

RESEARCH ARTICLE

Latitudinal specificity of plant–avian frugivore interactions

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Abstract

1. Broad-scale assessments of plant–frugivore interactions indicate the existence of a latitudinal gradient in interaction specialization. The specificity (i.e. the similarity of the interacting partners) of plant–frugivore interactions could also change latitudinally given that differences in resource availability could favour species to become more or less specific in their interactions across latitudes.
2. Species occurring in the tropics could be more taxonomically, phylogenetically and functionally specific in their interactions because of a wide range of resources that are constantly available in these regions that would allow these species to become more specialized in their resource usage.
3. We used a data set on plant–avian frugivore interactions spanning a wide latitudinal range to examine these predictions, and we evaluated the relationship between latitude and taxonomic, phylogenetic and functional specificity of plant and frugivore interactions. These relationships were assessed using data on population interactions (population level), species means (species level) and community means (community level).
4. We found that the specificity of plant–frugivore interactions is generally not different from null models. Although statistically significant relationships were often observed between latitude and the specificity of plant–frugivore interactions, the direction of these relationships was variable and they also were generally weak and had low explanatory power. These results were consistent across the three specificity measures and levels of organization, suggesting that there might be an interplay between different mechanisms driving the interactions between plants and frugivores across latitudes.

KEYWORDS

functional dissimilarity, interaction specificity, latitudinal patterns, phylogenetic distance, plant–frugivore interaction, taxonomic specificity

1 | INTRODUCTION

Mutualistic interactions between species are key drivers of population and community dynamics (Sasal & Morales, 2013; Suweis

et al., 2013). For example, seed dispersal mediated by animals influences the abundance and the distribution of the interacting species (Strauss & Irwin, 2004), which allows both plants and frugivores to persist across different geographic areas (Cain et al., 2000;

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Moegenburg & Levey, 2003). Although it is known that plant–frugivore interactions are affected by the species richness (García & Martínez, 2012), and the functional (Dehling et al., 2016) and phylogenetic (Rezende et al., 2007) diversity of the interacting species, it is still poorly understood how plant–frugivore interactions change across geographic space. In general, plant–frugivore interactions tend to be more specialized in temperate regions than in the tropics (Dalsgaard et al., 2017; Schleuning et al., 2012), but it is still unclear whether the specificity of these interactions also changes latitudinally. Here, we define specificity as the level of similarity of the group of species that interact with a focal species (Chomicki et al., 2019; Shefferson et al., 2019). Species specificity is expected to vary spatially given that environmental conditions (Devictor et al., 2010; Pellissier et al., 2018) and the identity of the interacting species change across space (Poisot et al., 2012, 2015).

Mechanisms ranging from neutrality to functional and phylogenetic constraints of the interacting species have been proposed to explain species interactions (Coelho & Rangel, 2018; Gómez et al., 2010; Peralta et al., 2020; Schleuning et al., 2014; Vázquez et al., 2009). Neutral theory assumes that individuals are ecologically equivalent (Hubbell, 2011), and in this context species interactions would occur following neutral stochastic processes (Coelho & Rangel, 2018). Differences in species traits can also affect species interactions such that a certain level of similarity between the morphological traits (i.e. trait matching) of the interacting species is needed for the interaction to occur (Garibaldi et al., 2015; Valenta & Nevo, 2020). For example, there is a trait matching between bird's bill size and plant's fruit size (Bender et al., 2018; Dehling et al., 2016) providing a morphological constraint on potential plant–frugivore interactions (Dehling et al., 2016). Thus, if trait matching is a strong driver of species realized interactions, one could expect birds to interact with a set of functionally similar plant species and plants to interact with a set of functionally similar bird species (Jordano et al., 2003). Moreover, plant–frugivore interactions can also be phylogenetically limited such that phylogenetically related species tend to interact with similar sets of species (Rezende et al., 2007). This suggests that, at least to some extent, there are functional and phylogenetic constraints in plant–frugivore interactions that limit the set of species that can potentially interact with each other. However, species interactions can also be affected by abiotic factors (Pellissier et al., 2018; Travis, 1996) and resource availability (Schleuning et al., 2012), such that changes in these conditions across the geographic space are expected to affect the level of functional and phylogenetic specificity of plant–frugivore interactions.

Species interactions have been proposed to be more specialized in the tropics (MacArthur, 1969; Schemske et al., 2009), although contrasting latitudinal patterns in interaction specialization have been observed for different taxa (Dalsgaard et al., 2011, 2017; Dáttilo & Vasconcelos, 2019; Schleuning et al., 2012). Latitudinal changes in the specificity of plant–frugivore interactions are likely to occur because of different factors. The broader functional resource diversity in the tropics might favour generalist species to

evolve traits that allow them to use the different resources available in these areas (Guimarães Jr et al., 2011; Wheelwright, 1988). This would lead plant–frugivore interactions to be less specific in the tropics. Alternatively, the higher climatic stability of the tropical region might allow species to potentially evolve narrower niches and specialize in specific resources that are constantly available in these areas (Belmaker et al., 2012; Fleming, 1986; Pianka, 1966). In this case, an inverse pattern would be observed, and plant–frugivore interactions would be more specific in the tropics. Latitudinal differences in the accessibility and nutritional composition of fruits could also be important drivers of differences in the specificity of plant–frugivore interactions across latitudes as these factors play an important role in promoting specialization or generalism in frugivores (Fleming, 1986).

Spatial patterns in the specificity of plant–frugivore interactions can be evaluated at different levels of organization ranging from populations to species and communities (Chown & Gaston, 2010; Gaston et al., 2008; Guimarães Jr, 2020). This is important to consider given that different mechanisms can drive the occurrence of such spatial patterns at different levels of organization (Gaston et al., 2008), and the trend might not be detected when the relationship is not assessed at the level the mechanism is acting. For example, populations of species might show latitudinal differences in the specificity of their interactions given variation in local conditions, where a latitudinal trend in the specificity of these interactions would be observed. However, these patterns could be obscured when assessed at the species level given that averaging the population responses across species could lead to a lack of specificity when these populations are responding in opposite directions across latitudes. Alternatively, a pattern might be detected at the species level, but not at the population level, when species respond differently to local conditions. In this case, the opposing responses of populations from different species found at the same sites would lead to a lack of latitudinal trend in interaction specificity at the population level, but when each species is considered separately, a trend could be observed at the species level. Likewise, a latitudinal gradient at the community level would be mainly observed when most of the co-occurring species in a community respond similar to changes in the local conditions across latitudes. Thus, considering different levels of organizations in the assessment of interaction specificity can provide additional understanding about how plant–frugivore interactions are structured across space.

Here, we used a global data set of interactions between plants and frugivores (Fricke & Svenning, 2020) to explore the prediction that these interactions should be more taxonomically, phylogenetically and functionally specific at lower latitudes because of the continuous availability of resources in these areas (Figure 1). We evaluated the consistency of these relationships considering a population, species and community context. A null model was used to determine whether the observed specificity of plant–frugivore interactions is higher or lower given what is expected due to latitudinal changes in species richness. Although we often

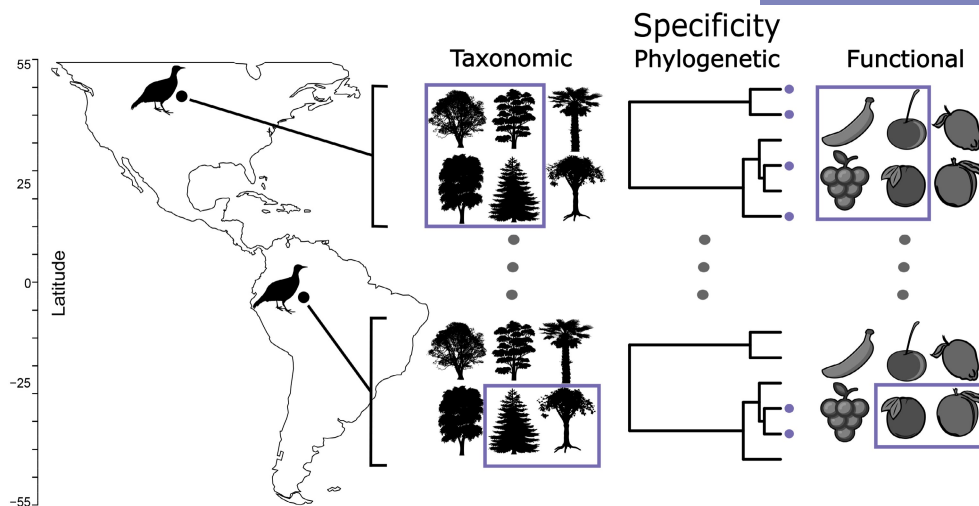


FIGURE 1 Species can be specialists in various ways. For instance, a frugivore species distributed across at least two locations in the Americas (left map), could specialize on a particular subset species (taxonomic; blue boxes), a particular subset of the plant phylogeny (phylogenetic; blue dots), or a specific subset of plants based on functional characteristics such as fruit size (functional; blue boxes). Given the constant resource availability in the tropics, we expect species to be more taxonomically, phylogenetically and functionally specific in their interactions at lower latitudes.

observed significant relationships between latitude and interaction specificity, these relationships were quite weak, challenging the expectation that there is a latitudinal trend in the specificity of species interactions. These results were consistent across populations, species and communities, suggesting that there are no latitudinal differences in the level of taxonomic, functional and phylogenetic constraints that could be affecting plant–frugivore interactions.

2 | METHODS

2.1 | Species data

We used data from plant–frugivore network interactions compiled by previous authors (Fricke & Svenning, 2020). We filtered the original data to keep only the interactions between plant and birds for our analyses ($\approx 74\%$ of the observed interactions). Data on species interaction were pooled based on geographic location where a network was sampled. For example, if a study sampled networks in 10 different sites, then each of those sites corresponded to a different network. Alternatively, if the same site was sampled or used by different studies, then the data for that site were pooled to obtain a single spatial network for that locations. This left us with plant–bird interaction data for 190 tropical and temperate sites (spanning $\approx 55^\circ$ in absolute latitude) comprising a total of 1254 bird species and 2225 plant species corresponding to 18,125 observed interactions between plants and birds (Figure S1). From these data, we generated one data set for birds and one data set for plants to measure the level of taxonomic, functional and phylogenetic specificity of their interactions. We acknowledge that there are potential gaps in global data sets of species interactions that could affect our analyses

(Poisot et al., 2021), and we took several steps to address some of these problems in our study (see text below). Ethical approval was not required as we used data openly available.

We obtained functional traits related to beak size and fruit size to measure the level of functional specificity of the interacting species given that these traits are important for plant–bird (hereafter plant–frugivore) interactions (Dehling et al., 2016; Jordano et al., 2003). For birds, trait data regarding (1) beak length measured from tip to skull along the culmen; (2) beak length measured from the tip to the anterior edge of the nares; and (3) beak depth and (4) beak width were acquired from the AVONET database (Tobias et al., 2022). We used the mean value of each trait for every species in our data set that had individuals measured in AVONET ($n = 1243$ species). Phylogenetic data from Jetz et al. (2012) were used for 1244 bird species. Consequently, 10 bird species were removed from the analyses because they were not available in the phylogeny by Jetz et al. (2012) and one bird species (*Cuculus clamosus*) was removed from the functional specificity analyses because it did not have data on beak length based on nares. For plants, we used seed mass as a proxy for fruit size given that data on plant seed size were more broadly available than measures associated with fruit size (e.g. maximum or minimum fruit length) and that there is a general positive correlation between seed size and fruit size (Fleming & Kress, 2011; Primack, 1987). Seed mass data from the BIEN, GIFT and TRY databases (Kattge et al., 2020; Maitner et al., 2018; Weigelt et al., 2020) were used for 1019 plant species. Additionally, we obtained phylogenetic information for 2221 plant species with the *U.PhyloMaker* R package that uses megatrees to generate phylogenies for several species (Jin & Qian, 2023). We also reran the plant phylogenetic analyses using finer phylogenetic data available in the BIEN database (Maitner et al., 2018) and similar results were obtained (see below and Supporting Information).

2.2 | Measuring the specificity of plant–frugivore interactions

We used binary interaction data to measure the taxonomic, functional and phylogenetic specificity of the interactions of each bird and plant species in our data set. Taxonomic specificity was measured as the fraction of species in a community that the focal species was observed to interact with (this is equivalent to normalized degree in network analyses). To compute functional specificity, we calculated the mean pairwise functional dissimilarity, based on Euclidean distance, for all the species that interacted with the focal species being considered using the `funrar` package (Grenié et al., 2017). To estimate phylogenetic specificity, we calculated the standardized mean pairwise phylogenetic distance for all the species interacting with the focal species being considered. A species should interact with at least two species at any given site in order for us to be able to calculate the specificity of their interactions. Thus, we only used species that interacted with at least two species that had functional and phylogenetic data available when estimating functional and phylogenetic specificity, respectively. Given that there are different phylogenies that are equally supported, we assessed phylogenetic specificity considering a set of 99 phylogenies for birds and plants (using the phylogenies obtained from BIEN) to evaluate whether our results could be influenced by the phylogeny being used in our analysis. We observed similar results regardless of the phylogeny used in our analyses (see [Supporting Information](#)).

2.3 | Null expectation of interaction specificity

The variability of functional and phylogenetic estimates is often influenced by species richness (Jarzyna & Jetz, 2016). For that reason, we calculated Z-scores to evaluate whether the observed patterns of functional and phylogenetic specificity of plant–frugivore interactions are higher or lower than what is expected considering the species richness of a given site. To achieve this, we generated 999 null values for functional and phylogenetic specificity for each bird and plant species in our study. For each species that was observed to interact with n partners in a site, null estimates for these interactions were obtained by randomly drawing n partners from the same site (or considering all sites, see text below) where the interactions were recorded. This allowed us to compare whether the observed specificity was higher or lower than when species interact with random (but the same number of) partners. The species pool considered for each null model consisted of the species that were sampled in the same site where the interactions were observed. Alternatively, we also considered a case where the species pool for our null model was sampled from all species found in our data set. We found similar results considering all species or only the species found at the same site (see [Supporting Information](#)), suggesting that the null space estimated at the sampled sites is often representative of the full null space. Z-scores were calculated as:

$$Z = \frac{x - \mu}{\sigma}$$

where Z is the standard score, x is the observed specificity, μ is the mean specificity calculated from the null models and σ is the standard deviation of the null models. Z-scores of zero indicate that there is no specificity (hereafter non-specificity) in interactions between plants and frugivores, where their interactions do not differ from random expectations. Negative Z-scores suggest that species are specific in their interactions and that they are interacting with partners that are more phylogenetically or functionally similar than randomly expected. This case is analogous to phylogenetic clustering caused by environmental filtering for species co-occurring in communities (Cavender-Bares et al., 2004). Positive Z-score values represent a case where there is 'anti-specificity' in the interaction between species, where species tend to interact with more phylogenetic or functionally dissimilar species. This is a case that is analogous to phylogenetic overdispersion in co-occurring species (Cavender-Bares et al., 2004). Significant specificity and anti-specificity from Z-scores are observed when values are below -1.96 and above 1.96 , respectively, while values falling within that interval represent non-specific interactions. A Z-score of 0 was assigned to species that were observed to interact with all available partners in a given site. To confirm that this decision did not affect our results, we rerun our population level analyses not considering instances where species interacted with all available partners and found the same results (see [Supporting Information](#)).

2.4 | Assessing the consistency in the specificity of plant–frugivore interactions

We evaluated the specificity of plant–frugivore interactions at the population, species and community levels. All of the specificity calculations were first performed at the population level, where interaction specificity was determined for each species observed to interact with a particular set of species in a sampled site. Specifically, specificity was calculated for all plant species that interacted with birds and for all bird species that interacted with plants within a specific site. At the species level, we averaged the population specificity estimates for all species in our data set that occurred in at least three different sites. At the community level, we averaged the population specificity estimates of all species occurring in a given site. For the community level analyses, we only considered sites where at least three species had been sampled.

We used each specificity estimate (i.e. the Z-scores obtained from our null models representing phylogenetic and functional specificity) as the response variable and absolute latitude as the predictor in our models to answer the question of whether interaction specificity changes across latitudes. Model structure was different across organizational levels. At the population level, we used phylogenetic generalized linear mixed-effect models (PGLMM) with species as random effect to account for variation across species in these parameters. These models also take into account the lack of phylogenetic independence of the species occurring at the different sites. PGLMM were fitted using the `phyr` package (Li et al., 2020) and R^2 values were extracted from these models using the `rr2` package

(Ives & Li, 2018). To assess the species level patterns, we utilized phylogenetic generalized least squares (PGLS) models given that species are not phylogenetically independent (Felsenstein, 1985; Freckleton et al., 2002). In these models, the mean absolute latitude of the locations where a species was sampled was the predictor. PGLS were fitted using the *caper* package (Orme et al., 2023). We used ordinary least squares to assess the community relationships given that we found no spatial autocorrelation in these models (see Figure S2).

2.5 | Missing trait data and species interactions

We only obtained functional trait data for ~50% of the plant species considered in our study, and most of these trait data were missing for plant species occurring in sites at lower latitudes (Figure S3). Species without trait data were removed from our functional specificity analyses. We acknowledge that this could have affected our analyses of the functional specificity of bird interactions. Although imputation techniques could have been used to obtain trait data for the plant species without traits in our study (Debastiani et al., 2021; Swenson, 2014), the use of such approaches is often challenging in situations where a high percentage of species have missing trait data (Johnson et al., 2021). For that reason, we did not use trait imputation approaches in our study.

The data set we used to assess the latitudinal specificity of plant–frugivore interactions was obtained from studies that used different sampling protocols to record the interaction between species (Fricke

& Svenning, 2020). Specifically, species interactions were recorded such that the observations captured the complete assemblage of interaction partners or just a subset of these partners. To confirm that our results were not affected by considering these different types of sampling design, we also ran our analyses considering only the cases where the complete assemblage of interaction partners was recorded. We found qualitatively similar results when considering cases where all interactions partners were recorded (see Supporting Information), indicating that the differences in sampling protocol used by the different data sources did not affect our results.

3 | RESULTS

3.1 | Specificity of plant–frugivore interactions across latitudes

Plant and frugivore interactions were generally non-specific, where they were often not significantly different from null models (i.e. Z-scores were often within the 95% confidence interval, see Supporting Information for details). We frequently found significant relationships between latitude and the specificity of plant–frugivore interactions, but these relationships were generally weak and most of the variance in our models remains unexplained (Table 1). The direction of these relationships also varied across the different estimates of specificity. There was a trend for plant species to be taxonomically anti-specific (i.e. interact with a higher fraction of bird species available) at higher latitudes, but this pattern was weak

TABLE 1 Taxonomic, phylogenetic and functional specificity of plant and frugivore interactions for the three levels of organization considered in our study.

Group	Specificity	Organization	Estimate	t-value	p-value	R ²
Plants	Taxonomic	Population	0.00180	5.402	<0.001	0.103
		Species	0.00218	3.357	0.001	0.037
		Community	0.00187	2.292	0.023	0.027
	Phylogenetic	Population	−0.00263	−1.163	0.245	0.048
		Species	0.00021	0.049	0.961	0.000
		Community	0.00150	0.461	0.645	0.001
	Functional	Population	−0.00873	−4.347	<0.001	0.065
		Species	−0.00597	−1.520	0.130	0.012
		Community	−0.00667	−2.312	0.022	0.029
Frugivores	Taxonomic	Population	0.00135	3.966	<0.001	0.188
		Species	0.00063	0.971	0.332	0.003
		Community	0.00183	2.304	0.022	0.028
	Phylogenetic	Population	0.00331	1.114	0.265	−0.000
		Species	0.00313	0.730	0.466	0.002
		Community	0.00551	1.654	0.100	0.015
	Functional	Population	0.00615	2.649	0.008	0.005
		Species	0.00975	2.631	0.009	0.036
		Community	0.00696	2.513	0.013	0.038

Note: Note that even for the significant (bold p-values) relationships, the slopes are small and the models have low explanatory power (i.e. small R²) evidencing the lack of latitudinal trend in the specificity of plant–frugivore interactions.

(Figure 2a–c). We found no relationship between the level of phylogenetic relatedness of the birds that plants interact with and latitude (Figure 2d–f), suggesting that plants are phylogenetic non-specific in their interactions across different latitudes. Plant species tended to be functionally specific (i.e. they interact with more functionally similar birds) in their interactions with birds at higher latitudes, although this relationship is weak and variable (Figure 2g–i). The strongest relationship we observed was for the functional specificity of plants at the population level ($\beta = -0.00873$, p -value < 0.001). In this case, a change of only ≈ -0.480 in the specificity of these interactions would be observed across the latitudinal extent ($\approx 55^\circ$ in absolute latitude) considered in our study. Given that the bounds for models that are non-significantly different from null relationships are between -1.96 and 1.96 , this further highlights the weaknesses of latitudinal changes in the specificity of these interactions. Overall, the level of taxonomic specificity showed by plants was

not correlated with the phylogenetic (Figure S5a–c) and functional (Figure S5d–f) specificity of their interactions. Alternatively, there was a positive relationship between the phylogenetic and functional specificity of plant interactions (Figure S5g–i), indicating that plants interact with birds that have similar levels of functional and phylogenetic dissimilarity.

Frugivore species also interacted with a higher fraction of plant species (i.e. taxonomic anti-specificity) at higher latitudes (Figure 3a–c), and these relationships were also weak and variable. Frugivores were phylogenetically non-specific (i.e. they had no phylogenetic preference) in their interactions with plants across latitudes (Figure 3d–f). However, frugivores tended to interact with more functionally distinct plant species at higher latitudes (Figure 3g–i). For birds, the strongest significant relationship observed was regarding their tendency to be functionally anti-specific across latitudes at the species level ($\beta = 0.00975$, p -value $= 0.009$). A change

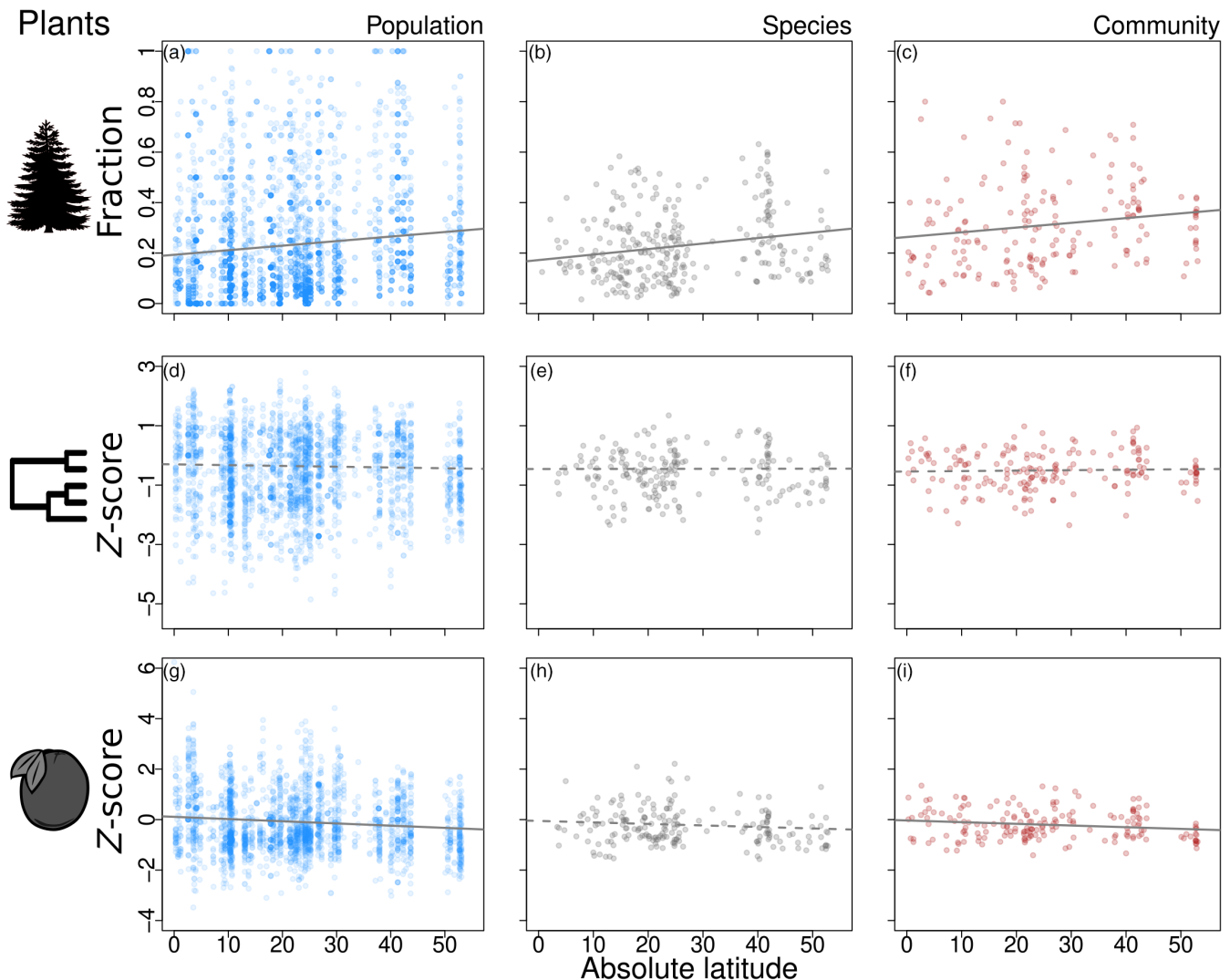


FIGURE 2 Relationship between the taxonomic (tree silhouette; a–c), phylogenetic (phylogeny silhouette; d–f) and functional (fruit silhouette; g–i) specificity of plant interactions with latitude for population (blue points), species (grey points) and community (red points) organization levels. In general, there is a high variation and lack of clear trend in the specificity of these interactions. Solid and dashed lines represent statistically significant and non-significant relationships, respectively. Fraction represents the fraction of observed interactions between plants and available interacting partners in a given site. Z-scores represent the the Z-score values obtained from our null models.

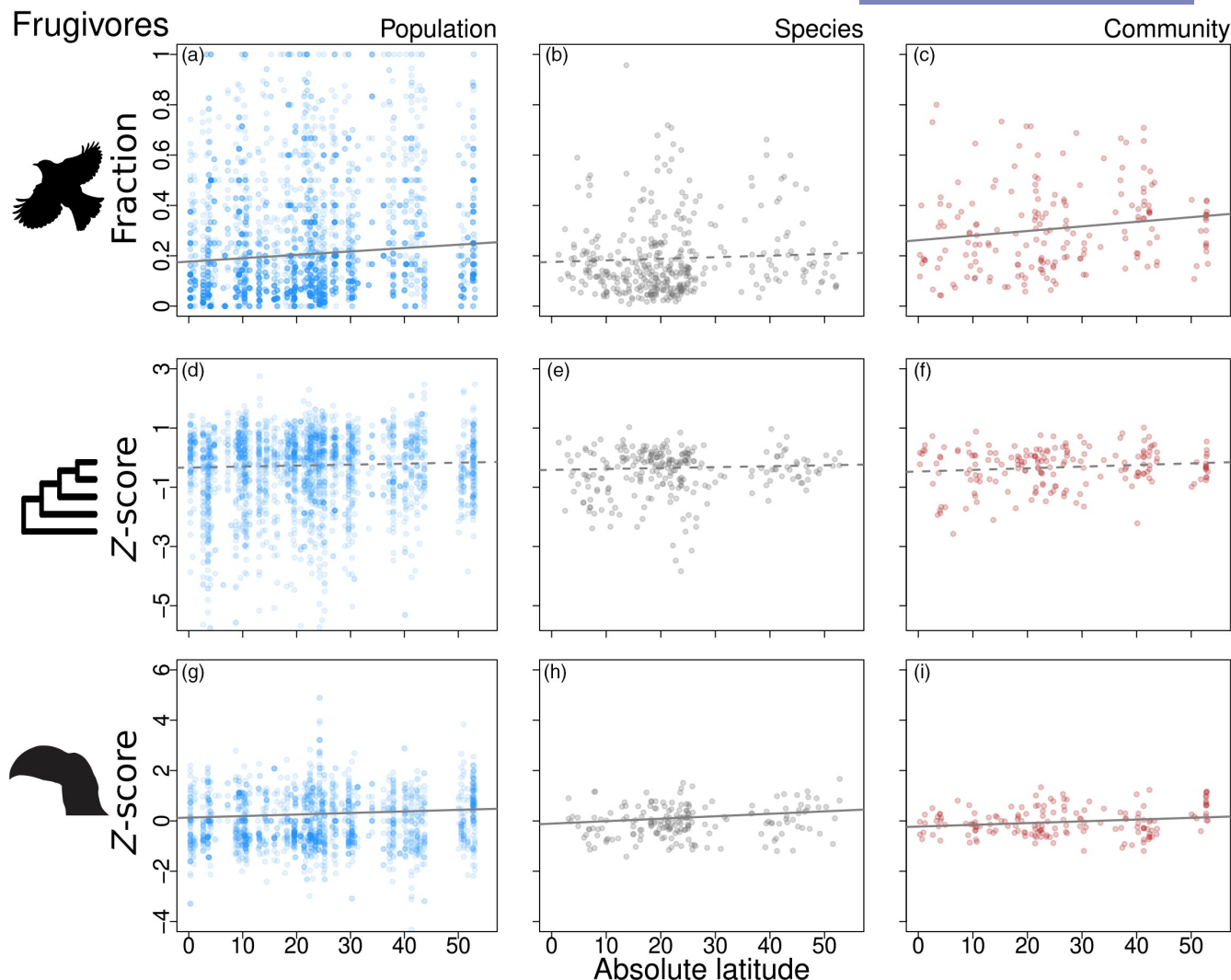


FIGURE 3 Relationship between the taxonomic (bird silhouette; a–c), phylogenetic (phylogeny silhouette; d–f) and functional (beak silhouette; g–i) specificity of bird interactions with latitude for population (blue points), species (grey points) and community (red points) organization levels. There is a large variation and no trend was observed in the specificity of these relationships. Solid and dashed lines represent statistically significant and non-significant relationships, respectively. Fraction represents the fraction of observed interactions between birds and available interacting partners in a given site. Z-scores represent the the Z-score values obtained from our null models.

of only ≈ 0.54 in the anti-specificity of these relationships would be observed across the latitudinal extent we considered, showing these relationships were also weak. We found a weak positive correlation between the taxonomic and phylogenetic specificity of frugivore interactions (Figure S6a–c), but there was no correlation between the other specificity estimates, suggesting that frugivores interact with plants that have different levels of taxonomic, functional and phylogenetic dissimilarity.

3.2 | Consistency of plant–frugivore interactions at different levels of organization

There was a general tendency for the specificity of plant–frugivore interactions to be consistent across the different levels of organization considered in our study. Functional specificity at the species

level for plants (Figure 3h) and taxonomic specificity at the species level for birds (Figure 3b) were the only instances where there was a disagreement with the other levels considered. These differences were in terms of the significance of the assessed relationships. However, the fact that the significant relationships were predominantly weak and variable indicates a general consistency in the evaluation of these trends across different levels of organization, where we only found limited evidence for latitudinal trends in the specificity of plant–frugivore interactions. Overall, the correlation between taxonomic and phylogenetic or functional specificity in plant interactions was either weak or non-significant whereas a moderate positive correlation between phylogenetic and functional specificity was observed across the three different levels of organization for plants (Figure S5). There is an overall absence of correlation between any of the specificity estimates for birds across the different levels of organization considered (Figure S6).

4 | DISCUSSION

We found negligible evidence for the occurrence of a latitudinal pattern in the specificity of plant–frugivore interactions given that, despite being often significant, these relationships were generally weak, variable and had low explanatory power. Plants and frugivores tended to interact with a relatively similar fraction of available species across latitudes, and these interactions did not exhibit any substantial latitudinal trend in the change of their phylogenetic and functional dissimilarity. Furthermore, the phylogenetic and functional specificity of plant–frugivore interactions often did not differ from null models (i.e. they were non-specific). This suggests that phylogenetic and functional constraints that affect plant–frugivore interactions might be relatively weak in the networks considered in our study, and that the strength of these constraints is likely not changing across latitudes. Moreover, the lack of strong correlation between taxonomic, phylogenetic and functional estimates of specificity indicates that these species could be potentially exhibiting different patterns in the specificity of their interactions for each dimension we considered. Together, our findings suggest that plants and frugivores are not showing considerable differences in the levels of taxonomic, phylogenetic or functional preferences of their interactions across latitudes, indicating that latitudinal trends in the specificity plant–frugivore interactions are not common.

The weak latitudinal trend for taxonomic anti-specificity exhibited by plants and frugivores can be explained by different factors. Latitudinal differences in resource availability could partially explain this tendency of species to interact with a higher fraction of available partners at higher latitudes. Resources are in general scarcer at higher latitudes (Kissling et al., 2007; Pianka, 1966; Schleuning et al., 2012), which would require species to utilize resources as they are available and consequently interact with relatively more species at higher latitudes compared to lower latitudes. Alternatively, it is also possible that the latitudinal gradient in species richness (Pianka, 1966) could have led to these results. We observed that sites sampled at higher latitudes have on average fewer species than sites sampled at lower latitudes (Figure S7). In this case, a species found in lower latitudes could interact with the same number of partners as a species found in higher latitudes, and higher latitude species would exhibit taxonomic anti-specificity, but not the species at lower latitude, simply because there are fewer potential interacting partners at high latitudes. This would explain the latitudinal trend we observed for taxonomic anti-specificity despite there being more obligate frugivores, which interact with more plant species than opportunistic frugivores (Mello et al., 2015; Schleuning et al., 2011, 2014), in the tropics.

A constant resource availability in the tropics could favour species to specialize in particular resources (Belmaker et al., 2012; Pianka, 1966) leading to a functional specificity. Conversely, a wide resource diversity in the tropics could also favour species to evolve traits that would allow them to use these different resources (Guimarães Jr et al., 2011; Wheelwright, 1988). This

would lead plant–frugivore interactions to exhibit a functional anti-specificity towards the tropics. We observed opposing (functional specificity and functional anti-specificity, respectively) latitudinal trends for birds and plants, where these relationships were highly variable. Such a lack of strength and high variability in these relationships that we observed could be explained if we assume that the occurrence of both of these evolutionary factors that affect plant–frugivore interactions is not restricted to tropical regions. If species across different regions have similar probabilities of becoming more specialized or generalist in their resource usage, species exhibiting functional specificity or functional anti-specificity in their interactions would be relatively evenly distributed across the globe, and no strong latitudinal pattern in these interactions would be observed. This would explain the similar proportions of functional specificity and anti-specificity that we observed across latitudes and the lack of a strong latitudinal trend in these relationships. These results could also be explained if there are no latitudinal differences in the accessibility or variability in nutritional content of available fruits as these factors also play an important role in the level of specialization or generalism that frugivores exhibit (Fleming, 1986). Moreover, if the considered species are not experiencing different levels of morphological barriers in their interactions (e.g. birds can swallow most of the fruits from co-occurring plant species (Machado-de Souza et al., 2019)) across latitudes, then latitudinal differences in the functional specificity of these interactions would also be unlikely to be observed.

Plant–frugivore interactions are usually phylogenetically non-random, such that closely related frugivores tend to interact with similar sets of plant species (Pigot et al., 2016; Rezende et al., 2007). Specifically, plant–frugivore interactions tend to be phylogenetically conserved in the tropics but not in temperate regions (Kissling & Schleuning, 2015). Our results fail to support this expectation, where we found that plant–frugivore interactions were generally phylogenetically non-specific across latitudes. Although coevolution between closely related species would favour plant–frugivore interactions to be phylogenetically specific (Charles-Dominique, 1993), introduced plants and frugivores can also strongly interact with native counterparts despite a lack of shared evolutionary history between the species (Herrera, 1985; Vizentin-Bugoni et al., 2019). This latter situation could obscure the phylogenetic specificity in the interactions between plants and frugivores, and no latitudinal trend would be observed regarding the phylogenetic specificity of these interactions. Furthermore, interaction patterns in plant–frugivore networks are often not inherited (Minoarivelo et al., 2014), which could also lead to phylogenetic non-specificity in these interactions. Additionally, an interplay between convergent evolution, where phylogenetically distant species evolve similar characteristics (Stern, 2013), and phylogenetic conservatism in traits (Cavender-Bares et al., 2004) across the species considered in our study could potentially explain the high variation we observed in phylogenetic specificity across latitudes.

Most plant (73%) and frugivore (50%) species considered in our study were found in only one site, which can potentially affect macroecological analyses (Qian et al., 2018). However, our species level analyses considered species that were found in at least three sites and they yielded virtually the same results as the population and community analyses, indicating that the species found in only one site are not responsible for the generally weak latitudinal trends in the specificity of plant-frugivore interactions that we observed at the population and community levels. Considering interaction frequency could also improve our results as functional constraints might affect the frequency of species interactions, but not the identity of the interacting partners. For example, a bird might consume large fruits more frequently, but it can also feed on small fruits occasionally. In this case, the bird will have several partners (i.e. it could be functionally anti-specific) despite having a clear preference for larger fruits. Nonetheless, similar results are often obtained when interaction frequency or binary data are used to assess plant-frugivore interactions (Schleuning et al., 2012; Vizentin-Bugoni et al., 2019), suggesting that these analyses are relatively robust to these different data types (Simmons et al., 2018).

Latitudinal patterns in species interactions are often observed (Dalsgaard et al., 2017; Dyer et al., 2007; Schleuning et al., 2012; Zvereva & Kozlov, 2021), but weak, or even absent, latitudinal trends are also frequently found (Kevan & Baker, 1983; Olesen & Jordano, 2002; Ollerton & Cranmer, 2002; Zvereva & Kozlov, 2021). This indicates that latitudinal trends in species interactions might not be so prevalent as previously suggested (Moles & Ollerton, 2016; Ollerton, 2012). In our case, this could be occurring due to an interplay between different mechanisms that affect plant and frugivore interaction specificity, where species-specific responses to latitude lead some species to specialize and some to anti-specialize in their interactions. For example, two groups of parasite species occurring in tropical and temperate regions exhibit different trends in their host specificity across these two regions (Rohde, 1978). This suggests that detecting latitudinal trends in species interactions might be challenging when considering large number of species given that different groups of species might exhibit opposing latitudinal trends in their interactions that could be obscured when considering all species simultaneously. Deconstructing these latitudinal patterns of species interactions could potentially improve our understanding of how different species specialize in their interactions across latitudes (Marquet et al., 2004). In this case, latitudinal patterns in species interactions could be decomposed by clade or biogeographic region, such that it becomes possible to disentangle how different factors are affecting these interaction patterns across different regions and groups of species (Terribile et al., 2009; Vásquez-Restrepo et al., 2023).

AUTHOR CONTRIBUTIONS

Cleber Ten Caten and Tad Dallas conceived the ideas and designed the methodology. Cleber Ten Caten formatted and analysed the

data. Cleber Ten Caten led the writing with contributions from Tad Dallas.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

R code and data to reproduce the analyses are available on figshare at <https://doi.org/10.6084/m9.figshare.22280629>.

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SUPPORTING INFORMATION

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

Figure S1: Locations where plant-frugivore interactions were sampled.

Figure S2: Moran's I values for the community levels analyses for plants (a–c) and frugivores (d–f) for taxonomic, phylogenetic and functional specificity.

Figure S3: Relationship between the absolute latitude of sampled sites and the fraction of plant species occurring at those sites that did not have trait data related to seed mass available.

Figure S4: Z-scores obtained from our local (red) and global (blue) null models for plants (a, b) and birds (c, d).

Figure S5: Correlations between the different specificity measures considered in our study for plants.

Figure S6: Correlations between the different specificity measures considered in our study for birds.

Figure S7: Latitudinal differences in species richness for plants (red points) and birds (blue points).

Table S1: Taxonomic, phylogenetic and functional specificity of

plant and frugivore interactions for the three levels of organization considered in our study considering only the cases where observations captured the complete assemblage of interactions partners.

Table S2: Phylogenetic and functional specificity of plant and frugivore interactions for the three levels of organization considered in our study using the global null model.

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