Short running title: Species centrality in climatic niche space

Bird species' network centrality varies differentially across species within their climatic niches

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Abstract

Understanding how the functional role of species within seed-dispersal networks varies across geographical and climatic gradients can reveal the drivers of network organization. Because bird-plant interactions differ depending on where these occur, species' centrality (a measurement of species importance in the networks) is expected to vary across species' geographic distributions. Using a global dataset of bird-plant seed-dispersal networks, we applied a cross-random mixed-effect model to evaluate the variation of 239 bird species' centrality within local networks across their occupied climatic conditions and in response to co-existing bird and plant diversities in those networks. Our model indicated that centrality did not vary significantly with the distance to the climatic niche centroid but increased with increasing bird diversity. However, by examining species' individual responses we found that centrality did vary with the distance to the climatic niche centroid, with 43% of the evaluated species (102) showing a negative relationship (higher centrality closer to the climatic niche centroid), whereas 51% of species (122) showed a positive relationship (higher centrality farther from the climatic niche centroid). The effect of bird diversity on individual species' centrality co-varied positively with that of plant diversity more than having opposite effects, regardless of the network's position within the climatic niche. Taken together, the variation in individual species' centrality within the occupied climatic conditions suggests the existence of areas where species achieve high centrality, which might form the substrate for evolutionary and ecological dynamics.

Keywords: centre-periphery hypothesis, frugivory, functional role, intraguild competition, mutualist networks, resources availability

Translated Title: La centralidad de las aves en redes de interacción varía dentro de sus nichos climáticos

Secondary Abstract

Entender cómo varía el rol funcional de las especies en las redes de dispersión de semillas a través de gradientes geográficos y climáticos puede informar acerca de las causas de la organización de estas redes. Puesto que las interacciones ave-planta pueden ser diferentes dependiendo en dónde sucedan, se espera que la centralidad de las especies (una medida de su importancia en las redes) varíe a lo largo de sus distribuciones geográficas. En este estudio, usamos un conjunto de datos global de redes de dispersión de semillas para evaluar la variación de la centralidad de las aves en las redes en las que participan. Esta evaluación de la centralidad se hizo en función de las condiciones climáticas que ocupan dichas redes dentro del nicho climático de las aves y de la diversidad de plantas y de otras aves que coexisten en esas redes. Nuestros modelos considerando todas las aves indicaron que la centralidad no varía significativamente con la distancia al centroide de sus nichos climáticos, sino que incrementa con la diversidad de aves. Sin embargo, al evaluar las respuestas por especies individuales encontramos que la centralidad sí varía con la distancia al centroide de su nicho climático, con 43% de las especies (102) mostrando una relación negativa (mayor centralidad a menor distancia del centroide) y 51% (122)

mostrando una relación positiva (mayor centralidad a mayor distancia del centroide). El efecto de la diversidad de otras aves en las respuestas individuales covarió positivamente con la diversidad de plantas, en lugar de tener efectos opuestos y sin importar la posición de las redes dentro del nicho climático. En suma, la variación de la centralidad de las aves en las redes ocupando diferentes condiciones climáticas dentro de sus nichos sugiere la existencia de áreas geográficas y climáticas donde las especies son más importantes para la organización de las redes, lo cual puede determinar la dinámica evolutiva y ecológica de sus interacciones.

Introduction

A broadly recognized ecological pattern is that some species have a disproportionate role in maintaining ecosystem functions in their communities (Mouquet et al. 2013). This is because species are not isolated entities, but are connected within complex networks of interactions. Keystone species tend to be more central (i.e., important) in networks by interacting with many other species via multiple direct and indirect pathways (Martín González et al. 2010; Mello et al. 2015; Escribano-Avila et al. 2018). Such central species may also influence the co-evolutionary convergence of traits of interacting partners (Guimarães Jr et al. 2011; Medeiros et al. 2018). Given their importance, the extinction of central species could increase co-extinctions, decrease network robustness and even cause negative cascading effects on the ecosystem balance (Emer et al. 2018). Species' centrality, however, is not a fixed trait and varies across the networks where a species participates within its geographic range. Thus, evaluating species' centrality requires moving from analyzing a species' role within a single ecological network to examining how that species' role varies across multiple networks, where it can be related to species' ecological traits such as their climatic (Grinellian) niches (Soberón 2007), phenotypic traits (e.g., Tobias *et al.* 2022), and extrinsic characteristics derived from their geographic co-occurrence with other species. Altogether, these traits allow for determining the spatial variation of species interactions and their drivers at broad spatial scales (Moulatlet et al. 2023).

Because the geographic distribution of species usually covers a range of environmental conditions at distinct localities, species' biotic interactions (e.g., partner composition, frequency, and dependency) vary along environmental gradients within their geographic ranges (Dehling et al. 2014). Species usually co-occur with a varied set of other species within their geographic ranges as described by the characterization of their diversity field (Villalobos and Arita 2010). The *diversity field* of a species characterizes the assemblages occupied across its range, describing its tendency to occur in species-rich or species-poor regions based on co-occurrence at broad spatial scales (Villalobos et al. 2013*a*) or co-existence at local scales (Pinto-Ledezma et al. 2020). Similarly, if we consider species from the same guild – which represent "arenas of intense competition" (Pianka 1980) – or those consumed as resources, the set of interacting species that co-occur with a focal species can be used to define its *interaction field* (Sánchez-Barradas et al. 2023). These concepts are important in understanding the variation in species centrality in interaction networks since a focal species can only interact with those species present in its diversity field because of co-occurrence limitations imposed by geographic and ecological boundaries (Dáttilo et al. 2020; Martins et al. 2022).

There is evidence that population characteristics vary along species' geographic ranges (Gaston 2009). A longstanding reported variation is the abundance decline from the centre towards the edge of the geographic range of a species (Brown, 1984). The main assumption behind this idea is that climatic conditions are more favourable and stable at the centre of a species' geographic range and become gradually less favourable towards the periphery (the Centre Periphery Hypothesis; Brown 1984; Martínez-Meyer *et al.* 2013; Pironon *et al.* 2017). The Centre Periphery Hypothesis has been systematically tested with discordant outcomes in the geographic space. The main criticism is that species abundances are not consistently higher at the centre of their geographic distributions (Sagarin and Gaines 2002; Lira-Noriega and Manthey 2014; Pironon et al. 2015). Instead, several studies have suggested that the climatic niche space (i.e. the climatic conditions where a species thrives) would be more appropriate to assess the species' abundance variability, mainly because such variability responds to the structure of climatic conditions, with higher population performance and abundance at the climatic niche centroid where optimal conditions are met (Maguire 1973; Hoffmann and Blows 1994; Martínez-Meyer et al. 2013; Lira-Noriega and Manthey 2014). Because species' relative abundances are one of the main factors that determine their role in an ecological network (Vázquez et al. 2007; Krishna et al. 2008), it seems plausible that the variation in species' centrality is associated with the location of those networks along the climatic niche space, as determined by the geographic distribution of a focal species.

The number of co-existing species in a network is also important for determining species’ centrality. Co-existing species affect the energetic costs of resource acquisition when these are limited (MacArthur 1960; Hall et al. 1992), and can lead to species displacement by stronger competitors, thus shaping the organization of mutualistic networks (de M. Santos et al. 2012; Dáttilo et al. 2014). As such, a focal species may be more or less central in the networks it participates within its range depending on the number of co-existing species (Cazelles et al. 2016; Pedraza and Bascompte 2021). The need to include co-existing species as driving factors of the centrality variation in ecological interactions has been recently highlighted (Early and Keith 2019), but few attempts to map those interactions have been made so far (Braz et al. 2020). Assuming the existence of areas within a species’ geographic range where climatic conditions are optimal to reach high centrality, an intriguing and poorly understood issue is whether the co-existing species from different trophic levels influence the chances of a focal species becoming more central in these areas.

Here, we used a dataset of 314 seed-dispersal networks from 11 biogeographical regions (Figure S1; Holt et al. 2013) to examine how bird species' centrality varies across the climatic niche space, considering the number of co-existing bird and plant species (i.e., the measured diversity of plant and bird species in each network). We chose bird-plant seed-dispersal networks because they are excellent model systems to evaluate species' ecosystem functions (Schleuning et al. 2015). Birds have wide distributions and are the main seed dispersers, establishing mutualistic interactions with most angiosperms' families, which is fundamental for biodiversity maintenance (Fleming and John Kress 2011). Moreover, seed dispersal networks have been studied in basically all continents and biogeographical regions (Windsor et al. 2022), making it possible to compile datasets of global relevance. As predicted by the Centre Periphery Hypothesis, we expected that centrality would be higher at the centre of the climatic niche space for most of the selected species, but it can be influenced by both bird and plant species co-existing in the networks as potentially representing competition and resource availability, respectively.

We envisioned five possible scenarios for the interplay of climatic niche space and the numbers of co-existing bird and plant species in determining bird species centrality (Figure 1a-e). (1) Centrality can be the highest closer or farther from the climatic niche centroid (Figure 1a). In any of these two possibilities, 2) bird and plant diversities have no effects on centrality (Figure 1b); (3) Both bird and plant diversities affect centrality either positively (e.g., due to foraging specialization and higher resource availability) or negatively (e.g., due to increased competition and lower resource availability) (Figure 1c). (4) Bird and plant diversities have opposing effects on centrality. This scenario could reflect, for example, a negative effect of bird diversity on centrality (due to increasing competition) and a positive effect of plant diversity on centrality (due to higher resource availability) across a bird's climatic niche (Figure 1d). (5) Only bird or plant diversity has an effect on centrality (Figure 1e). Overall, these hypothetical scenarios are not mutually exclusive, but rather gradients that can advance our understanding of how species' centrality within mutualistic networks varies across their climatic niches over broad spatial scales.

Methods

Species data

We used the dataset of individual species centrality in bird-plant seed-dispersal networks compiled by (Moulatlet et al. 2023). This dataset consists of studies describing mutualistic networks of seed dispersal compiled from the scientific literature, using the Web of Science (WoS), Scopus and Google Scholar databases, from two specialised databases (the Interaction Web Data Base [https://www.nceas.ucsb.edu/interactionweb] and Web of Life [http://www.web-of-life.es/2.0/index.php]) and other databases containing plant-frugivore interaction data (see more details in Moulatlet el. 2023). We selected 239 focal species from 42 bird families. Due to the nature of our main tested variables (distance to the niche centroid), we considered only those species that were present in at least two local networks to represent their climatic variability across their geographic ranges (Table S1).

Species centrality in networks

Species centrality was determined based on four species-level centrality metrics for each individual network: i) degree (the number of links of each species), ii) betweenness (the proportion of the shortest paths linking any pair of nodes in a network), iii) closeness (the shortest connections between a species and every other network species) and iv) Katz centrality (a measure of the distance, in terms of all possible pathways, between the focal node and all other nodes of the network). Each metric was first standardised by calculating the z-scores in each network to allow for comparison among different networks. The z-score standardization was done by subtracting species values for each metric from the mean values of the same metric for all species presented in each network, divided by the standard deviation. Then, the four metrics were combined using a PCA analysis, where the first PCA axis (PC1) represented the centrality of species, with the highest positive values associated with those species that are more central in a network, as has been suggested in previous studies (Dáttilo et al. 2016; Guimarães et al. 2017; Maia et al. 2019; Burin et al. 2021). The centrality values were calculated for each species in the individual networks. For the convenience of interpreting PC1 values from 0 (more peripheral) to the highest positive value (more central), PC1 values were rescaled to non-zero, positive-only values by adding up the absolute value of the minimum score plus a millesimal unit to each centrality value (Cruz et al. 2022; Moulatlet et al. 2023). In this manner, all PC1 values were greater than zero while keeping the original order and distance among them. The first PC explained >75% of the total variance for each network. Except for the Katz metric, which was calculated using a custom R code written by the second author of this article, the other metrics were calculated using the R package bipartite (Dormann 2011).

Explanatory variables

Our predictor variables of species' centrality were the position of each network within the climatic niche space relative to its centroid, and the number of co-existing plant and bird species in each network (diversity of bird and plant species) as coarse proxies for resource availability and competition, respectively (Figure 1).

The number of co-existing plant and bird species have been suggested as general proxies for biotic interactions by previous studies that focused on proposing ways to infer interactions (Morales-Castilla et al. 2015; Gravel et al. 2019; Sánchez-Barradas et al. 2023). Also, classic ecological theory predicts competition to be stronger in species-rich regions (Yoder et al. 2010). For instance, at broad spatial scales, the number of co-existing species of the same guild or clade has been used as a proxy for the number of potential interactions (Gotelli et al. 2010; Machac 2020). This is the case when considering the complete geographic distribution of species as in the characterization of species' fields' describing the taxonomic, phylogenetic or functional structure of co-occurrence within species' ranges (Villalobos et al. 2013*b*). The interaction fields have been used to infer interactions and their resulting biogeographic consequences (Villalobos et al. 2017), as well as the history of invasions (Kusumoto et al. 2019; Pinto-Ledezma et al. 2020; Maitner et al. 2022).

We used the ellipsoid envelope model (EEM, Farber & Kadmon, 2003) to characterize species' climatic niches based solely on their geographic occurrences and climatic data (i.e., presence-only method). EEM is grounded on classic niche theory, which states that species are unevenly distributed along climatic gradients with a tendency towards optimal conditions (i.e. niche centroid; Hutchinson 1959; Maguire 1973; Brown 1984) and thus can be modelled as a bell-shape function in multivariate climatic space that is best represented by an ellipsoidal shape, yielding a closer approximation to the fundamental niche of a species (Farber and Kadmon 2003; Jiménez et al. 2019). In contrast, common niche modelling methods like climate envelope (e.g., BIOCLIM) or machine learning models (e.g., MaxEnt) do not make an explicit assumption about the niche shape and thus defining the niche centroid is not straightforward (Jiménez et al. 2019). The idea of a niche centroid representing the optimal conditions for a species has been supported by the overall positive relationship between climatic suitability and species' abundance as well as genetic diversity (Martínez-Meyer et al. 2013; Lira-Noriega and Manthey 2014; Weber et al. 2017), including the application of EEMs particularly for birds (Osorio-Olvera et al. 2020*b*). Finally, EEMs are suitable for modelling a high number of species, as they require considerably fewer assumptions and decisions regarding parameters (Nuñez-Penichet et al. 2021).

The environmental variables used to characterize species niches in EEM were obtained from WorldClim v.2.1 (Fick and Hijmans 2017) at a resolution of 30' (~1 km^2 at the Equator). We extracted climatic data for each occurrence record with the R package terra (Hijmans et al. 2022). We selected variables BIO1 (Annual Mean Temperature), BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO12 (Annual Precipitation), BIO16 (Precipitation of Wettest Quarter) and BIO17 (Precipitation of Driest Quarter), as these are suitable variables to delimit the niche space based on temperature and precipitation (Nuñez-Penichet et al. 2021).

To build EEMs, we first downloaded from the Global Biodiversity Information Facility database (GBIF; https://www.gbif.org/) a maximum of 1000 spatially random occurrences for each species using the rgbif R package (Chamberlain et al. 2022). The number of occurrences is sufficient to represent the geographic distribution of a species (Herkt et al. 2017) and, importantly, to characterize its environmental preferences as derived from ecological niche models (van Proosdij et al. 2016). We cleaned the data by removing duplicates and records with uncertain or missing coordinates. We also removed records at distances less than 15 km from one another (spatial thinning; Nuñez-Penichet et al., 2021). We used the cleaned records of each species and the selected climatic variables to build its EEM using the default parameters of the *ell_model* function (modelling method “covmat”, confidence level = 95% and single replicates) of the R package ellipsenm2 (Cobos et al. 2022). The error assumed for the occurrence data was 5%, meaning that 5% of the occurrence data are potentially climatic outliers, and therefore not included in the EEM. From each model, we identified the niche centroids, i.e., the values that characterized the centre of species climatic niche and that can be interpreted as the optimal climatic conditions for species’ performance (Hoffmann and Blows 1994; Soberón 2007).

Finally, to obtain the distance of each network to the centroid of the species’ climatic niche (a vector of bioclimatic values) we calculated the Euclidian distance of the climatic conditions where each network was located to the niche centroid. We used as input a matrix of the bioclimatic values (i.e., the same used in the EEMs, the columns) as obtained from the geographic location of the network where the focal species occurred (rows). The Euclidian distance was then calculated from each row to the vector of bioclimatic values that represent the centroid of the niche space. Our analytical tests were performed using only occurrence information, following Weber et al., (2017) who indicated that occurrence data could be used to map and describe environmental suitability as a surrogate for abundance information. A summary workflow can be found in Figure 2.

The niche centroid predictor variable was not correlated to the bird and plant diversities across all networks, whereas these two latter variables showed moderate correlation. Pearson's correlation between plant diversity and niche centroid was $r = 0.016$ ($p = 0.37$), between bird diversity and niche centroid was $r = 0.079$ ($p < 0.0001$) and between bird and plant diversity was $r = 0.46$ ($p < 0.001$).

Data analysis

We modelled the relationship between bird species' centrality (PC1, response variables) and the predictor variables (distance to the climatic niche centroid and bird and plant diversity) by fitting a crossed-random effect linear mixed-model with Gaussian distribution using the R package lme4 (Bates et al. 2015). All response and explanatory variables were scaled prior to the analyses using the function scale, from the base R package. This step is necessary when variables have distinct magnitudes (Bates et al. 2015). This function first "centres" each column from the dataset by subtracting each value by the column's mean. Then, the values are "scaled" dividing them by the column's standard deviation. Our model included a) single, 2-way and 3-way interaction of the three predictor variables (distance to the centroids, birds and plant diversity) as fixed-effect terms and b) a by-species (grouping factor) cross-random terms, meaning that both the intercept and the slopes were not fixed for the grouping factor and allowed to vary for each tested variable (equation 1). We started with a maximum model (Barr et al. 2013), where the cross-random terms were multiplicative, but that had to be modified to avoid singularity issues. These issues occur when the estimated variance-covariance matrix for one or more random factors has either perfect or near-perfect positive or negative correlations, or one or more variances are closer to zero (Barr 2021). We fixed model singularity by replacing the multiplicative with additive terms and by constraining all covariance parameters to zero, according to Barr (2021) (equation 1).

$$\mathrm{PC1} \sim \mathit{nichedist} \times \mathit{nbirds} \times \mathit{nplants} + (\mathrm{nichedist} + \mathrm{nbirds} + \mathrm{nplants} \mid\mid \mathrm{species})$$

Equation 1. PC1 is the species' centrality measurement obtained as the first axis of the PCA analysis; nichedist (distance to niche centroid), nbirds (diversity of birds) and nplants (diversity of plants) are fixed-effect terms; the species term stands for the species' scientific names and was modelled as the grouping-factor in the random term of the model. Equation 1 is written using the syntax of the lme4 R package. Fixed effects are shown in italics, while the random term is shown between brackets. The multiplier symbol indicates that slopes are calculated for each variable separately and by their two- and three-way interactions. The double-bar instead of a single-bar syntax in the random term indicates that the model is set to constrain all covariance parameters to zero.

The inclusion of the predictor variables as fixed terms allowed us to test which of them (and their interactions) had the highest global explanatory power for species' centrality. This test was done by simulating (n = 1000) fixed effects posterior distributions to build empirical Bayes means and 95 % confidence intervals estimates, using the Gelman sim technique (Gelman and Hill 2006), available in the R package merTools (Knowles et al. 2024). The model's goodness of fit was obtained with Pseudo-R square, the conditional coefficient of determination for Generalized mixed-effect models, available in the R package MuMIn (Bartoń 2023). Associated p-values were calculated using the lmerTest R package extension for the lme4 package (Kuznetsova et al. 2017). The model's overdispersion was tested by performing a simulation of the residuals and evaluating diagnostic plots available in the R package DHARMa (Hartig and Lohse 2022). We tested for models' dispersion using the function testDispersion with Pearson's Chi-squared test option and the one-side hypothesis test (Harrison 2015). Test values larger than one indicate overdispersion; our model dispersion value was 0.82.

Because we were also interested in the individual species' responses to each variable, we calculated the marginal effects (hereafter referred to as "slopes"), i.e., the partial derivative (*d*) of the regression equation for a regressor of interest. The *d* refers to an infinitesimal change in the slope values rather than a one-unit change (as commonly done in simple regression models). The slope for each variable by species was calculated using the function *slopes* of the R package marginaleffects (Arel-Bundock et al. 2024). For each species, we calculated the slope direction (positive or negative) as the difference between the initial and final slope estimate along the values of each variable for each species. Given our modelling choice, we did not address p-values for the slopes of the random terms as it is not generally clear that the null distribution of the computed ratio of sums of squares was really an F distribution, for any choice of denominator degrees of freedom (Bolker et al. 2009). Altogether, the slope directions allowed us to classify each species according to our proposed hypothetical scenarios indicated in Figure 1. Packages sjPlot (Lüdecke 2024) and merTools (Knowles et al. 2024) were used for data visualization.

Results

Our global model (pseudo-R square = 0.13) indicated that, considering all bird species evaluated and their networks, centrality did not change significantly with distance to niche centroid ($b = -0.01$, $P = 0.703$) and plant diversity ($b = 0.015$, $P = 0.590$). Only bird diversity had a significant positive effect on birds' centrality ($b=0.06$, $P < 0.05$) (Figure 3). We also found no significant two-way or three-way interaction effects involving distance to niche centroid, plant diversity and bird diversity (Figure 4).

By comparing the slope direction of the variables for each species' responses, we classified bird species into our hypothetical scenarios (Table 1). Overall, 94% of the evaluated species (224 out of 239 species) had regression slopes different from zero. Half of the evaluated species (51%; 122 out of 239 species) had a positive slope between their centrality and distance to their niche centroid across their occupied networks, with centrality increasing towards their niche border. A slightly lower number of species, representing 43% (102 species) of the total, showed a negative slope between centrality and niche centroid distance, with centrality increasing towards their niche centroid.

For 62% of the species (63) whose centrality increased towards the niche centroid (decreased with niche centroid distance; negative slope), the slopes of bird and plant diversity had the same direction between them (Table 1); with 90% of these species (57) also having negative slopes for these predictors (i.e., centrality decreasing when bird/plant diversity increased; Table 2). For 45% of species (55) whose centrality decreased towards the niche centroid (increased with niche centroid distance; positive slope), the slopes of bird and plant diversity showed similar directions between them (Table 1); with 65% and 35% of these species showing negative and positive slopes for both variables, respectively (Table 2).

For 28% of species (29) whose centrality was negatively related to niche centroid, the slopes of bird and plant diversity had opposite directions (Table 3). Out of these species, 62% had negative slopes for plant diversity and positive for bird diversity. For the species whose centrality was positively related to niche centroid distance, 58% showed negative slopes for plant diversity and positive for bird diversity, and 42% had positive slopes for bird diversity and negative for plant diversity (Table 3).

Discussion

Determinants of species' centrality variation

Our results revealed how the interplay between climatic niche conditions, plant diversity, and bird diversity influence the variation of bird species centrality within seed-dispersal networks. Previous studies have addressed how bird species centrality in seed-dispersal networks is related to their species' geographic and evolutionary traits (Pigot et al. 2016; Burin et al. 2021; Moulatlet et al. 2023). However, to our knowledge, this is the first study evaluating how bird centrality varies across their geographic ranges in relation to their occupied climatic niches and how this variation follows the predictions of the Centre Periphery Hypothesis in the climatic space (Martínez-Meyer et al. 2013). Based on the assumption that the optimal conditions for a species' highest fitness are at the centre of its climatic niche (Maguire 1973; Brown 1984), we expected the species' centrality to be the highest closer to their niche centroid. However, our global model revealed that our expectation could not be generalized among bird species, as centrality was not significantly related to the distance to the niche centroid. Our results on the individual species (by-group factor in our model) indicated that centrality values do vary along their climatic niches. Centrality tends to decrease away from the centroid of the climatic niche (as obtained from the slope directions) for about half of our evaluated bird species (102 out of 239), whereas the other half (122) showed the opposite pattern with centrality increasing away from the niche centroid. Therefore, despite the distance to the niche centroid had no significant effect in the model, virtually all bird species studied had slopes different from zero, which implies the influence of climatic conditions in the variation of species' centrality across their geographic ranges.

The predictions of the Centre Periphery Hypothesis as applied to species' roles within networks were not supported. Instead, our model showed that centrality was positively related to the number of co-existing bird species, so the co-existence of bird species was more influential in explaining the variation in individual species' centrality. A high number of co-existing bird species may suggest that no resource limitation would otherwise lead to niche segregation and a high number of specialist (i.e. not central) species (Tilman 1982). Indeed, the high diversity of co-existing species can increase generalism (i.e. high centrality) (Palacio et al. 2016). This may be related to the fact that more generalist bird species tend to achieve a higher abundance (Osorio-Olvera et al. 2020*a*) so that they can interact with more plant species and with higher visitation frequency.

Higher centrality closer to the niche centroid and the effect of plant and bird diversity

The centrality of 43% of the evaluated bird species increased towards the centroid of their climatic niches, where the climatic conditions are optimal (Maguire 1973, Martínez-Meyer et al. 2013). Most likely, for those species the optimal climatic conditions are the most important driver of their interaction role as they could allow species to attain high abundances (Martínez-Meyer et al. 2013, Weber et al. 2017, Osorio-Olvera et al. 2020) and therefore higher number of interactions (Laurindo et al. 2020; Pizo et al. 2022). Previous studies suggested that bird species can be at their ecophysiological optimum at the niche centroid (Hoffmann and Blows 1994) when compared to the niche border, where climatic conditions would not be adequate (VanDerWal et al. 2009; Perez-Navarro et al. 2022). Our results, however, should be interpreted with caution as our analyses do not allow us to determine if climatic conditions are the most important driver since other untested factors could also be influencing species interaction roles.

Our results suggest that optimal climatic conditions for a focal bird species do not solely influence its centrality in mutualistic networks, as has been previously found for plant species (Gómez and Perfectti 2012), but that plant and bird diversities are also key factors in determining species centrality within the niche space. For these 43% species, centrality decreased as bird and plant diversity decreased for the great majority (90%). Thus, when a species is more central close to its niche centroid, it is also more central where plant and bird diversity are the highest.

The effect of bird and plant diversities can be discussed separately. On one hand, co-existing plant species might define species centrality because it increases the chances of a focal bird species establishing links with more plant partners and becoming a generalist in terms of their consumed resources (Dehling et al. 2014). On the other hand, it may increase the chances of specialization between birds and plants by increasing the possibilities of trait-matching, especially in resource-rich networks (Medeiros et al. 2018). Our results suggest that the first case was more likely when the species were more central close to the niche centroid. It is important to note that we considered the total number of co-existing plant species reported within the studied networks, which can certainly be lower than the actual number of available plant species in the community. Given that not all plant species in a community are necessarily dispersed by birds, we consider our approach conservative, while still informative based on empirical information.

The effect of bird diversity suggests that the number of co-existing bird species reduces the access to resources for the populations at the centre of the climatic niche space, displacing the populations to the niche border (Case & Taper 2000). The increasing number of co-existing bird species might indicate a limiting factor when resources are not sufficient for ecologically similar species (MacArthur 1960; Palmer et al. 2003). If that assumption holds, the co-existence with a high number of ecologically similar species may define centrality (de M. Santos et al. 2012; Maia et al. 2019; Dáttilo et al. 2022). However, for the species whose centrality was higher towards the niche centroid, this was not the case. The high number of co-existing bird species may not necessarily indicate competition, but it somehow facilitated species to be more central. This could be the case for species from high-diversity systems, such as tropical forests. In these systems, the possibilities of increasing network links are higher and may not be limited by competition (Chesson 2000; Weiher and Keddy 2001).

Higher centrality at the niche border and the effect of plant and bird diversity

Despite almost half of our evaluated species (102) showing that centrality tends to be higher towards their niche centroid, the other half of bird species (122) increased their centrality towards their niche border. For 45% (55 species) of these species, the number of co-existing bird and plant species had a similar slope direction, being mostly negative (36 of 55 species – 65%). This result suggests that species were more central far from their niche optima, where plant and bird diversity were the lowest. For those bird species, the high number of co-existing bird species may lead to species displacement in resource-limited regions. It is noteworthy that for ~40% of the species with the highest centrality closer to their niche border, the influence of bird and plant diversity had opposite directions, being most of the species more central where the number of co-existing bird species was the highest and the number of co-existing plant species the lowest (29 out of 50 species – 58%). For these species, an increased number of co-existing bird species may lead to a high centrality of a focal species in networks with higher levels of specialized species (Bascompte et al. 2003).

The interplay between the variables

For a small number of species (15%) there was no effect of the occupied climatic conditions in their centrality, but the number of co-existing bird and plant species did affect their centrality. This result suggests that for some species 1) centrality is a species' characteristic that is independent of their occupied climatic conditions, and/or 2) that the strength of biotic factors may override the effect of climate, i.e., that the complex effects of these interactions in the evaluated networks may outpace the effects of climatic conditions in determining the areas in which species can be central in their occupied networks across its climatic niche space. Further investigation on the evolution of species interactions may help elucidate the interplay between the tested variables.

The interactions of focal species in ecological networks across their complete geographic ranges could serve as a template to identify hot- and coldspots of species interactions, for example in the context of the geographic mosaic theory of coevolution (Thompson 2009). In this context, hotspots would be those areas where the centrality of a focal species increases with plant diversity and decreases with bird diversity in a network, whereas coldspots of interaction would then be those areas where centrality is either negatively or not related to plant diversity and positively related to bird diversity. The importance of mapping the conditions where species become more central is important because central species may drive the coevolution of both plant and bird species in a community (Bascompte et al. 2003; Medeiros et al. 2018). However, the possibilities of establishing links with plant species vary according to the biogeographic region where the network is located (Kissling et al. 2012) as well as the habitat type (Friedemann et al. 2022) and quality (Emer et al. 2018). The study of interaction networks along climatic niches of species could reveal how interactions are being established and evolving in the landscape, but its application would require finer-scale data on pairwise species interactions such as measures of adaptation and selection (Thompson 2009).

Conclusions

We evaluated how the centrality of bird species in seed-dispersal networks varies within their climatic niches and how this variation depends on the interplay with the number of co-existing bird and plant species. The number of co-existing bird species was the variable that mostly influenced centrality variation. Although we did not find a global effect of the distance to niche centroid on species' centrality, individual species responses indicated a pervasive influence of the occupied climatic conditions on centrality, with 94% of species showing non-zero slopes, warranting further investigation on the potential drivers of centrality variation. For instance, species' traits such as morphological or life history characteristics may shape the observed relationships. These traits could be related to different ecological and evolutionary hypotheses that remain to be tested in this context. In addition, actual information on resources and competitors' variation, beyond the coarse proxies used here, is scarce in the literature and should be considered in further studies, as we found that the number of co-existing plant and bird species are key factors in determining species centrality. Conducting studies including other taxa and types of interactions would help us to understand the factors that determine the spatial and climatic variation of species' centrality and contribute to the potential conservation of species and their ecosystem services. Further investigation on the spatio-temporal variation of interactions such as those in temporally dynamic networks is certainly needed and will enhance our understanding of the drivers of species' centrality.

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Tables

Table 1. Classification of species into the hypothetical scenarios presented in Figure 1. The classification was made based on the combination of the direction of each predictor's slope (nichedist – the distance to the niche centroid, plant and bird diversity) as regressed with the response variable (species' centrality) derived from the global model.

Slope direction Plant and Bird Diversity	Slope (nichedist): negative	Slope (nichedist): no effect	Slope (nichedist): positive
No effect	0 (0%)	1 (7%)	2 (2%)
Opposite direction	29 (28%)	6 (40%)	50 (41%)
Same direction	63 (62%)	6 (40%)	55 (45%)
Single variable effect	10 (10%)	2 (13%)	15 (12%)
Total	102 (100%)	15 (100%)	122 (100%)

Table 2. Classification of species whose interaction between plant and bird diversity had the same direction (see Figure 1 for details). The classification was made based on the combination of the direction of each predictor's slope (nichedist – the distance to the niche centroid, plant and bird diversity) as regressed with the response variable (centrality) derived from the global model.

Slope direction Plant and Bird Diversity	Slope (nichedist): negative	Slope (nichedist): no effect	Slope (nichedist): positive
Negative	57 (90%)	5 (83%)	36 (65%)
Positive	6 (10%)	1 (17%)	19 (35%)
Total	63 (100%)	6 (100%)	55 (100%)

Table 3. Classification of species whose interaction between plant and bird diversity had opposite directions (see Figure 1 for details). The classification is made based on the combination of the direction

of each predictor's slope (nichedist – the distance to the niche centroid, plant and bird diversity) as regressed with the response variable (centrality) derived from the global model.

Slope direction Plant and Bird Diversity	Slope (nichedist): negative	Slope (nichedist): no effect	Slope (nichedist): positive
Plant diversity (-)/ Bird diversity (+)	18 (62%)	6 (100%)	29 (58%)
Plant diversity (+)/ Bird diversity (-)	11 (38%)	0 (0%)	21 (42%)
Total	29 (100%)	6 (100%)	50 (100%)

Figure captions

Figure 1. Schematic representation of the possible scenarios for the interplay among climatic niche space, and the number of co-existing bird and plant species (i.e., bird and plant diversities) in determining individual species' centrality. The variables bird diversity (B), plant diversity (P) and the distance to the climatic niche centroid were used to explain the centrality of bird species with a cross-random mixed-effect model. For either direction of the effect of the climatic niche space (a), centrality does not change with bird and plant diversities (b), bird and plant diversities have similar effects on centrality (c), bird and plant diversities have opposing effects on centrality (d), or only bird or plant diversity has a significant effect on centrality (e).

Figure 2. Methodological workflow. The steps after downloading the data used in this article are given in the text boxes. The climatic niche centroid of each network was calculated by first characterizing the species' climatic niche space based on its geographic distribution (blue dots) and then estimating the distance from the network's position (red dots), defined by the conditions at its coordinates (a), to the centre of such niche space (b). Bird and plant diversity were obtained from individual seed-dispersal networks as the number of co-existing birds and plants, respectively (c).

Figure 3. Statistical relationships between bird species' centrality (PC1) and the evaluated predictor variables from the global cross-random mixed-effects model.

Figure 4. Simulated median ± confidence interval (95%) of the global model's fixed effect terms as calculated from their posterior distributions. The combination of variable names indicates the interaction between them.