Bird species’ centrality in seed-dispersal networks varies within 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 mechanisms driving network organization. Using data for 157 bird species from all continents, we evaluated the variation of species' centrality within local networks across species' climatic niches (occupied climatic conditions) and in response to proxies of competition (number of co-occurring bird species) and resource availability (number of co-occurring plant species). We found that species' centrality increases towards the climatic niche centroid for most bird species. The effect of competition on species' centrality was usually opposite to that of resources (i.e., when one was positive, the other was negative), regardless of the network's position within the climatic niche space. Taken together, our results show that species' centrality within seed-dispersal networks is influenced by the climatic suitability of network location, supporting the niche centrality hypothesis, whereas competition and resource availability exert opposing effects.

Introduction

A broadly recognized pattern in ecology 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 and are connected within complex networks of interactions, where keystone species tend to be more central (Martín González *et al.* 2010; Mello *et al.* 2015) by interacting with many other species via multiple direct and indirect pathways (Escribano-Avila *et al.* 2018). Such central species may also influence the co-evolutionary convergence of traits of interacting partners (i.e. trait matching; Guimarães-Jr et al., 2011). Giving their importance, the extinction of central species from networks could increase coextinctions and decrease network robustness (Emer *et al.* 2018). Evaluating species' centrality requires moving from the "network" to the "species" analytical perspective. Contrary to evaluating the spatial variation of interactions as described by network properties at particular sites or communities with the "network" perspective (Dupont *et al.* 2009; Perea *et al.* 2013; Trøjelsgaard & Olesen 2013), the "species" perspective involves the consideration of those networks where the focal species participates across its geographical distribution. From this perspective, species' ecological attributes such as their climatic (Grinellian) niches (Soberón 2007) and phenotypic traits (e.g., Tobias *et al.* 2022) can be combined with their network properties (i.e. centrality) and those derived from their geographic co-occurrence (i.e., competition and resources availability). In combination, these species' properties allow determining the spatial variation in how species interact with each other and their drivers at broad spatial scales (Windsor *et al.* 2022).

Because the geographic distribution of species usually covers different environmental conditions at distinct localities, their biotic interactions can vary along environmental gradients within their geographic ranges (e.g., partner composition, frequency, and dependency) (Dehling *et al.* 2014). In this sense, the number of co-occurring species (i.e., those with overlapping ranges) within the range of a focal species determines its diversity field. Accordingly, if we consider species from the same guild or their resources, the set of species that have been reported to co-occur with a focal species can be used to define its interaction field and thus potential competitors or resources, respectively (Sánchez-Barradas *et al.* 2023). These concepts are important in understanding the variation in species centrality in mutualistic networks, since a focal species can only interact with those species present in its diversity field, and not with those that are not present therein because of co-occurrence limitations imposed by geographic and ecological boundaries (Martins *et al.* 2022).

There is evidence that the variation in biotic interactions along species' geographic ranges could be determined by population characteristics (Gaston 2009). For instance, species abundance is usually considered to 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 [CPH]; Brown 1984; Martínez-Meyer *et al.* 2013; Pironon *et al.* 2017). The CPH has been systematically tested with discordant outcomes in geographic space, such that species abundances are not always higher at the centre of their geographic distributions (Brown, 1984, Sagarin & Gaines 2002; Lira-Noriega & Manthey 2014; Pironon *et al.* 2015; Dallas *et al.* 2017; Santini *et al.* 2019). 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 arrangement of climatic conditions with higher population performance and abundance at the niche centroid where optimal conditions are met (Hoffmann & Blows 1994; Lira-Noriega & Manthey 2014; Maguire 1973; Martínez-Meyer *et al.* 2013). Because species relative abundance is one of the main factors that determines their role in a network (Krishna *et al.* 2008; Vázquez *et al.* 2007), it thus seems plausible that the variation in species' centrality in ecological networks could be associated with the location of those networks along the climatic niche space, as determined by the geographic distribution of a focal species.

Competition is also important for determining species' centrality within networks because it may increase the energetic costs of resource acquisition (Hall *et al.* 1992; MacArthur 1960), but also because it can lead to species displacement by stronger competitors and shape the organization of mutualistic networks (Dáttilo *et al.* 2014; de M. Santos *et al.* 2012). Moreover, competition reduces the ability of each species to adapt to local environmental conditions at their range limits (Case & Taper 2000). Thus, a species may be more or less central in networks depending on the number of co-existing competitors across its range (Cazelles *et al.* 2016; Pedraza & Bascompte 2021). In the same vein, species co-occur with different sets of resource species across their range, determining the potential interaction links that a focal species can establish in the networks it participates across its occupied localities (Dehling *et al.* 2022). Therefore, the interaction field of a species can be used to define the number of potential competitors as well as resources across its geographic range (Sánchez-Barradas *et al.* 2023). Assuming the existence of areas within a species' geographic range where climatic conditions are optimal allowing it to reach high centrality, an intriguing and poorly understood issue is whether competition and resources influence the chances of a species to become more central in these areas.

Using a species perspective within seed-dispersal networks, we here investigated the variation in bird species' centrality along their climatic niches and how it is related to competition (measured as the number of co-occurring bird species, i.e., the diversity field of bird species) and resource availability (measured as the number of co-occurring plant species, i.e., the diversity field of plant species). We chose seed-dispersal networks because they are excellent model systems to evaluate species' ecosystem functions (Schleuning *et al.* 2015) and because birds have wide distributions and are the main seed dispersers, establishing mutualistic interactions with most angiosperms' families, an interaction that is fundamental for biodiversity maintenance (Fleming & 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 put together datasets of global relevance.

In this study, we used a dataset of 314 seed-dispersal networks with 1264 bird species and 2903 plant species/morphospecies from 11 biographical regions to ask how bird species centrality from seed-dispersal networks varies within their climatic niche spaces. Our hypothesis was that the centrality of each focal bird species within seed-dispersal networks is higher at the centre of the climatic niche space, according to the predictions of the CPH. Moreover, we envisioned four possible scenarios for the interplay among climatic niche space, competition, and resource availability in determining species' centrality (Table 1). In scenario *a*, the centrality of a focal species should be higher at the centre of its climatic niche with no effect of competition and resource availability. In this case, a focal species' centrality is higher where the climatic conditions are optimal, independently of its biotic interactions. In scenario *b*, a focal species is more central towards its niche centre, but its centrality is also influenced by competition and resource availability acting in opposite directions, with the focal species being more central towards the niche centre where more resources are available and there is less competition or vice-versa. In scenario *c*, both resources and competition are higher at the niche centre, so that the focal species is more central when overall diversity is high. Alternatively, in scenario *d*, a focal species may not be more central at its niche centre, but at the niche border, where less resources are available and because competition may reduce the access to resources for the populations at the centre of the climatic niche space. Overall, these four 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 searched in the repositories GitHub (https://github.com) and DRYAD (https://datadryad.org).

For each bird species in the dataset, we downloaded the geographic ranges (i.e., extents of occurrence) from the Birdlife project (www.birdlife.org). We then selected 157 focal species (Table S1) from thirty-seven families based on two criteria that aimed to minimize sampling bias (Borregaard & Rahbek 2010): 1) species that were present in at least five networks, considering the minimum number of degrees of freedom needed in our data analysis (see below); and 2) species whose occurrences in the networks were not spatially clustered within their geographic ranges. For the second criterium, we visually inspected the spatial distribution of networks where each focal species participates within their geographic ranges.

Species centrality in networks

Species centrality was 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. 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 to those species that are more central in a network, as has been suggested in previous studies (Burin *et al.* 2021; Dáttilo *et al.* 2016; Guimarães *et al.* 2017; Maia *et al.* 2019). The centrality values were calculated for each species in the individual networks. Because each species has been present in at least five networks, centrality values were calculated for each species in each network it occurs. For convenience when interpreting the PC1 values and ranking species 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.

Explanatory variables

Our predictor variables of species' centrality were the position of each network within the climatic niche space relative to its centre (see below), resource availability and competition, as measured by the number of co-occurring plant and bird species in each network, respectively (Figure S1). The number of potential competitors as well as resources was defined by the number of both plant and bird species in the interaction field of a focal species (Sánchez-Barradas *et al.* 2023).

We used the ellipsoid envelope model (EEM, Farber & Kadmon, 2003) to characterize species' climatic niches based on their geographic occurrences. EEM yields a closer approximation to a fundamental niche estimate than other methods that fit arbitrary shapes to the occurrence points in climatic space (Jiménez *et al.* 2019). Furthermore, 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). 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). 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). EEMs were built for each focal species using the ellipsenm R package (Cobos *et al.* 2022).

The environmental variables used to characterize species niches in EEM were obtained from the WorldClim v.2.1 (Fick & Hijmans 2017) at a resolution of 10' (~18.5 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 climatic niche spaces (Nuñez-Penichet *et al.* 2021).

To characterize climatic niches of species it is important to delimit the accessible area of a modelled species prior to the modelling (Barve *et al.* 2011). For that, we determined the accessible area as the convex polygon with 100 km buffer around the occurrence points of each species. The bioclimatic variables were masked to that area. Then, we built EEM using the default parameters of the *ell_model* function (modelling method "covat", confidence level = 95% and single replicates) of the R package ellipsenm (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 centroid, i.e., the values that characterized the centre of species climatic niche and that can be interpreted as the optimal conditions for species' performance (Hoffmann & Blows 1994; Soberón 2007).

Finally, to obtain the distance of each network to the centroid of the species' climatic niche (i.e., network's niche position), we calculated the Mahalanobis distance of the climatic conditions where each network was located to those conditions at the niche centroid. Based on the distribution of values of all Mahalanobis distances, as assessed with a histogram, we excluded those networks with distances 25% greater than the median values (3rd quartile), as they were visually inspected as possible outliers. 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.

Predictor variables were not correlated to each other across all networks. Pearson's correlation between resources and niche position was $r = -0.05$ ($p = 0.002$), between competition and niche position was $r = -0.002$ ($p = 0.91$) and between competition and resources was $r = 0.46$ ($p < 0.001$).

Data analysis

We used simple and multiple linear regression models to test the relationship between species' centrality (PC1; dependent variable) and the explanatory variables network distance to niche centroid, competition, and resources availability. All variables were scaled prior the analyses using the function "scale", from the base R package. The variables competition and resources availability were tested with their raw or log-transformed values in independent models for each species to fit the assumptions of normality. Model selection was done by choosing the one with the lowest Akaike Information Criterium corrected for small samples (AICc; Anderson & Burnham 2002). All three predictor variables were kept in the models at a first moment. Then, we proceeded with a stepwise selection of the variables on the previously selected best models using the function "step", from base R. The standardized beta coefficients of each species model (only models significant at $r2 > 0.2$ and $p < 0.05$) were then classified in the hypothetical scenarios presented in Table 1.

We also tested whether the centrality values of each focal species (PC1, dependent variable) differed among scenarios (independent variable) using one-way Analysis of Variance (ANOVA) followed by the post-hoc Tukey test. This analysis was done to test whether species centrality values (i.e., high, or low centrality within the range of all species centrality values) were an indicator of each focal species relation with the tested variables.

Results

Regression models were statistically significant for 90 of the 157 species studied (58%). Out of the species with significant models, the most representative families were Thraupidae (14 species, 15.5%) and Tyrannidae (10 of species, 11.1%). In the statistically significant models, the standardized beta coefficients for resources showed no directional trend when compared to standardized beta coefficients for niche position (Figure 1a); while the standardized beta coefficients for competition were negatively related with the standardized beta coefficients for niche position (Figure 1b).

Effects of niche, competition, and resources on species' centrality

For the 90 bird species whose regression models were significant, we found that 27 of them (30%) showed higher centrality towards the centre of their niche spaces; 17 species (18.9%) were more central towards the border of their niche spaces; and for 45 species (50%) centrality was not related to the niche position (Figure 2).

Only four species (*Camptostoma obsoletum* [Tyrannidae], *Dumetella carolinensis* [Mimidae], *Euphonia chlorotica* [Fringillidae] and *Phoenicurus phoenicurus* [Muscicapidae]) were more central at the niche centre without having significant standardized beta coefficients for competition and resource variables (scenario *a*; Figure S2a). For 20 species whose resources and competition had significant opposite effects when being more central at the niche centre (scenario *b*), six of these had a negative effect of resources, meaning more resources and less competition at the niche centre, whereas seven species had a positive effect of resources, meaning more resources and less competition at the niche border (Figure S2b). The other seven species had no resource effect (standardized effect equals zero).

Under scenario *c*, the direction of the standardized beta coefficients was the same for three species, meaning that competition and resources were also positively related to centrality at the niche centre (Figure S2c). An exception was *Pachyramphus polychopterus* (Tityridae), who had negative direction for all variables, meaning that its centrality was highest at the niche centre, where there was less competition and less resources. Seventeen species fell within scenario *d*, with their centrality being positively related to the niche position, meaning that species' network centrality increased with the distance to the niche centroid (Figure 2d). For these species, the majority had opposite effects of resources and competition, so that when one was positive, the other was negative (and vice-versa). Only the species *Colius striatus* (Coliidae) had both competition and resources with same effect direction (negative).

The other half of bird species showed no relationship between their network centrality and niche position, being only affected by resources and/or competition (Figure S3), with varying effects of these two variables. Apart from *Tangara xanthocephala* (Thraupidae), which had positive standardized beta coefficients for both competition and resources, all the other species had opposite effects of resources and competition.

The ANOVA test for differences in species' centralities between scenarios (Figure 3A) showed that centrality values of species classified within each the four scenarios were not significantly different. The mean centrality of the 157 initially selected species was similar to that of the 90 species significantly related to the evaluated variables (4.48 and 4.49, respectively; Figure 3B).

Discussion

Our results revealed how the interplay between climatic niche position, resource availability, and intraguild competition can define the variation of the role that bird species play within seed dispersal networks. Previous studies have addressed how centrality of bird species in seed-dispersal networks is related to their geographic, evolutionary and environmental characteristics (Burin *et al.* 2021; Moulatlet *et al.* 2023; Pigot *et al.* 2016), but, 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 (CPH) in climatic space (Martínez-Meyer et al. 2013). We could evaluate the variation in centrality of focal species in multiple networks (minimum 6 and maximum 79) within their climatic niche spaces, and thereby show that the variation in species' centrality suggests the existence of climatically suitable areas where species can achieve high abundance and high centrality, which might form the substrate for evolutionary and ecological dynamics.

Centrality closer to the niche centre and the effect of competition and resources

Our results showed that for 30% of the evaluated bird species the centrality was higher 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 allow species to attain high abundances (Martínez-Meyer et al. 2013, Weber et al. 2017, Osorio-Olvera et al. 2020). Indeed, species roles may be highly dictated by species' abundances in the network they participate (Laurindo *et al.* 2020; Pizo *et al.* 2022). Previous studies suggested that species can be considered to be at their ecophysiological optimum at the niche centre (Hoffmann & Blows 1994) when compared to the niche border, where climatic conditions would not be adequate (Perez-Navarro *et al.* 2022; VanDerWal *et al.* 2009). Thus, this result is an agreement with the predictions of the CPH, when applied to the niche space instead of the geographical space (Osorio-Olvera et al. 2020).

For the species under scenarios *b* and *c*, centrality did increase with increasing resources towards the climatic niche centroid. 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 & Perfectti 2012), but that the resources are also a key factor in determining species centrality along the niche space. On one hand, resources might define species centrality when more resources increase the chances of a focal species to establish links with more plant partners and to become a generalist (Dehling *et al.* 2014). On the other hand, more resource may increase the chances of specialization (i.e. making species less central) between birds and plants by increasing the possibilities of trait-matching, especially in resources-rich networks (Medeiros *et al.* 2018), although specialization has also been associated with lower resource availability (Schleuning *et al.* 2012). As we could not find differences in the centrality values for the species classified into our four hypothetical scenarios, indications of specialization could not be tested. Thus, our results only suggest that increasing resources availability may help to make a species more important in its interactions towards its niche centre, effectively combining the benefits of both abiotic and biotic factors. It is important to note that we considered resource availability as the total number of 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 at least while still informative based on empirical information.

We also found that for the species classified under the scenarios *b* and *c*, it was possible that centrality was higher towards their niche centre when competition was lower at that same position. Indeed, we predicted that when competition was the highest at the niche centre, species would be more central in networks away from this centre (i.e., towards their niche border), as competition would reduce 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 need to include competition as a driving factor of varying ecological interactions across species geographic ranges has been recently highlighted (Early & Keith 2019), but few attempts to map those interactions have been made so far (Braz *et al.* 2020). Intraguild competition has been proposed as a limiting factor when resources are not sufficient for ecologically similar species (MacArthur 1960; Palmer *et al.* 2003). If that assumption holds true for seed-dispersal networks, competition with ecologically similar species may define centrality, as higher competitors may be in advantage for resource acquisition and may even cause the displacement of weaker competitors (Dáttilo *et al.* 2022; de M. Santos *et al.* 2012; Maia *et al.* 2019).

Centrality at the niche border and the effect of competition and resources

Despite several of the evaluated species showed higher centrality towards their niche centre, as predicted by the CPH in climatic niche space, around 18% of the species (scenario *d*) showed that their centrality was highest towards the niche border. Contrary to our predictions, for 40% of these species, competition was also the highest at the niche border, so competition does not seem to negatively affect the role of these species in their interaction networks. Instead, the higher co-occurrence of species in a network may be related to the role executed by species. For example, an increased number of co-occurring species may lead to a high centrality of a focal species when the competitors tend to be more specialized (Bascompte *et al.* 2003).

No niche effect with opposite effect of competition and resources

Results for half of our evaluated species (n = 45) did not fit any of our scenarios. Indeed, for these species there was no effect of the occupied climatic conditions in their centrality, but the presence of competitors and availability of resources did affect their centrality. This result highlights the importance of interspecific biotic interactions in driving specie's centrality, which 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 competition in the evaluated networks may outpace the effects of climatic conditions in determining the areas in which species can be central in their interactions across its climatic niche space.

Despite centrality values being quite variable among the evaluated species, no difference in species' centrality values were detected among the proposed scenarios. As such, independent of potential differences among species and their particular values of centrality (low or high, on average), the interactive role of species across their occupied networks is influenced by the climatic conditions of such network locations relative to the optimal conditions for the species (i.e., their niche centroid). Accordingly, the effect of climatic suitability on species could be extended to other aspects of their performance beyond population dynamics (e.g., abundance structure, as originally proposed by the Centre-Periphery hypothesis in climatic space; Martínez-Meyer et al. 2013) such as their ecological role and importance and its impact on evolutionary dynamics (Thompson 2005; Burin *et al.* 2021).

Ecological meaning of the scenarios

Our approach can lend support to the theory of the geographic mosaic of coevolution (Thompson, 2005). Applying the assumptions of the geographic mosaic of coevolution, 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. In this case, hotspots would be those areas where the centrality of a focal species increases with resources availability and decreases with competition in a network, whereas coldspots of interaction would then be those areas where centrality is either negatively or not related to resource availability and positively related to competition. The importance of mapping the conditions where species become more central is 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 approach of geographic mosaic of coevolution to study 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

In this study 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 between resource availability and competition. We also found that these two factors can have opposite or the same direction effects in explaining centrality depending on the position of the network within the species' climatic niche space. Actual information on resource and competition variation, beyond the proxies used here, is scarce in the literature and should be considered in further studies, as we found that they are key factors in determining species centrality. By conducting studies including other taxa and types of interactions that help us understand the factors that determine the spatial and climatic variation of species' centrality will contribute to the understanding and potential conservation of species and their ecosystem services.

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Table

Table 1. Schematic representation of the conceptual hypothesis tested in this study with the respective references. The variables competition (C), resources (R) and the distance to the climatic niche centre (N) were used to explain the centrality of a focal species in multiple regression models. Depending on the direction and slope of the relationship between centrality and the variables (positive or negative [regular lines]), species could be classified into four hypothetical scenarios (a, b, c, and d).

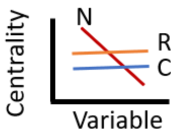
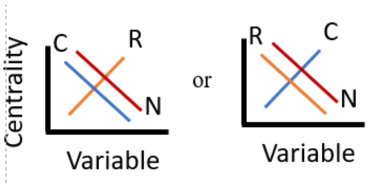
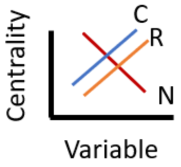
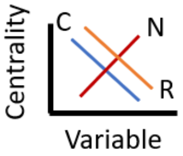
Hypothesis	Scenarios	Graphical representation	References
Centrality is higher at the centre of the niche space	a) No effects of resources and competition		(Brown 1984; Martínez-Meyer *et al.* 2013; Pironon *et al.* 2017)
	b) Opposite effect/direction of resources and competition		(Case & Taper 2000; Hall *et al.* 1992; MacArthur 1960)
	c) Same effect/direction of resources and competition		(Guimarães Jr *et al.* 2011)
Centrality is higher at the border of the niche space	d) Resources and/or competition drives species away from the niche optima		This study

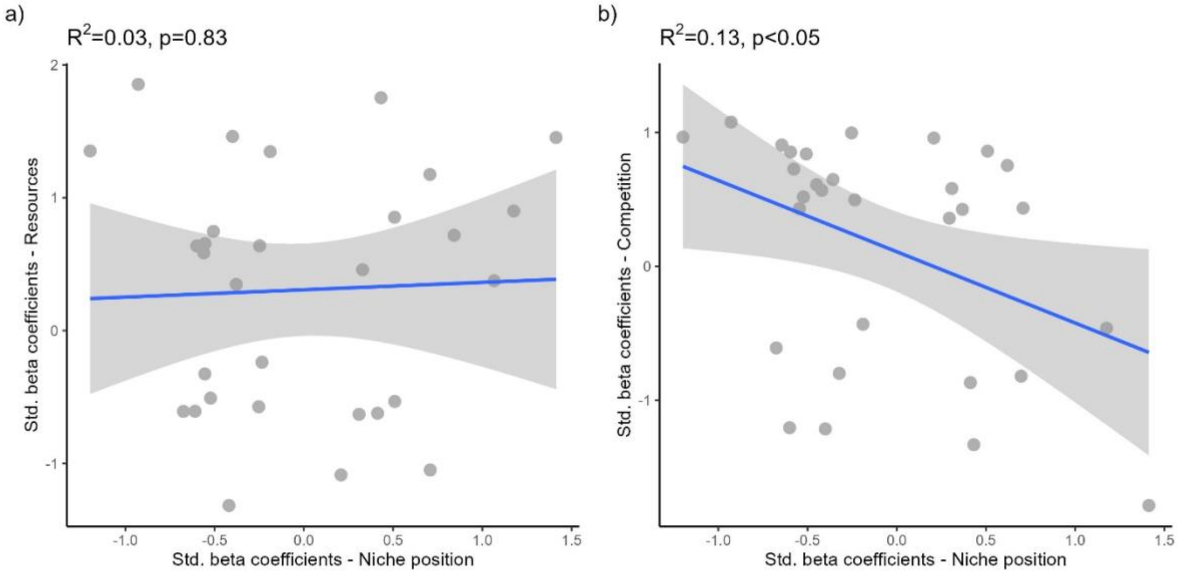
Figure captions

Figure 1. Relation between the standardized beta coefficients from regression models between resources and niche position (a), and between competition and niche position (b), as obtained for each focal species.

Figure 2. Standardized beta coefficients for each focal species as obtained from multiple regression models. For each species, the standardized beta coefficients can be positive or negative, and the magnitude of the value in relation to zero (dashed line) indicates the effect size. Standardized beta coefficients are shown for the variables niche position (a), competition (b) and resources (c) in relation to the mean centrality values in all the networks the species participated. Generalized additive models were adjusted for the relationship between mean centrality values and each of the variables.

Figure 3. Mean centrality values as represented by a) the distribution of the mean centrality values of each focal species in the hypothetical scenarios a, b, c and d explained in Figure 1 plus the scenario where there was no significant relation between a focal species centrality and the distance to the niche centre (No niche effect); and b) the count of 157 species initially selected (grey bars) and the 90 species that were significantly related to the tested variables (red bars).

Fig. 1



a)
R^2=0.03, p=0.83
Std. beta coefficients - Resources
Std. beta coefficients - Niche position
2
1
0
-1
-1.0
-0.5
0.0
0.5
1.0
1.5
b)
R^2=0.13, p<0.05
Std. beta coefficients - Competition
Std. beta coefficients - Niche position
1
0
-1
-1.0
-0.5
0.0
0.5
1.0
1.5

Fig 2.

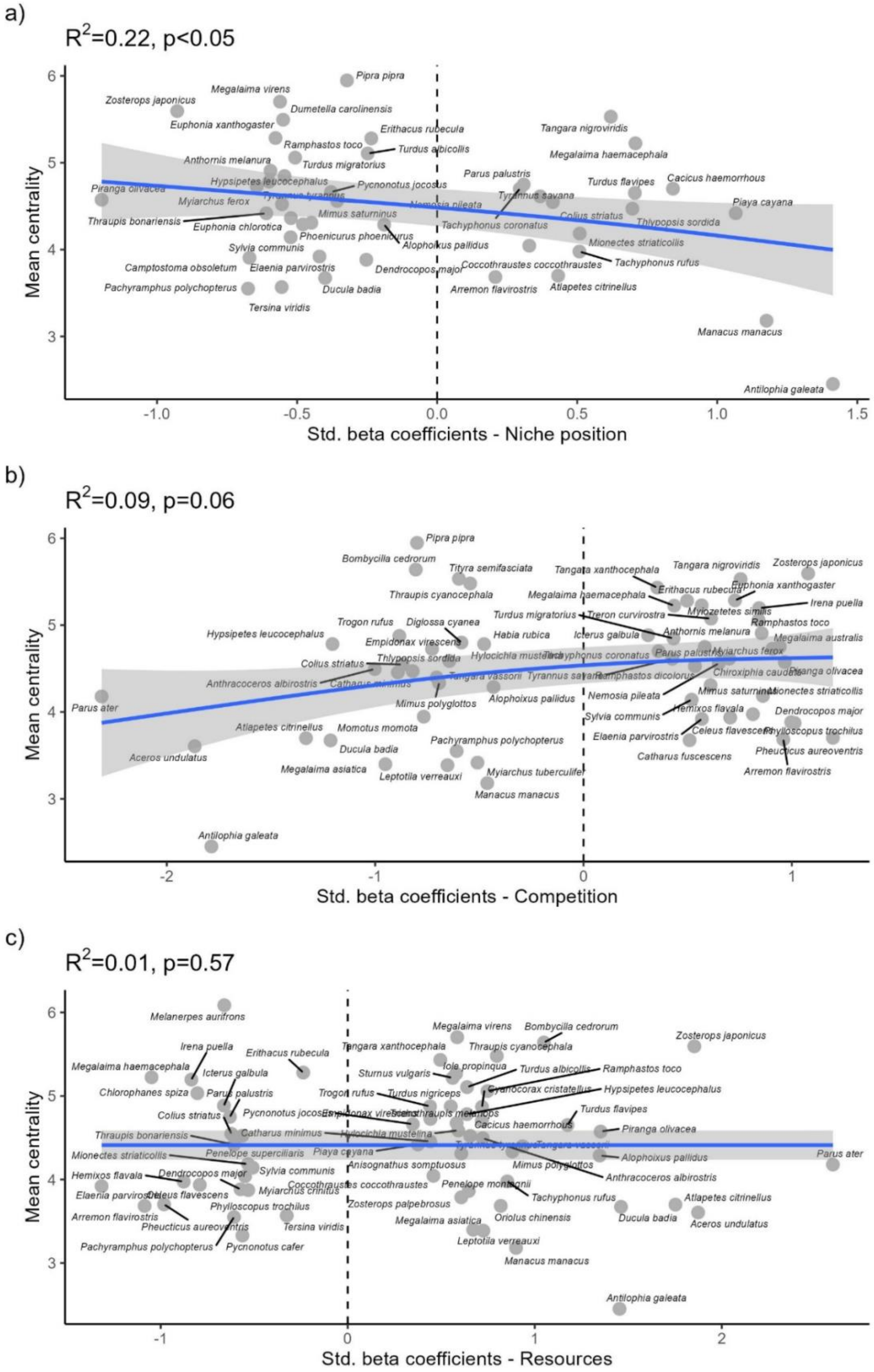
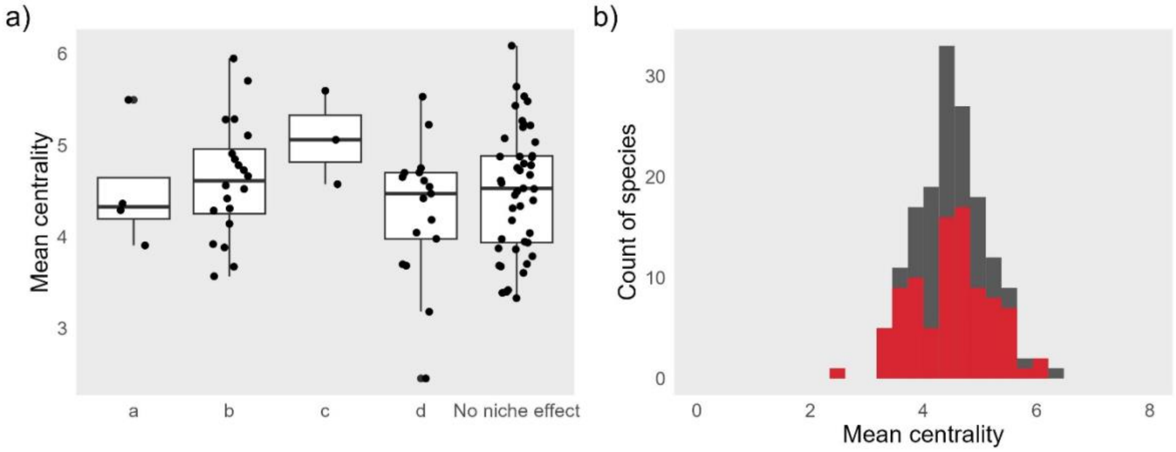

a)
R²=0.22, p<0.05
Mean centrality
6
5
4
3
Std. beta coefficients - Niche position
-1.0
-0.5
0.0
0.5
1.0
1.5
Pipra pipra
Megalaima virens
Zosterops japonicus
Dumetella carolinensis
Euphonia xanthogaster
Erithacus rubecula
Tangara nigroviridis
Ramphastos toco
Turdus albicollis
Megalaima haemacephala
Anthornis melanura
Turdus migratorius
Parus palustris
Hypsipetes leucocephalus
Pycnonotus jocosus
Turdus flavipes
Cacicus haemorrhous
Piranga olivacea
Tyrannus tyrannus
Myiarchus ferox
Nemosia pileata
Tyrannus savana
Piaya cayana
Colius striatus
Thraupis bonariensis
Mimus saturninus
Thlypopsis sordida
Euphonia chlorotica
Tachyphonus coronatus
Phoenicurus phoenicurus
Mionectes striaticollis
Sylvia communis
Alophoixus pallidus
Tachyphonus rufus
Camptostoma obsoletum
Elaenia parvirostris
Dendrocopos major
Coccothraustes coccothraustes
Pachyramphus polychopterus
Ducula badia
Arremon flavirostris
Atlapetes citrinellus
Tersina viridis
Manacus manacus
Antilophia galeata
b)
R²=0.09, p=0.06
Mean centrality
6
5
4
3
Std. beta coefficients - Competition
-2
-1
0
1
Pipra pipra
Bombycilla cedrorum
Tityra semifasciata
Tangara xanthocephala
Tangara nigroviridis
Zosterops japonicus
Thraupis cyanocephala
Megalaima haemacephala
Erithacus rubecula
Euphonia xanthogaster
Irena puella
Turdus migratorius
Treron curvirostra
Myiozetetes similis
Trogon rufus
Diglossa cyanea
Ramphastos toco
Hypsipetes leucocephalus
Empidonax virescens
Habia rubica
Icterus galbula
Anthornis melanura
Megalaima australis
Hylocichla mustelina
Tachyphonus coronatus
Parus palustris
Myiarchus ferox
Colius striatus
Thlypopsis sordida
Chiroxiphia caudata
Piranga olivacea
Tangara vassorii
Tyrannus savana
Ramphastos dicolorus
Anthracoceros albirostris
Catharus minimus
Mimus saturninus
Mionectes striaticollis
Parus ater
Alophoixus pallidus
Nemosia pileata
Mimus polyglottos
Hemixos flavala
Dendrocopos major
Sylvia communis
Atlapetes citrinellus
Momotus momota
Celeus flavescens
Phylloscopus trochilus
Elaenia parvirostris
Pachyramphus polychopterus
Ducula badia
Pheucticus aureoventris
Aceros undulatus
Catharus fuscescens
Megalaima asiatica
Myiarchus tuberculifer
Arremon flavirostris
Leptotila verreauxi
Manacus manacus
Antilophia galeata
c)
R²=0.01, p=0.57
Mean centrality
6
5
4
3
Std. beta coefficients - Resources
-1
0
1
2
Melanerpes aurifrons
Megalaima virens
Bombycilla cedrorum
Zosterops japonicus
Irena puella
Erithacus rubecula
Tangara xanthocephala
Thraupis cyanocephala
Megalaima haemacephala
Icterus galbula
Sturnus vulgaris
Iole propinqua
Turdus albicollis
Ramphastos toco
Chlorophanes spiza
Parus palustris
Trogon rufus
Turdus nigriceps
Cyanocorax cristatellus
Hypsipetes leucocephalus
Turdus flavipes
Colius striatus
Pycnonotus jocosus
Empidonax virescens
Trichothraupis melanops
Cacicus haemorrhous
Thraupis bonariensis
Catharus minimus
Hylocichla mustelina
Piranga olivacea
Tyrannus tyrannus
Tangara vassorii
Mionectes striaticollis
Penelope superciliaris
Piaya cayana
Anisognathus somptuosus
Mimus polyglottos
Alophoixus pallidus
Parus ater
Hemixos flavala
Dendrocopos major
Sylvia communis
Anthracoceros albirostris
Myiarchus crinitus
Coccothraustes coccothraustes
Penelope montagnii
Elaenia parvirostris
Celeus flavescens
Tachyphonus rufus
Phylloscopus trochilus
Zosterops palpebrosus
Atlapetes citrinellus
Arremon flavirostris
Megalaima asiatica
Oriolus chinensis
Ducula badia
Aceros undulatus
Pheucticus aureoventris
Tersina viridis
Leptotila verreauxi
Pachyramphus polychopterus
Pycnonotus cafer
Manacus manacus
Antilophia galeata

Fig 3.


a)
Mean centrality
6
5
4
3
a
b
c
d
No niche effect
b)
Count of species
30
20
10
0
0
2
4
6
8
Mean centrality