctic (Appendix SC, Figure SC1). From the dataset, we selected interactions between fleshy-fruited plants and avian frugivores, with partners identified at the species level and for which we had information on focal traits (see below). Fifty-eight per cent of communities did not have information on interaction frequencies, and when they did, the frequencies represented different aspects of frugivory (e.g., number of visits vs. number of seeds dispersed). Thus, to preserve a high number of comparable communities, we decided to work with binary information on interaction occurrence.

We compiled information on fruit and bird characteristics and their phylogeny. In the case of plants, traits were obtained from FRUBASE (Jordano 2007) and Atlantic datasets (Bello et al. 2017) as well as 48 other studies or websites. We recorded fruit width (mm) and lipid content according to the classification of the Atlantic dataset (1: <10% of content, 2: 10%–20%, 3: >20%). Our data were very imbalanced with respect to such classification (level 1: 630 species, level 2: 55 species and level 3: 115 species). Thus, we decided to classify fruits either as lipid-poor (<10% of lipid content in the pulp) or not. In our communities, lipid-poor fruits tended to be sugary (Appendix SC, Figure SC3). We could obtain complete information on traits for 506 out of the 799 plant species. To impute missing trait data, we used the average value of the trait at the genus level. This method performed better than a random forest imputation (Stekhoven and Bühlmann 2012) and provided a good match with observed data (see details in Appendix SA, SA.1). Plant names were standardised using the TaxoStand package (Cayuela et al. 2012), and we obtained plant phylogeny from the V.PhylomMaker package using the GBOTB.extended tree (Qian and Jin 2016). For birds, we obtained beak width (mm) from Avonet (Tobias et al. 2022) and the proportion of frugivory in their diet from Elton traits (Wilman et al. 2014). We used bird phylogeny from BirdTree, averaging across 100 trees (Jetz et al. 2014).

### 2.2 | Frugivory Joint Species Model

To model species interactions, we built a Bernoulli joint species frugivory model (based on Pizo et al. 2021) in which the probability that a bird and a plant species interact depended on their abundances, trait-matching and phylogeny. To detect the presence of biogeographical trends, the strength of trait-matching

was not fixed but varied with latitude and insularity (i.e., whether communities were on islands or in the mainland).

In our model, the expected probability that a bird interacted with a given plant was a function of the abundance of both species and bird responses to fruit diameter and lipid content in the pulp (i.e., if it was lipid-poor or not). We used normalised degree as a proxy of species abundances (following Fricke et al. 2022) because both variables are related (Fort, Vázquez, and Lan 2016). However, ND can also be affected by trait-matching and the span of species phenologies (González-Castro, Yang, Nogales, and Carlo, 2012). Thus, we performed additional tests to evaluate if it was indeed a reasonable proxy of species abundances. We ran simulations of species interaction based on their abundance and traits. Reassuringly, we could accurately recover simulated responses to fruit traits, trait-matching parameters and biogeographical trends using ND instead of abundance during model fitting (Appendix SA, Figure SA8). Furthermore, in observed data, ND correlated with species abundances (Figures SA3 and SA4) and very infrequently with species traits (in <20% of our communities in all cases).

Beyond neutral processes and trait-matching, our model accounted for unmeasured interaction-relevant plant traits that could share a common evolutionary history (e.g., secondary compounds in fruits Cipollini 2000). To this end, we included random effects with a Gaussian decaying covariance structure informed by plant phylogeny at the family level (Pizo et al. 2021). We also included the identity of communities as a random term in the intercept to consider different sampling efforts across studies and in the slope of the effect of normalised degree to consider that the strength of neutral processes can vary with community richness (Vázquez et al. 2009). The response of frugivores to fruit traits was sampled from a multivariate normal distribution whose mean values depended on bird beak width and degree of frugivory. We quantified morphological trait-matching as the effects of beak width on the response of frugivores to fruit diameter within a community. A positive value implies that the slope of bird responses to fruit diameter increases with beak width making the interaction more probable. Similarly, the effects of the degree of frugivory on bird responses to lipid-poor fruits measured nutritional trait-matching. In both cases, larger values of trait-matching imply that the effect of bird traits on how they respond to fruit characteristics is stronger (i.e., stronger trait-matching, Appendix SB, Figure SB1). The model considered the possibility that birds with close phylogenetic association could behave more similarly than what is expected based on the measured traits. Depending on the value of a phylogenetic strength parameter (i.e.,  $\rho$  in equation SB7) the variance–covariance of bird responses to fruit traits could go from being independent from phylogeny to fully structured by it. Finally, to quantify changes in trait-matching at macroscales, its strength could vary across communities as a function of latitude and insularity.

Prior to model parameterisation, we scaled and standardised all continuous covariates (mean=0, SD=1). We fitted the model using a Bayesian approach with weakly informative priors in Stan through R and monitored convergence and adequate sample size of posteriors (Carpenter et al. 2017). We evaluated model fit by means of posterior-predictive checks on the proportion of

realised interactions within communities (i.e., network connectivity) and on species pairwise interactions (i.e., who interacts with whom). For details on model specifications, including priors, see Appendix SB.

### 2.3 | Functional Consequences of Trait-Matching

To estimate the functional complementarity and irreplaceability of bird species within communities, we performed simulations of frugivory based on the posterior of interaction probabilities. In each community, we distributed 10,000 foraging events between all plants and bird species according to their pairwise interaction probabilities (Appendix SB, equation SB2). We simulated 10,000 foraging events to ensure variance stabilisation across simulations and to allow the occurrence of interactions with low probabilities (Appendix SB, Figure SB3). To characterise complementarity, we measured the differences in the size and lipid content of fruits consumed by dissimilar bird species during the simulations. First, we identified the widest and narrowest-beaked birds (based on  $q_{0.25}$  and  $q_{0.75}$ ) and calculated the mean diameter of the fruits they consumed. We quantified complementarity due to morphological trait-matching as the difference between the diameter of fruits consumed by wide and narrow-beaked birds relative to the range of diameters found in the community. In this way, we could compare communities with different ranges of fruit sizes. We followed the same procedure and compared the mean lipid score of fruits (0: if lipid-poor, 1: otherwise) consumed by the most versus least frugivorous birds to quantify complementarity due to nutritional trait-matching. We repeated the simulation process 1000 times using a sample from the joint posterior of our model each time and calculated the mean and credible intervals of differences in fruit sizes and lipid scores. Our simulations are stochastic and include interaction uncertainty; hence, birds can switch partners between realisations (i.e., it allows for interaction rewiring, CaraDonna et al. 2017).

To estimate the irreplaceability of bird species, we quantified changes in the traits of the fruits consumed with or without them in the community. In particular, we quantified changes in the size of fruits if we removed interactions performed by (i) the

widest and (ii) narrowest-beaked species. Similarly, we looked at changes in the lipid score when we removed interactions by (iii) the least and (iv) most frugivorous birds (based on  $q_{0.25}$  and  $q_{0.75}$ ). We considered that greater changes in the traits of fruits consumed by the bird assemblage implied a higher irreplaceability of the missing species. We estimated mean and credible intervals of such changes across frugivory simulations ( $N=1000$ ).

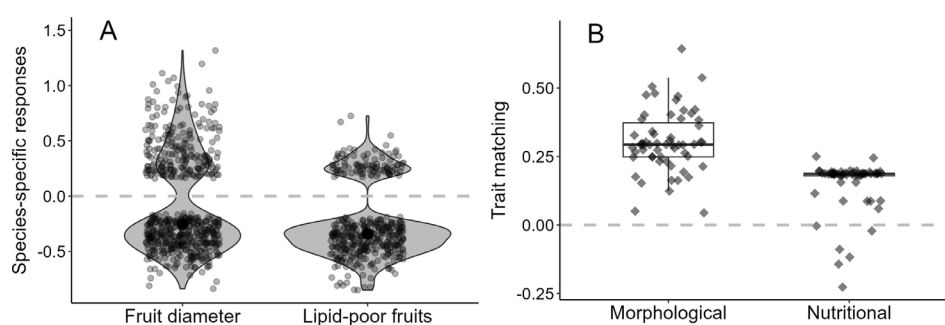
## 3 | Results

### 3.1 | Description of Communities

Our dataset contained 6883 pairwise interactions between 799 plant and 733 bird species from 84 and 76 families. Communities harboured contrasting levels of plant richness (mean=28 species; [6, 88]  $q_{0.05}$  and  $q_{0.95}$ ) and bird richness (mean=25, [7,76]  $q_{0.05}$  and  $q_{0.95}$ ) with a negative trend with respect to latitude. On average, birds were larger and more frugivorous in tropical areas than in temperate ones, and fruits were also larger in the tropics (Figure SC4). In addition, tropical communities harboured species with a wider range of trait values (Table SC1). We did not find any biogeographical pattern with respect to lipid content (Figure SC4C and Table SC1), with lipid-poor fruits being common in all communities (representing on average 76% of fruiting species, [0.56, 1]). Regarding insularity, we did not detect any clear pattern with respect to fruit and bird characteristics, but on islands there were on average half as many bird species as in mainland communities (17 vs. 37).

### 3.2 | Trait-Matching Trends

Our joint species frugivory model performed very well at predicting the observed proportion of realised interactions within communities ( $R^2=0.99$ ) and, on average, it correctly predicted 77% of specific pairwise interactions ([68, 85]  $q_{0.05}$  and  $q_{0.95}$  Appendix SB, Figure SB2). In the studied communities, 42.3% of birds tended to respond to fruit diameter (> 85% of the posterior had the same sign as the posterior mean, i.e.,  $f$ -value  $\geq 0.85$ ) and 30.3% of them responded to lipid content ( $N=589$  and 421, respectively). In general, when we detected a response to fruit



**FIGURE 1** | (A) Violin plot of species responses to fruit traits (diameter and lipid-poor fruits) when they were responsive to them ( $f$ -value of posterior distributions  $\geq 0.85$ ). Each point corresponds to the response of a bird species to a fruit trait within a community ( $N=589$  for diameter and  $N=421$  for the lipid content of fruits). (B) Boxplot of community-level parameters of morphological and nutritional trait-matching. Positive values of morphological trait-matching imply that the slope of bird responses to fruit diameter increases with their beak width making interactions more probable. The same applies for nutritional trait-matching (i.e., the degree of frugivory increases the probability of interacting with lipid-poor fruits). Each point represents trait-matching within a community ( $N=59$ ).

traits, model estimates were negative, with the probability of interaction decreasing with fruit diameter and in lipid-poor fruits (Figure 1A).

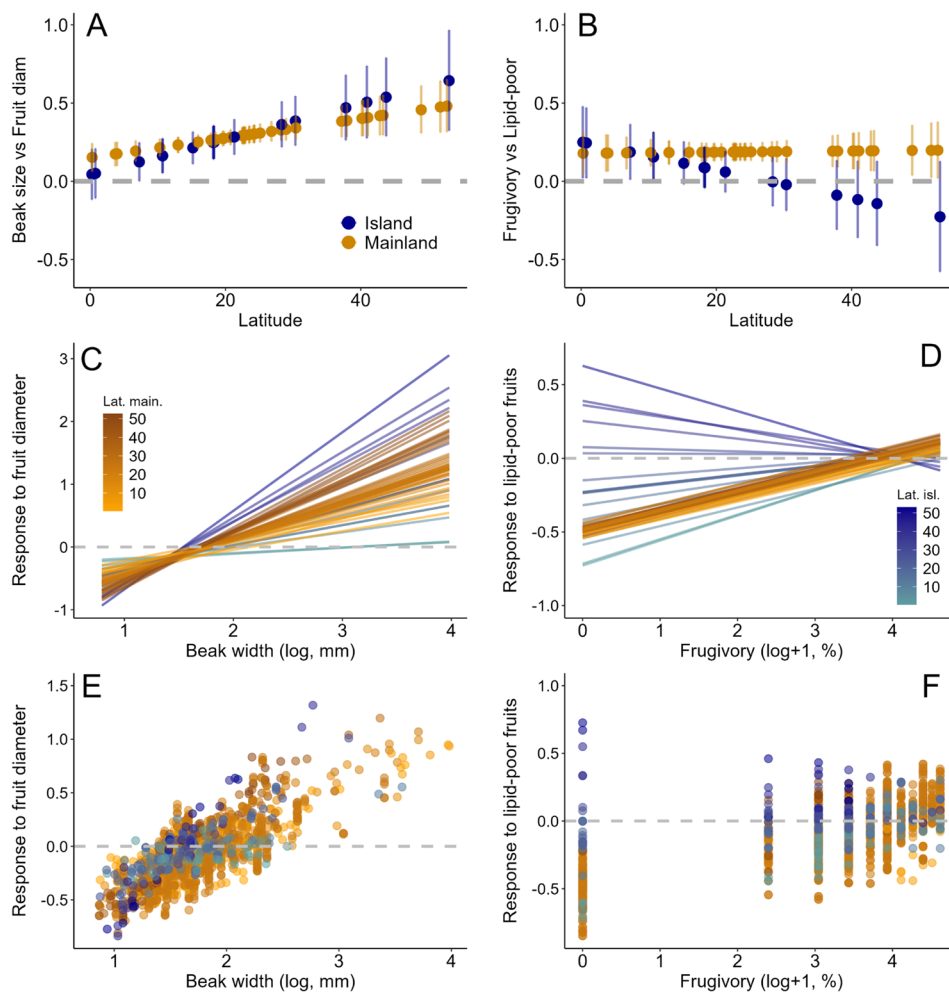
Avian responses were modulated by bird traits according to trait-matching rules. In 95% of communities, we detected a clear positive effect of beak width on bird responses to fruit diameter ( $f$ -value  $\geq 0.95$ ). In 77% of communities, we detected a positive effect of the degree of frugivory of birds on their response to lipid-poor fruits (Figure 1B).

Birds with narrow beaks responded negatively to fruit diameter, while those with wide beaks tended to do so positively (Figure 2, left panels). The rate of change in these responses is a measure of the strength of morphological trait-matching, which increased with latitude, especially on islands (Table 1). In contrast, the strength of nutritional trait-matching remained similar across latitudes. In addition, changing the degree of frugivory very rarely changed the sign of the response of birds to lipid-poor fruits (Figure 2, right panels). Insectivorous (less frugivorous) species tended to avoid lipid-poor fruits, but frugivorous species

did not usually respond to this trait (Figure 2F). In some temperate islands, the sign of nutritional trait-matching reversed (Figure 2B), with insectivorous birds responding positively to lipid-poor fruits rather than negatively (Figure 2D,F). However, the uncertainty around the estimates of nutritional trait-matching on these islands was high.

### 3.3 | Functional Consequences of Trait-Matching: Complementarity and Irreplaceability of Bird Species

In 74% of the studied communities, narrow-beaked birds foraged on different fruits than the wide-beaked species (i.e., differences in the size of fruits consumed did not overlap zero, Figure 3A). The complementarity of large and small birds increased with latitude, although these communities did not necessarily show the highest irreplaceability (Figure 3B, Figure SC5A). Irreplaceability of large and small birds was related to a greater extent to the range of fruit diameters within communities (Pearson correlation  $r = 0.54$ ,  $p < 0.01$ ,  $N = 59$ ) than



**FIGURE 2** | Estimated values of (A) morphological and (B) nutritional trait-matching across communities. Points show posterior means of trait-matching parameters and lines represent credible intervals. (Middle and lower panels) To visualise trait-matching strength, we plotted the response of frugivores to fruit diameter and lipid-poor fruits as a function of their beak width and degree of frugivory. (C, D) Mean values of partial model predictions (only accounting for the trait on the x-axis) of frugivores responses to fruit traits according to their beaks and diets. Each line represents one community. (E, F) Mean values of posterior distributions of estimates of bird responses to fruit traits. Each point represents one bird species in a community.

**TABLE 1** | Summary of the effects of biogeographical variables on morphological and nutritional trait-matching.

Predictor	Trait-matching	Mean	CI	<i>f</i> -value
Latitude	Morphological	<b>0.08</b>	<b>[0.02, 0.14]</b>	<b>0.99</b>
Island		-0.1	[-0.29, 0.08]	0.83
Lat*Island		0.08	[-0.05, 0.18]	0.82
Latitude	Nutritional	-0.01	[-0.07, 0.08]	0.55
Island		0.06	[-0.19, 0.34]	0.67
Lat*Island		<b>-0.12</b>	<b>[-0.26, 0.02]</b>	<b>0.92</b>

Note: Mean values of posterior distributions, CI—0.95 credible interval, *f*-value—proportion of posterior distribution with the same sign as the posterior mean. Responses with an *f*-value  $\geq 0.9$  are in bold; those with an *f*-value  $> 0.8$  and  $< 0.9$  are in italics.

to the range of bird responses to this trait ( $r=0.26$ ,  $p=0.05$ ,  $N=59$ ). In temperate communities, the range of bird responses to fruit diameter was high, but available fruits were of similar sizes (Figure SC6). Regarding complementarity related to nutritional trait-matching, it only occurred in 24% of the studied communities (Figure 3C), leading to a low irreplaceability of birds (Figure 3D, Figure SC5B).

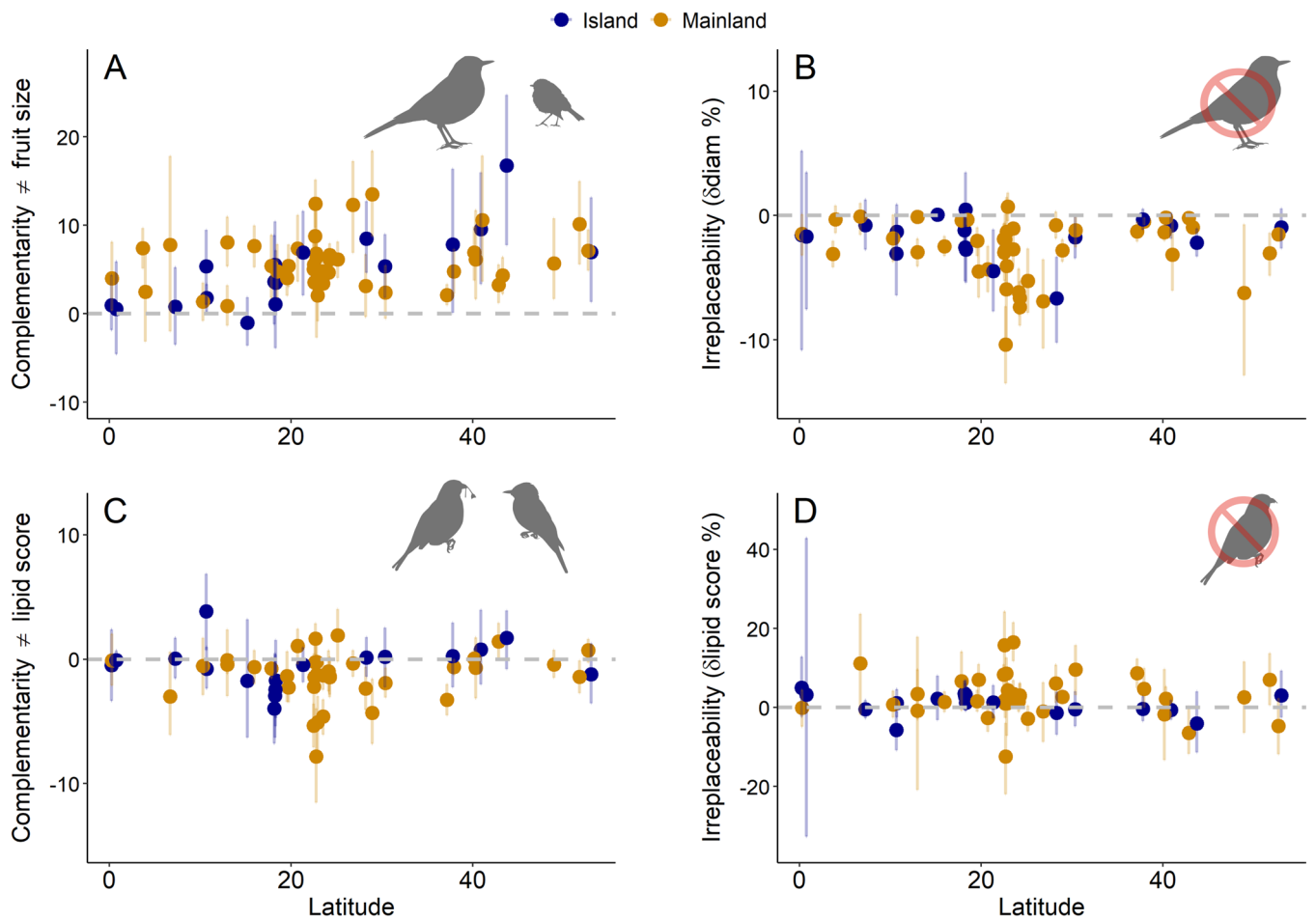
#### 4 | Discussion

Our work shows that trait-matching affects avian frugivory on a global scale, and hence, differences in bird beak width or degree of frugivory imply a change in how they respond to the size and lipid content of fruits. This is particularly clear for morphological trait-matching, which is stronger in temperate areas leading to high functional complementarity between large and small birds. However, we show that increased complementarity does not necessarily imply increased irreplaceability of species.

We found a general negative response of birds to fruit diameter (Figure 1A), highlighting that size-driven constraints are widespread in avian frugivory (Olesen et al. 2011). Even though birds can manipulate fruits in multiple ways (i.e., gulping, mashing or pecking them), and there could be changes in foraging behaviour depending on resource availability (Rey and Gutierrez 1996), our results show that interaction probability between birds and fruits tends to decrease with increasing fruit size. In line with trait-matching rules, these negative responses of birds to fruit diameter turned positive in wide-beaked species in 95% of our communities (Figures 1B and 2, left panels). We also found that the strength of the morphological trait-matching increased with latitude (Table 1), despite tropical areas having a wide range of bird and fruit sizes (Table SC1). Stronger morphological trait-matching at high latitudes is consistent with the high degree of specialisation of plant-frugivore interactions found in these areas (Schleuning et al. 2012; Dalsgaard et al. 2017). Temperate birds rely on fruits for overwintering, breeding, and migration, but fruit resources are available over relatively short periods of time (González-Varo et al. 2022; Herrera 1982; Mudrzyński and Norment 2013; Tattoni et al. 2019; Ting, Hartley, and Burns 2008). It is likely that birds optimise their foraging intake by consuming fruits that are easier to handle (Courtney and Sallabanks 1992), especially during times of high fruit demand and availability.

Nutritional trait-matching was generally weaker than morphological trait-matching (Figure 1B) and birds often negatively responded to lipid-poor (sugary) fruits (Figure 1A). This can reflect the importance of insectivorous species in the studied communities (Figure 2D,F). For example, tyrant flycatchers (Tyrannidae) were responsible for 8% of the pairwise interactions observed in the Neotropics, and in the Palaearctic, passerines with mixed diets (Turdidae, Sylviidae and Muscicapidae, Carnicer, Jordano, and Melian 2009) accounted for 14.5% of the interactions. The importance of insectivorous birds on frugivory has been previously highlighted at local scales (Herrera 1984) and within the Neotropical realm (Pizo et al. 2021). Here, we show that this also applies globally, something important because insectivorous species have often been overlooked in frugivory studies (Carlo, Camargo, and Pizo 2022). For frugivorous birds, we expected a positive response to lipid-poor fruits because they can assimilate sugars more easily (Levey and Martínez del Río 2001). However, we found that highly frugivorous birds were not responding to this trait (Figure 2F). Frugivorous birds may consume lipidic and sugar-rich fruits to ensure their daily energy intakes (Blendinger et al. 2022) and, at high latitudes, to compensate for thermoregulation costs during winter (Herrera 1982). We did not find a latitudinal trend in nutritional trait-matching (Figure 2B), probably because variability in this trait was low. In most communities, lipid-poor fruits dominated the fruiting assemblage (Figure SC4C). Nonetheless, it is also possible that our results are affected by the coarse grain classification of fruits as lipid-poor or not. It allowed us to detect general patterns of nutritional trait-matching (Figure 1B) but may not be sufficient to detect latitudinal trends (Figure 2B). To date, there are important knowledge gaps with respect to the lipid content of fruit pulps. In this study, we gathered traits of 1313 plant species but only 38% contained quantitative information about lipid content. We hope that including tools such as near-infrared reflectance spectroscopy in frugivory studies will help to overcome this limitation (Rothman et al. 2009).

Compared to the mainland, islands showed larger changes in the strength of morphological trait-matching with increased latitude (Table 1, Figure 2). In the tropics, morphological trait-matching was weaker on islands than in the mainland, whereas in temperate areas it tended to be stronger (Figure 2, left panels). This is in line with previous studies that found generalised frugivory on tropical islands (Naniwadekar et al. 2019) and a high degree of specialisation on temperate ones (González-Castro, Traveset, and Nogales, 2012). Our results suggest a more flexible integration



**FIGURE 3** | Complementarity of birds with distinct beaks and diets measured as differences in the (A) diameter and (C) lipid content of the fruits they consume. Values further away from zero imply a greater complementarity among dissimilar birds. Irreplaceability of birds with (B) the widest beaks and (D) the most frugivorous diets measured as changes in the mean diameter and lipid score of fruits consumed by the bird assemblage after removing their interactions. Greater changes imply a higher irreplaceability. In all panels, points depict mean values across 1000 simulations and lines represent 90% credible intervals. Silhouettes: (A, B) *Turdus* and *Erithacus* represent wide and narrow-beaked species. (C, D) *Cotinga* and *Tyrannus* represent highly frugivorous and insectivorous species. Source of silhouettes: [www.phylopic.org](http://www.phylopic.org).

of non-native fruits in bird diets near the tropics and a greater complementarity of small and large birds at high latitudes. The interaction between insularity and latitude reversed nutritional trait-matching in temperate islands (Table 1 and Figure 2B), which implies that insectivorous birds preferentially forage on sugary rather than on lipidic fruits (Figure 2F). This agrees with the “interaction release” hypothesis, which states that species on islands can expand their feeding niche using novel resources (Traveset and Navarro 2018). Yet, the uncertainty of nutritional trait-matching estimates was high and frequently overlapped zero in island communities. Future work filling important knowledge gaps on island frugivory and an increase in geographical coverage (e.g., sampling the underrepresented Pacific and Oceanic archipelagos, Nogales et al. 2024) will allow us to draw more robust conclusions.

The prevalence of trait-matching across communities (Figure 1B, Figure 2A,B) suggested that birds with contrasting beaks and diets would play complementary roles. This was confirmed for morphological, but not for nutritional trait-matching (Figure 3, left panels). Morphological trait-matching led to opposite responses of large and small birds to fruit size (Figure 2E), and hence, they tended to interact with different fruits (Figure 3A).

In contrast, most frugivorous birds acted as generalist foragers with respect to lipid content (Figure 2F), overlapping their fruit diets with those of insectivorous species (Figure 3C). These results call for caution in assuming that trait-matching necessarily leads to functional complementarity. This only occurs if it implies opposite responses of birds to fruit traits, and hence, some degree of specialisation in the type of fruits consumed. It is important to note that our estimates of complementarity focus on the size and lipid content of fruits, but bird-fruit interactions can depend on other traits, such as secondary compounds, the concentration of certain micronutrients or the presence of carotenoids (Delhey et al. 2023; Levey and Martinez del Rio 2001). The response of birds to these fruit traits may depend on their own characteristics (e.g., kidney size or mating systems), potentially leading to other dimensions of complementarity not covered in our study.

As expected, latitudinal trends in morphological trait-matching led to a high complementarity of large and small birds in temperate communities, and especially on islands (Figure 3A). However, they did not necessarily play irreplaceable roles (Figure 3B, Figure SC5A). In temperate areas, birds with contrasting beaks responded very differently to fruit diameter, but fruits within the

communities were of similar size (Figure SC6). As a result, the size of fruits consumed by the bird assemblage did not change much after removing the interactions performed by the largest or smallest birds. These results highlight that complementarity is probably a necessary but not a sufficient condition for the irreplaceability of species. Our estimates of irreplaceability are based on our modelled interaction probabilities derived from binary interaction data, considering species responses to traits and using normalised degree as a proxy for species abundance. A more realistic way to predict the consequences of species loss would require a more mechanistic and hence more data-rich approach (Morán-López et al. 2020). For instance, we need to consider the possibility that fruits that would have been consumed by the missing birds are now available for the rest of the species. Reporting interactions at fine temporal scales rather than pooling them across seasons will allow us to incorporate such dynamism (CaraDonna et al. 2021). It will inform us about how birds respond to changes in fruit availability across the season (Carlo et al. 2024), the effects of phenological overlap on interaction probabilities (Vizentin-Bugoni et al. 2020), and to consider compensation mechanisms due to competition release (e.g., after the departure of migrant frugivorous birds from communities, Ohkawara, Kimura, and Satoh 2022). It would also be important to report frugivory interactions together with estimates of fruit abundances. This information was available in only 10% of the studied communities, and it often included only a subset of plant species. Consequently, we had to use normalised degree as a proxy for abundance limiting our ability to model abundance-driven compensation mechanisms. In sum, even though communities tend to suffer interaction deficits after bird losses (Cordeiro and Howe 2003; Fricke, Tewksbury, and Rogers 2018; Holbrook and Loiselle 2009), it is unclear if the remaining species can compensate, at least partially, for such losses (as it occurs in adaptive foraging, Valdovinos et al. 2013). Reporting interactions in more detail will allow us to incorporate this degree of realism into our models.

## 5 | Conclusions

Our work shows that trait-matching affects frugivory on a global scale, and hence, birds with contrasting beaks and diets respond differently to fruit traits within communities. However, having different responses to fruit traits does not necessarily imply functional complementarity or irreplaceability of birds. For complementarity to occur, birds with contrasting trait values need to show opposite responses to fruit traits. This only occurred for morphological trait-matching where narrow-beaked species responded negatively to fruit size while wide-beaked species responded positively. We found that the strength of morphological trait-matching increased with latitude and especially on islands, leading to a higher functional complementarity between large and small birds. Yet, an increased complementarity did not necessarily imply a higher irreplaceability of species because it also depended on fruit trait variability within communities. As a result, latitudinal trends in species irreplaceability were not trivial.

### Author Contributions

T. Morán-López, M. Schleuning, D. García and J.M. Morales devised the ideas of the work. T. Morán-López wrote the first draft. T. Morán-López

and MSC gathered and curated data. T. Morán-López and J.M. Morales performed data analyses. All authors provided input during the writing process and have approved the final version of this work.

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### Data Availability Statement

Data and the code are available at <https://zenodo.org/records/14632524>; (doi: [10.5281/zenodo.14632524](https://doi.org/10.5281/zenodo.14632524)).

### Peer Review

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.