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DOES NICHE CENTRALITY PREDICT TRAIT VARIATION IN THE ANTIOQUIA WREN?

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Abstract. The niche centrality hypothesis predicts that individuals near the niche centroid have higher fitness due to more favorable environmental conditions. In this study, we evaluated the effect of the niche structure of the Antioquia Wren on 20 different traits grouped into four datasets: morphology, genetic diversity, coloration and acoustics. We tested the relationship with distinct niche configurations using minimum volume ellipsoids, and evaluated the relationship between the distance to the niche centroid and trait values through ordinary linear and generalized linear squared regression models. We found positive relationships for variables associated with beak morphology and crown feathers hue. Conversely, we found a negative relationship with birdsong frequency and the distance between longest primary and first secondary flight feathers. All effects of the niche structure on traits were weak (<0.2). We found no consistency in the relationship between niche structure and the remaining 13 traits. We identify potential mechanisms underlying both positive relationships and the absence of trait–niche relationships. Our findings emphasize that factors such as biotic interactions, climatic heterogeneity, range size, niche breadth, centroid position, and intrinsic trait variability are likely to shape how species conform to the niche centrality hypothesis.

Key words.—Birdsong, color, minimum volume ellipsoid, genetic diversity, morphology, niche structure.

Introduction

Ecological traits offer insights into how species adapt to their environments and their roles within the ecosystem (Webb et al., 2010). The study of individual or population variation in these traits along geographical, trophic, and climatic gradients provides information about organismal responses to environmental pressures and structural limitations (e.g., Martínez-Gutiérrez et al., 2018; Delhey et al., 2019; Mota-Vargas et al., 2023). The relationship between functional traits and the environment is the result of historical selective pressures, individual and population variability, and their consequences in terms of fitness. These relationships have been conceptualized within ecological niche theory (e.g., Kearney et al., 2010; Yañez-Arenas et al., 2012; Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2020).

The ecological niche has been defined as the interaction between a species and all aspects of its biotic and abiotic environment that allow it to maintain viable populations over time (Hutchinson, 1957; Soberón, 2007). Such interactions may limit species' ranges through the movement of individuals (Soberón, 2007), or through interactions between morphological traits and occupied environments (i.e., realized niche; Maguire, 1973; Rejmanek and Jenik, 1975). In 1973, Maguire proposed that the niche has an internal structure, in which the best-adapted individuals

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or populations are found near optimal environmental conditions, in other words, the species' niche centroid. This is known as niche centrality hypothesis and serves as reference for analyzing intraspecific variation in individual and population traits such as abundance, genetic diversity, or morphology (Ingram et al., 2018).

The conceptualization of the niche centrality hypothesis encompasses individuals, populations, or whole species responses to environmental gradients (Maguire, 1973). Although different studies have examined the relationship between population trait variation and niche structure, most of them focus primarily on abundance (e.g., Yañez-Arenas et al., 2012; Martínez-Meyer et al., 2013), population size (e.g., Osorio-Olvera et al., 2019; Cordier et al., 2025), and genetics (e.g., Lira-Noriega and Manthey, 2014; Diniz-Filho et al., 2015; Ochoa-Zavala et al., 2022). Therefore, there is a tendency to overlook functional traits that may vary in response to environmental changes and reflect differences in fitness among individuals. These functional traits can be associated with the species morphology, acoustic signals, or coloration (Delhey et al., 2023; Zimova et al., 2023; Appleby et al., 2024), which have not yet been examined within the context of the niche centrality hypothesis.

Research on morphological traits has shown that differences in body size often arise in response to environmental factors, reflecting adaptations to abiotic conditions that may be linked to variation in resource availability and individual condition (James, 1982). This variation includes changes in wing length in environmental gradients (Yom-Tov et al., 2006), body mass associated with the expansion and contraction of geographical ranges (Bradshaw et al., 2014), and variation in bill musculature as an evolutionary adaptation (Deeming et al., 2024). Similarly, environmental conditions can affect how birds transmit and interpret acoustic signals (Medina and Francis, 2012). Birdsong characteristics, such as song performance, can impact individuals' survival (Rivera-Gutierrez et al., 2010b). Additionally, larger adult song repertoires are positively associated with better individual condition (Gil and Gahr, 2002) and greater energy investment in singing, reflected by higher frequency peaks and broader bandwidths (Kroodsma, 2017), as well as more song complexity (Bradbury and Vehrencamp, 2011; Catchpole and Slater, 2008). Moreover, there is a well-documented relationship between a bird's plumage color and individual quality, measured through variables such as hue (Saks et al., 2003), brightness (D'Alba et al., 2011), and saturation (Butler et al., 2011). These variables are related to carotenoid pigments, which are crucial for maintaining the nervous and immune systems in birds (Saks et al., 2003).

Here we analyzed how different trait sets (i.e., morphological, color, genetics, and acoustics) varied as a function of the distance to the niche centroid of the Antioquia Wren (*Thryophilus sernai),* an endangered and microendemic Colombian bird species that inhabits dry and semi-deciduous forests along the Cauca River canyon in the department of Antioquia (Lara et al., 2012; Fjeldså, 2020). This species is an ideal model to evaluate the niche centrality hypothesis due to its restricted distribution, its position along a precipitation gradient, and the availability of information on various ecological traits (e.g., Lara et al., 2012; Zapata et al., 2020; Betancur Ortiz et al., 2024; Restrepo-Arias et al., 2025). We explored whether morphological, color, genetic, and acoustic attributes of the Antioquia Wren were associated with its climatic niche structure, as predicted by the niche centrality hypothesis (Maguire, 1973). Additionally, we examined the consistency of the trait-centroid relationship across various niche configurations (e.g., different environmental predictors) to investigate how different niches may influence our understanding of the centrality hypothesis.

We hypothesize that optimal environmental conditions near the niche centroid enhance individual performance, leading to better conditions expressed as i) larger body size, longer legs, peak, and wings, related to more resource availability; ii) higher genetic diversity; iii) higher birdsong performance (represented by the bandwidth, frequency, and duration) reflecting higher energy deployment and song complexity exhibited by higher entropy values; iv) higher hue and brightness but less saturation which are related with carotenoids and individual quality. If these predictions are correct, then evaluating traits in the context of niche structure would provide an indirect estimate of population status. Also, understanding the variation in ecological traits in relation to niche structure could be an interesting approach to analyze how different environmental pressures may influence the state of a particular trait.

Materials and Methods

Methodological overview

We captured Antioquia Wren individuals during eight years in different localities. We also measured several morphological traits, including weight, beak width and height, tarsus length, wing length, hallux length, and tail length. We then collected blood samples for molecular analysis and estimated individual heterozygosity using microsatellites. Additionally, when possible, we collected feather samples to assess color characteristics such as brightness and spectral saturation. Furthermore, we recorded the songs of different individuals to analyze acoustic traits, including peak frequency, bandwidth, and duration. To

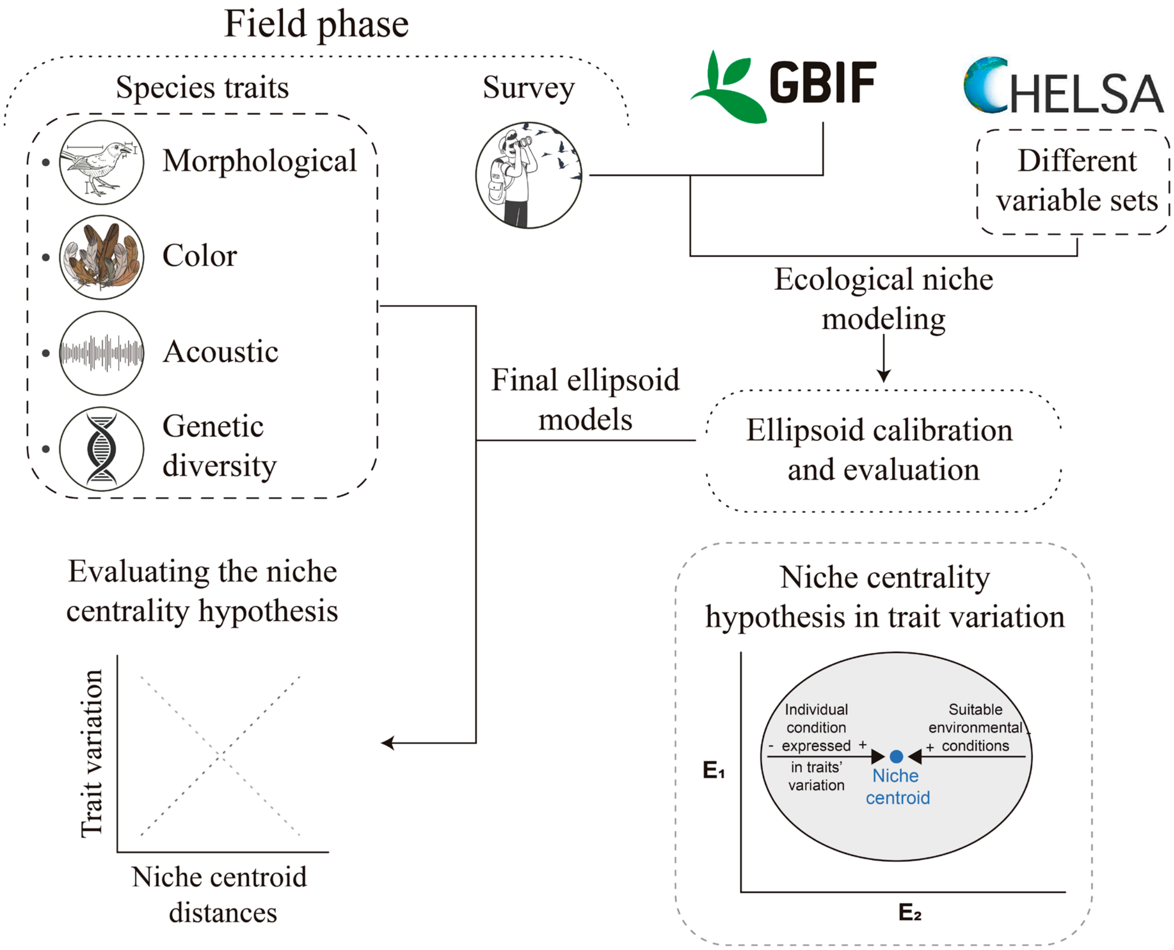

Figure 1. Workflow diagram of our study framework. We also expose the niche centrality hypothesis. E1 and E2 are the hypothetical environmental variables 1 and 2, respectively.

evaluate the niche centrality hypothesis, we created and evaluated different niche configurations using an ellipsoid hypervolume-based modeling algorithm and several environmental predictors. Finally, we developed Ordinary Least Squares (OLS hereafter) and Generalized Least Squares (GLS hereafter) regressions to analyze the variation in each trait as a function of distance from the niche centroid (Fig. 1).

Field phase

We conducted a field sampling phase between 2015 and 2023 as part of a bird monitoring program at the Hidroituango Hydroelectric Project in the Cauca River canyon, between the Western and Central Andes, in the Department of Antioquia, Colombia (Fig. 2). This area is mainly composed of dry and semideciduous forests and tropical rainforests in an elevational range between 340 and 1200 m.a.s.l. (Fig. 2). To capture the birds, we used mist nets close to their territories to increase capture probability. We recorded the coordinates in each capture event, measured morphological traits, collected blood, and feathers from the crown for color analysis (see below). Further, we performed directional recordings of songs from individuals of the Antioquia Wren (see below). Finally, we marked each captured individual with a unique metal and two plastic rings with two distinctive color combinations to distinguish individuals in the field.

We conducted this study in accordance with Colombian law and the Code of Ethics of the Animal Behavior Society, as well as the ABS/ASAB guidelines for the use of animals in research and teaching. Animals were not kept in captivity and were not exposed to any experimental treatment. The capture/collection of biological samples and specimens is covered by a permit for the collection of wild specimens for non-commercial purposes, issued by the National Environmental Licensing Authority (ANLA) through resolution 0524 to the Universidad de Antioquia.

Morphological traits

We followed the protocol for measuring functional traits in birds proposed by López-Ordoñez et al. (2016). We measured weight using a digital scale, beak width and height (at the level of the nostrils), and tarsus length (as

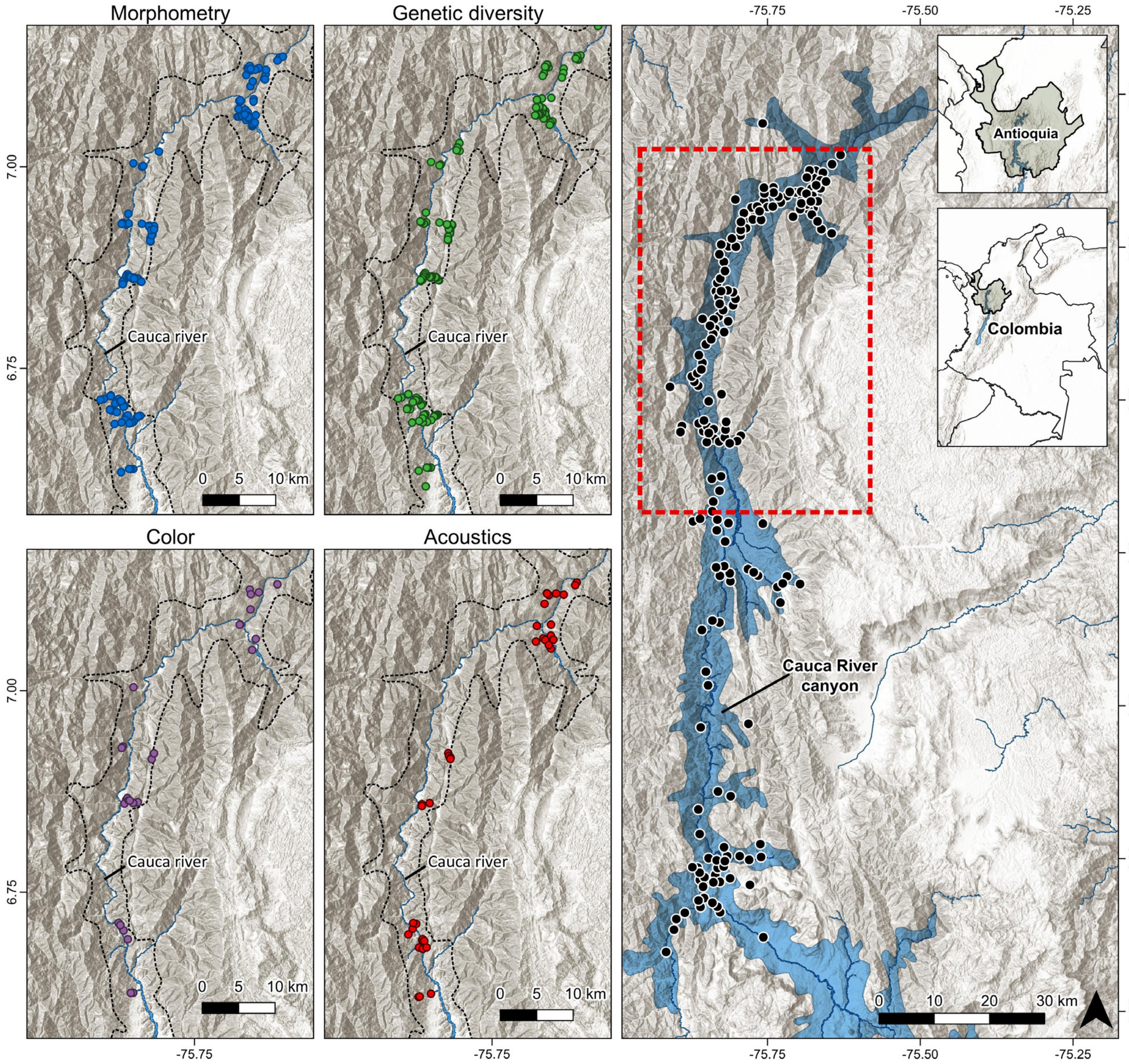

Figure 2. Spatial locations of survey sites (color dots) and final occurrences of the Antioquia Wren from GBIF used for the ecological niche model (black dots). The red dotted box shows the geographic location of the field sample phase. We also point out the Cauca River canyon within each traits box in dotted black lines.

the distance between the bony protrusion at the tibiotarsal articulation and the front of the last scale at the base of the toes) using a digital vernier calliper. Further, we measured wing length (as the distance between the carpal and the tip of the primary feather), distance between longest primary and first secondary flight feathers (LP-FSF distance hereafter), and tail length (as the longest inner tail feather) using a ruler with a perpendicular stop. We used only adult data for our analysis because the morphometric measures in immature specimens could produce bias in the results due to the lack of full development of the traits. Finally, we excluded data with missing coordinates and averaged the values of recaptured individuals across sampling years resulting in 154 individuals with morphometric data.

Molecular data and genetic diversity

We took blood samples of approximately 20 µL by brachial venipuncture using 0.4 mm diameter hypodermic needles and capillaries and stored them in Queen's lysis buffer for molecular analysis (Seutin et al., 1991). Genomic DNA extraction was performed using the Salting Out protocol (Miller et al., 1988). To assess individual genetic diversity, we used four microsatellites (Hle284, Hle315, TA-C6-7, ThPl30) reported by Bowie et al. (2012), Brar et al. (2007), and Cabe and Marshall (2001). These four microsatellite loci were polymorphic within a set of 15 microsatellite markers tested by Restrepo-Arias et al. (2025).

We used the methodology proposed by Schuelke (2000) to amplify the microsatellites and fluorescently label PCR products. Reactions were performed in a 10 µL volume using 1X PCR buffer, 0.2 mM dNTPs, 7.5% bovine serum albumin, a specific concentration of MgCl2 marker for the species (Table S1), and 0.5 units of Taq Polymerase (Thermo Fisher). We used three primers for each reaction: i) a reverse primer (final concentration of 0.5 µM), ii) a hybrid direct primer that had a universal M13 (-16) tail incorporated at the 5' end (final concentration of 0.1 µM), and iii) a universal M13 (-16) primer labeled with one of three fluorochromes VIC, FAM, NED (final concentration of 0.4 µM). We then performed a PCR using a touch-down protocol (95°C for 5 min; followed by 25 cycles of 95°C for 30 sec, 55-65°C for 80 sec, 72°C for 30 sec, 20 cycles of 95°C for 30 sec, -5°C from the initial banding temperature for 80 sec, 72°C for 30 sec, 72°C for 30min). Each locus was amplified separately, and capillary electrophoresis was performed using an ABI 3500 HD genetic analyzer with Ladder GeneScan LIZ 600 (Applied Biosystems), combining three or four loci in each run. The PCR products were run on an ABI3500 applied biosystems in Genes (Colombia), and allele sizes were determined using Geneious (Biomatters Ltd).

We used Arlequin 3.5.2.2 (Excoffier and Lischer, 2010) to test Hardy-Weinberg equilibrium (HWE) for all locus and linkage disequilibrium for each pair of loci. For each microsatellite, evidence of null alleles or genotyping errors due to stuttering and dropout of large alleles was assessed using Microchecker 2.2.3 (Van Oosterhout et al., 2004).

We obtained microsatellite genotypes from 165 individuals and used the "mlh" function of the Rhh R package (Alho et al., 2010) to estimate Multilocus Heterozygosity for each individual. To estimate individual heterozygosity across the set of microsatellites markers, we used the Internal Relatedness Index (IR hereafter; Amos et al., 2001). In IR negative values indicate higher heterozygosity, while positive values indicate higher homozygosity. We used IR among other metrics, because it explains more variation in fitness than other metrics and it is more accurate for species with low genetic diversity such as the Antioquia Wren (Amos et al., 2001; Restrepo-Arias et al., 2025).

Spectrophotometry and colorimetric variables

We obtained 5-10 feathers from the crown (Quesada and Senar, 2006) of 33 individuals and excluded immature and moulting birds from the analysis. Despite the low variation in color between the crown and the mantle of the Antioquia Wren, we focused on the crown patch because this plumage region exhibits conspicuous coloration in the species. Then, we calculated the reflectance spectrum of every plumage sample by spectrophotometry. Additionally, we restricted the reflectance spectra to values between 300 and 700 nm, as this range corresponds to the avian visual spectrum (Hill and McGraw, 2006), with reflectance values recorded at 1 nm intervals. Further, we set the black reference by placing the probe on a dark surface with no light emission, and the white reference by taking readings from a WS-1 reflectance standard. We placed the feathers one a low reflectance surface (<2%) and illuminated them using a UV-VIS bifurcated optical fiber connected to a Deuterium-Halogen light source (DH-2000 BAL; Ocean Optics) that emitted in the UV and visible light range. We used a FLAME-S-XR1-ES Ocean Optics spectrophotometer coupled to the OceanView software, version 1.6.7 (https://oceanoptics.com/product/oceanview/) to perform all measures. For each measurement, we maintained an angle of 90° and distances of 2 mm.

Also, to process the raw spectrometric data and calculate color traits, we applied local regression smoothing using the "procspec" function of pavo R package (Maia et al., 2019) with a span parameter of 0.25 to reduce voltage spikes and smooth the reflectance spectra. For each plumage sample, we took three measurements and averaged across them. For each average spectrum we measured the mean brightness (B2), the visible spectral saturation (S2) and hue (H3) by the "summary" function of the R pavo package.

Acoustic analysis and measurements

We recorded 44 Antioquia Wren individuals defending their territories. We defined a territory as an area defended by a dominant male, occasionally accompanied by a female (Betancur Ortiz et al., 2024). We also assumed that the dominant male was the individual who sang most actively and was more aggressive (Rose, 2013; Hall et al., 2015). Due to this species' complex singing repertoire, we searched for at least four territories in each locality to obtain a representative sample of song variation. We recorded each dominant male during the morning (from 5:30 to 10:00 hours), mainly at dawn when males were most vocally active. We followed them throughout their territories while recording, or we recorded opportunistically if a dominant male sang suddenly, and it was identified. Once we recorded an individual, we used mist nets to capture and marked him with a metal ring and a unique combination of color bands to avoid resampling individuals. Then we saved the recordings in Waveform audio file (.WAV) format at a sampling rate of 44.1 kHz and 16 bits. We recorded using three pieces of equipment: a Marantz PMD661 recorder, a Tascam DR-100-MkIII recorder, and a SENNHEISER ME67 highly directional microphone.

To reduce potential variability introduced by differences in recording equipment, all audio files were amplitude-normalized using the "normalize" function from the tuneR package in R (Ligges et al., 2023). This function centers and scale the waveform of a Wave or WaveMC object to a canonical interval corresponding to the Wave format. By applying this normalization step prior to acoustic measurements, we ensured that traits from signals with comparable energy profiles, thereby improving the reliability of cross-individual comparisons. Finally, we measured the average entropy, band width 90%, duration 90%, frequency 95%, and peak frequency of each recording using Raven Pro-1.6.1 (Yang K. Lisa Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2023) and a window with the following parameters: Window size of 910 points, type: Hann, time grid overlap: 50%, time grid hop size: 475 samples, frequency grid DFT size: 1024 samples, spacing: 43.1 Hz averaging spectra: 1. We chose these measurements because they provide a comprehensive and comparable picture of song repertoires in this species (Tubaro, 1999; Ey and Fischer, 2009).

Ecological niche modeling

Occurrence data.—We obtained 2,945 occurrences of the Antioquia Wren from the Global Biodiversity Information Facility (GBIF, 2025). These occurrences included data from different sources such as monitoring programs at Hidroituango hydroelectrical project (53%), EBIRD (43%), sound databases (3%), and iNaturalist (1%). We applied three filters to these occurrences to improve the quality of the data for the niche model. First, we removed occurrences above 1200 m elevation following the species' elevational range (Lara et al., 2012). To achieve this, we used the "elevation_3s" function of geodata R package v0.6-2 (Hijmans et al., 2024) to obtain a digital elevation model at 90 m resolution. Then we used the "extract" function of terra R package (Hijmans, 2023) to extract elevation data for each occurrence and removed those above 1200 m elevation. To avoid potential bias in climatic conditions due to georeferencing uncertainty, we removed iNaturalist observations because their coordinates are often intentionally obscured for restricted or sensitive species (Contreras-Díaz et al., 2023). Further, we deleted occurrences that presented low precision (less than two decimal positions). Third, we used a custom function based on the spThin R package (Aiello-Lammens et al., 2015) to apply a spatial thin of 1 km to the occurrences to reduce spatial autocorrelation of the data and to obtain a single occurrence per pixel. Once we applied these filters, we obtained a database of 178 occurrences as our final database for niche modeling. We did not include our trait data (see below) because most of the records were already reported in GBIF data (monitoring programs at Hidroituango Hydroelectrical project).

Accessible area

For niche model projection in geography, we defined an accessible area or "**M**" (Soberón and Peterson, 2005; Barve et al., 2011). To achieve this, we used the intersection of The Nature Conservancy (TNC) terrestrial ecoregions (Olson et al., 2001) where at least one occurrence was reported, and then we applied a 50 km buffer to the occurrences simulating the possible species' dispersion field. This framework allowed us to limit the projection of the niche in geography for species with a known restricted range within larger ecoregions (Rojas-Soto et al., 2024).

Environmental variables

To estimate the ecological niche of the Antioquia Wren, we used the environmental data from Chelsa v2.1 (Krager et al., 2017) at 30 arc-second resolution (~1 km at the equator). We selected the Chelsa database over other sources because it includes orographic corrections that improve precipitation estimates in tropical montane regions (e.g., the Cauca Canyon). We selected 11 variables from Chelsa's database that are ecologically important for the Antioquia Wren, based on our empirical knowledge, field observations, and previous studies (Lara et al., 2012; Betancur Ortiz et al., 2024). These variables included 10 bioclimatic variables and net primary productivity, which mainly describe the dry and semideciduous forests and tropical rainforests that the Antioquia Wren inhabits (Table S1). Then, we combined the 11 variables into different datasets, ensuring a minimum of three variables per combination, which resulted in 1,981 distinct sets. However, because some variables in certain sets were highly correlated, we used the final occurrence database to extract the values of the 11 variables and performed a Spearman correlation test (Díaz-Vallejo et al., 2024). Afterwards, we retained the variable sets that presented low correlation estimates (rho < |0.8|), obtaining 183 groups of variables (see online repository https://doi.org/10.6084/ m9.figshare.30281851). Finally, we masked the 183 variables set using the accessible area (**M**) previously estimated. This framework is based on Osorio-Olvera et al. (2020), in which different candidate niche models are evaluated to find the parameters for niche configuration.

Niche modeling

To estimate the niche of the Antioquia Wren, we used a minimum volume ellipsoid modeling approach. This method suggests that the realized fundamental niches are convex, assuming an ellipsoidal configuration when multiple dimensions are considered (Jiménez et al., 2019; Etherington, 2021; Carrasco et al., 2022). Estimating niches using this method provides a clear structure for testing how different species' traits respond as a function of distance from the niche centroid (Yañez-Arenas et al., 2020).

For ellipsoid calibration, we used the "ellipsoid_calibration" function of ellipsenm R package (Cobos et al., 2022). We considered 183 sets of variables and two methods for ellipsoid construction, namely the covariance-variance matrix (COVMAT hereafter) and the minimum volume ellipsoid (MVE hereafter). Both methods present differences in centroid position and ellipsoid size. Firstly, the COVMAT method locates the centroid at the center of the entire data distribution. At the same time, the MVE method may modify the centroid position and the covariance matrix. Further, the ellipsoid size is smaller for MVE ellipsoids than that estimated by the COVMAT method (Etherington, 2021). However, due to different random partitions, which can lead to different niche models selected, we made a bootstrap of 100 random partitions (80% for training and 20% for testing). Therefore, for each sample partition, we evaluated the 183 sets and both ellipsoid methods, for a total of 366 candidate niche models in each bootstrap replicate. To select the best combination of variable set and ellipsoid method in the 100 random partitions, we used the ellipsenm function "calib_ellipsoid". This function evaluates the best ellipsoid configuration using a training and testing dataset and estimates the AUC ratio (>1) throughout a partial ROC and the omission rate (<5%) based on the test data. Finally, for each sample partition, we selected the best niche model configuration (i.e., best variable composition and ellipsoid method), prioritizing the lowest omission rate and subsequently the highest AUC ratio. If among the 100 replicates a particular niche model was selected twice or more times, we counted it as unique configuration.

Once we obtained the best niche model configuration, we used the "ellipsoid_model" function from ellipsenm to create the niche models. To achieve this, we used the final occurrences dataset (i.e., 178 occurrences) to create 10 replicates for each of the 56 ellipsoid configurations, using the random subsample option in the same proportion (i.e., 80% training and 20% test) as during the niche model calibration process. Each replicate included 95% of the data to avoid potential environmental outliers. Then, we used the average distance centroid from all replicates for each niche model configuration. Because our trait datasets were independent from the occurrences used for the niche modeling, we assessed potential bias and differences in niche centroid distances between the final occurrences and the traits datasets. To do that, we calculated the mean centroid distance for each trait set and for the final occurrence database. Afterwards, we compared them using the Mann-Whitney U test (Mann and Whitney, 1947; Wilcoxon, 1992). This test compares the two independent group medians to determine whether they come from the same data population ($P \leq 0.05$). We repeated the procedure for each 56 COVMAT and MVE method niche model proved. Furthermore, to explore the spatial agreement and centroid distance variation among niche models we employed two approaches. First, we mapped the 5th and 10th percentile lower niche centroid distances of each model and overlapped them to observe the spatial variation and coincidence of centroid distances in geography. Second, we considered the mean suitability layer of each niche model and reclassified as presence if the environmental conditions in a pixel are included inside the ellipsoids, and as absence if those climates were outside. Then we overlapped the binarized layers to explore the coincidence of suitability in geography.

Statistical analyses

To test the relationship between species' traits and the distance to the niche centroid, we related all traits to the Mahalanobis distance of the 56 ellipsoid configurations. First, we tested the OLS regression assumptions of normality (Shapiro-Wilk test) and homoscedasticity. To verify the homoscedasticity assumption, we performed a linear regression analysis between the squared regression residuals and their model-fitted values, evaluating that the residuals were constant across all fitted values. We also considered linear, quadratic, and logistic fitting of the data. Additionally, we compared them using the Akaike Information Criterion (AIC; Akaike, 1998) to determine the best regression configuration based on the nature of the data. Secondly, we assessed whether there was spatial autocorrelation among the residuals of each regression model using the "morans.test" function of the spdep package to estimate Moran's index (Bivand, 2022). In cases where the above assumptions were not met and there was no spatial autocorrelation (i.e., Moran's I; $P \geq 0.05$), we used a GLS through the "gls" function from the nlme R package (Pinheiro and Bates, 2023). On the other hand, when we found spatial autocorrelation (i.e., Moran's I; $P < 0.05$), we incorporated a spatial correlation structure into the GLS, evaluating the most common spatial structures used in ecological studies such as exponential, gaussian, and spherical configurations (Dorman et al., 2007), and selected the best linear model using the AIC.

Once we obtained the best modeling approach for trait-distance relationship, we averaged the best regression (i.e., OLS or GLS) estimates and calculated their 95% confidence interval, grouping them according to the method used to construct the ellipsoid (i.e., COVMAT or MVE). Therefore, if the confidence intervals did not reach zero, we considered the features to be consistent in their directionality (i.e., positive or negative) regarding the distance to the centroid. Then, for the consistent trait-distance relationships, we assessed which regression model were statistically significant ($P < 0.05$) and verified similarities among the configurations of those ellipsoids.

Finally, to assess whether the sample sizes in the traits datasets were sufficient to detect meaningful effects in our regression models, we conducted a power analysis. This test evaluates the probability of correctly rejecting a false null hypothesis and depends on parameters such as the sample size, effect size, and significance level. We set the significance level at 0.05 and used the degrees of freedom and the coefficient of determination (R^2) for each regression to estimate the power of the models using the function "pwr.f2.test" from the pwr R package (Champely, 2023).

Results

Traits data and ellipsoid models

From the 100 data partitions used to evaluate the 183 candidate sets, we obtained 56 ellipsoid configurations (i.e., variable set and ellipsoid method) that satisfied the evaluation criteria (see online repository). From these, 32 corresponded to ellipsoids built using the MVE and 24 to the COVMAT ellipsoid method. We also found that the most frequently selected set (i.e., the set 726) included the COVMAT method, and the following variables: mean diurnal temperature range (bio2), isothermality (bio3), minimum temperature of the coldest month (bio6), precipitation of the coldest quarter (bio19), and net primary productivity (npp). We also found high geographical consistency and agreement towards low elevations near the center of the Canyon in the 56 niche model configurations (Fig. 3). Similar results were observed for distances below the 5th and 10th percentiles of the niche centroid. However, we observed great variation in distances below the 5th percentile, compared to the 10th percentile centroid distances (Fig. 3).

We found more variation in centroid distances among the different variable sets than between the two methods to create the ellipsoids (Fig. S1). However, we observed a tendency of non-statistically significant difference between the distribution of traits' centroid distances and the final occurrence dataset across the 56 variable sets (Fig. S2). We found that in most cases for color (87.5%), genetics (71.4%), and morphometric (57.1%) traits, there was a non-significant difference between the centroid distance of each trait dataset and the final occurrence database ($P>0.05$). Conversely, for the acoustic traits, we found that the centroid distances were statistically similar in 39.3% of the cases regarding the final occurrences (Fig. S3).

Morphometric traits and niche structure

None of the morphological traits met the OLS assumptions, and only weight presented spatial autocorrelation in the residuals (Moran's I; $P \leq 0.05$). Therefore, we evaluated the relationship between each trait and centroid distances using GLS linear regressions but including a spatial matrix only for the weight. Furthermore, we found that linear regression showed a more appropriate fit (i.e., lower AIC), except for the weight and culmen, which also presented two and one quadratic GLS regression, respectively (see online repository).

We observed a consistent relationship between the LP-FSF, beak height, and width with the centroid distance (Fig. 4A). We found that larger LP-FSF distances are present near the niche centroid (negative relationship; Fig. 4B). Whereas we found that higher and wider beaks are present far from the niche centroid (positive relationship; Fig. 4C and D). We also noted that, despite a consistent relationship between these traits and the centroid distance, not all regressions were statistically significant (LP-FSF: 28%; beak height: 17.9%; beak width: 91.1%; $P \leq 0.05$). Further, the relationship of the centroid distance on those traits was weak (i.e., $R^2 < 0.1$). On the other hand, the remaining morphological traits exhibited both positive and negative relationships with the niche centroid distances, showing less consistency. For traits such as tail length, commissure, culmen, and weight, at least one regression model was statistically significant, despite inconsistent relationships with centroid distances (see online repository).

Genetic diversity and niche structure

We found that microsatellite RhPl30 exhibited a significant deviation from Hardy-Weinberg equilibrium, presenting an excess of heterozygotes compared to the three remaining polymorphic markers (Table S3). However, no microsatellites showed evidence of null alleles. Therefore, we retained ThPl30 in the analyses, as its removal did not yield different results.

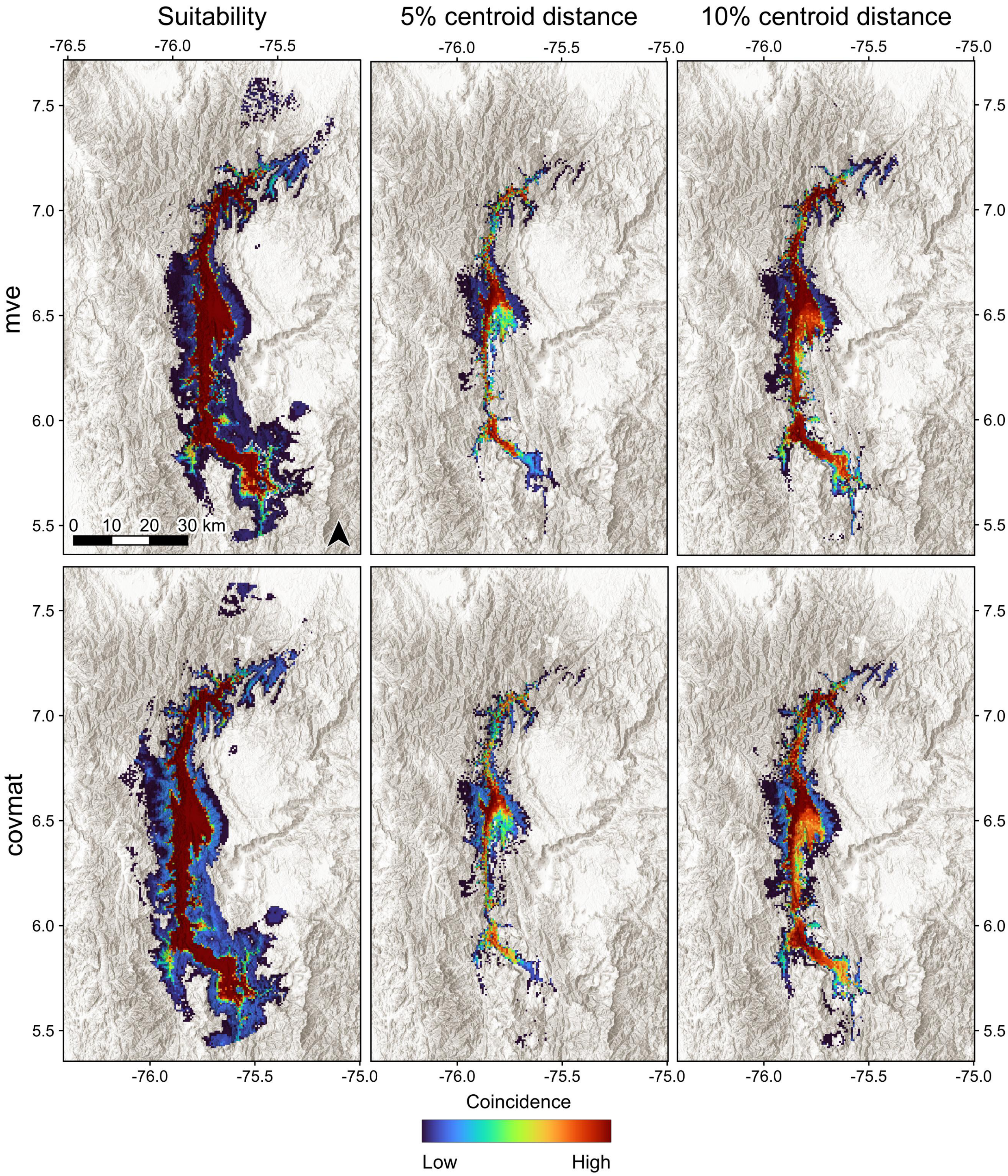

Figure 3. Spatial coincidence of the suitability and 5th and 10th percentiles of the centroid distances of all 56 model configurations. The maximum coincidence for COVMAT and MVE ellipsoids was 24 and 32 models, respectively.

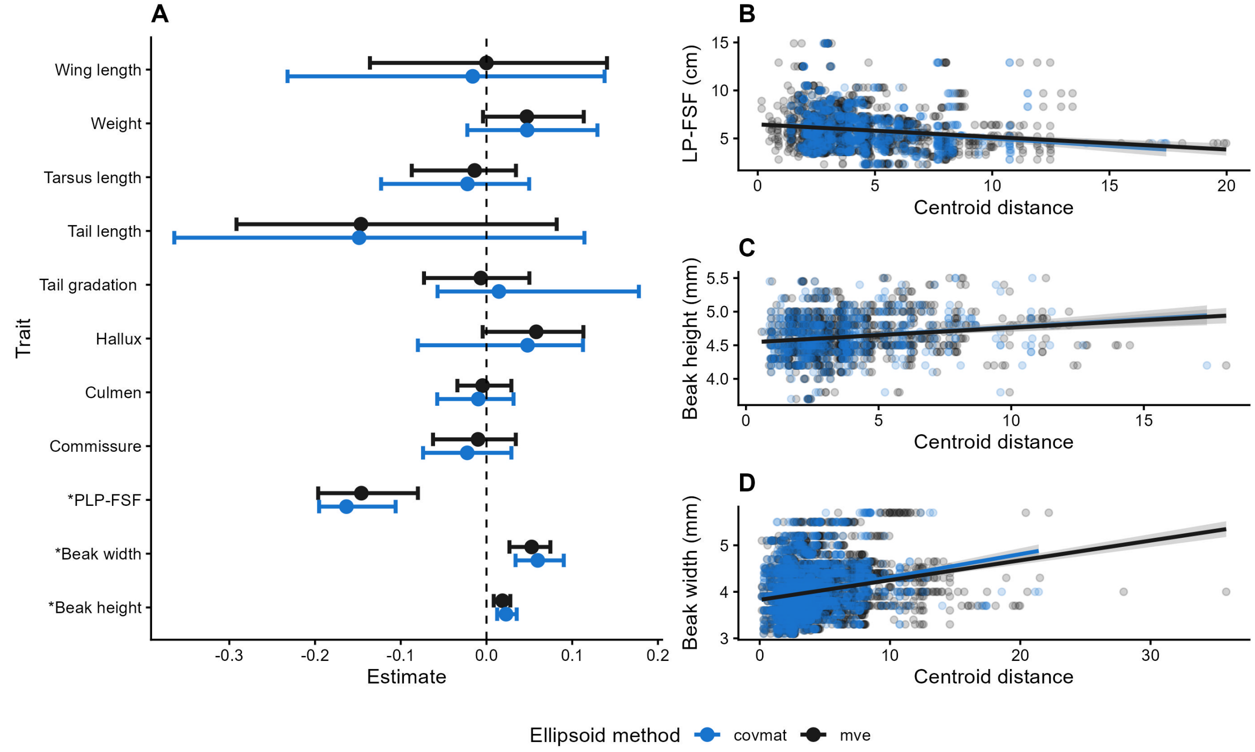

Figure 4. Relationship between morphometric traits and the centroid distance for each of the 56 niche models. A) Mean estimate and its 95% confidence interval. B) Relationship between LP-FSF distance and niche centroid; C) Relationship between beak height and niche centroid; D) Relationship between beak width and niche centroid. The points in each panel represents statistically significant models. * Traits that presented a consistent relationship (all negative or positive).

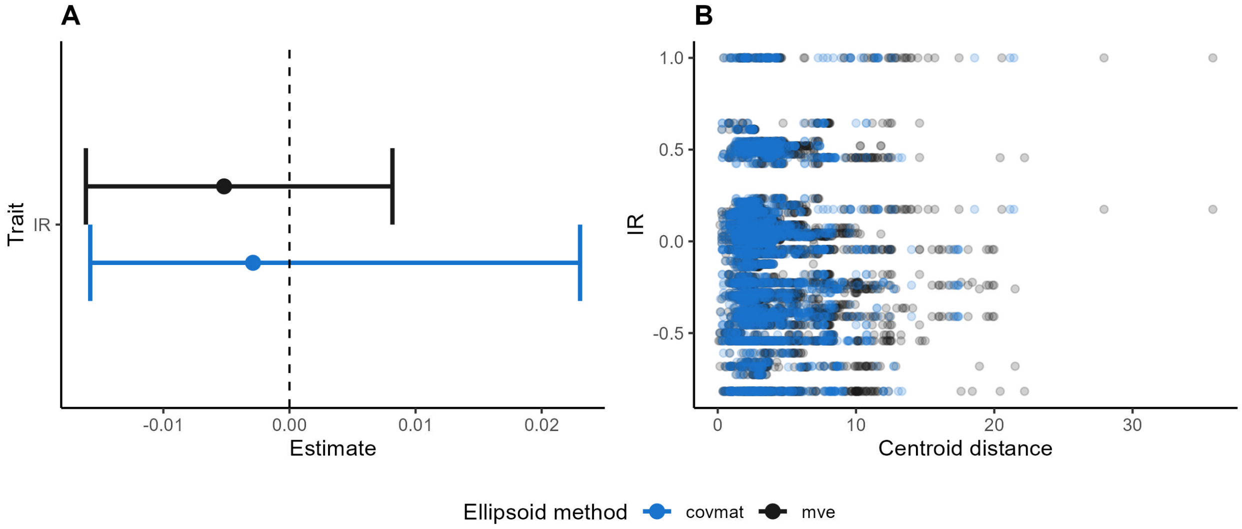

Figure 5. Relationship between the Internal Relatedness index (IR) and the centroid distance for each of the 56 niche models. A) Mean estimates of regressions and their 95% confidence interval. B) Representation of the genetic diversity data, but no significant models were obtained.

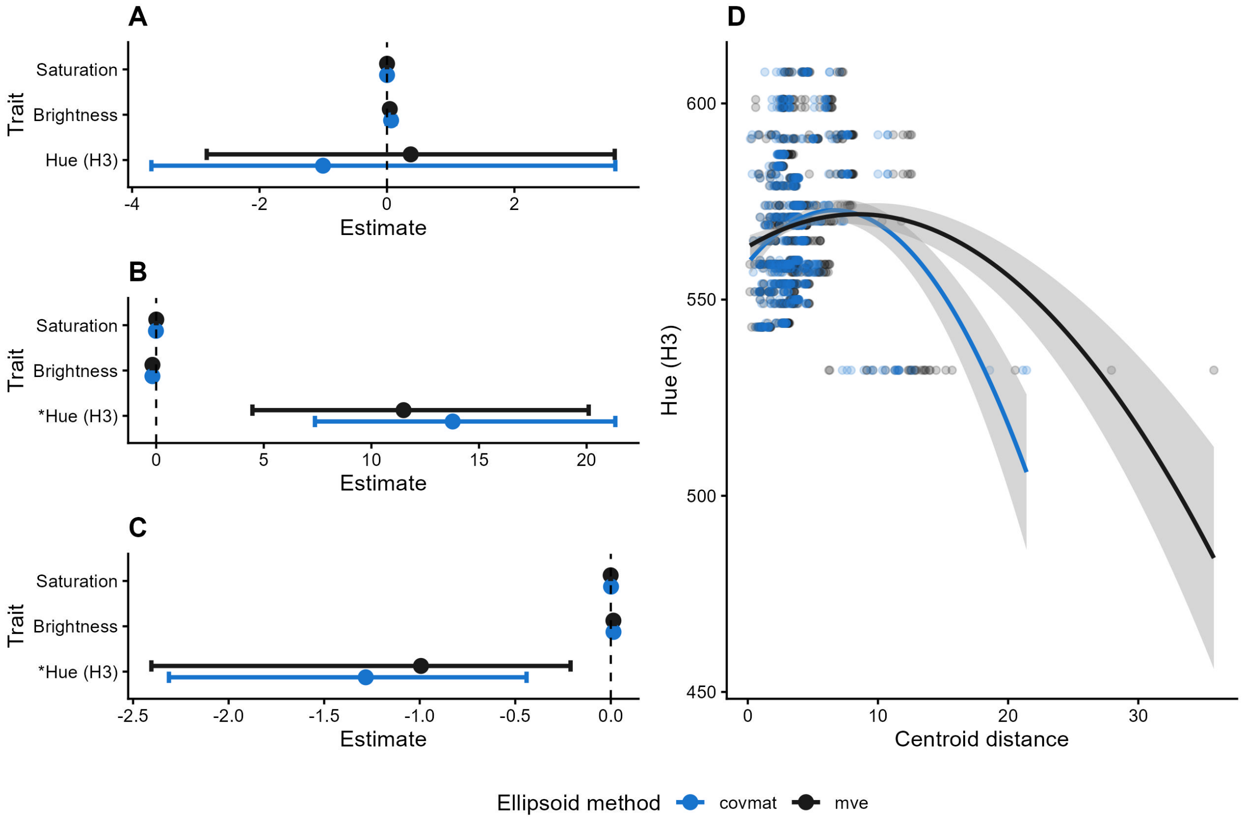

Figure 6. Relationship between color traits and the centroid distance for each of the 56 niche models. A) Mean estimate of regressions and their 95% confidence interval for linear models' regressions. B) Linear term (first-order coefficient) estimates and their 95% confidence intervals from hue (H3) quadratic regression. (C) Quadratic term (second-order coefficient) estimates and their 95% confidence intervals from H3 quadratic regression. D) Relationship between hue and niche centroid. * Traits that presented a consistent relationship (all negative or positive).

We noted that the Internal Relatedness index (IR) did not fulfill the OLS assumptions nor showed evidence of spatial autocorrelation (Moran's I; $P \geq 0.05$). Therefore, we evaluated the relationship between the IR and centroid distances using GLS linear regression, showing no consistent relationship and non-statistical significance (Fig. 5). Therefore, it is possible to find a positive or negative weak relationship between IR and centroid distance, depending on the niche configuration (i.e., identity and number of variables).

Color traits and niche structure

We found that regressions for all color traits fulfilled the OLS assumptions and that there was no evidence of spatial autocorrelation (Moran's I; $P \geq 0.05$). Not all regressions were statistically significant (H3: 71.4%; brightness: 16.1%; saturation: 3.6%). We also noted that hue (H3) presented a quadratic relationship (better fit in 91.1% of regressions) with the centroid distance (Fig. 6A, B and C; see online repository). Individuals presenting higher H3 values were not necessarily near the niche centroid, but rather at an intermediate distance (~10 units; Fig. 6D). The effect of the centroid distance on hue was weak (i.e. mean R^2=0.2).

Acoustic traits and niche structure

We found that the regressions for bandwidth (90%), peak frequency, and 95% frequency fulfilled the OLS assumptions, while those for duration and entropy did not; therefore, we analyzed these last two using GLS models. We did not find evidence of spatial autocorrelation in any of the regression models (i.e., GLS and OLS; Moran's I; $P \geq 0.05$). Best fit regressions for bandwidth (90%), peak frequency, and entropy were all linear. For song duration, a GLS quadratic regression was selected 34 times, while for the 95% frequency, OLS quadratic models were used 10 times; the remaining cases corresponded to linear GLS and OLS regressions.

We found that the duration, peak frequency, and frequency 95% presented a consistent negative relationship

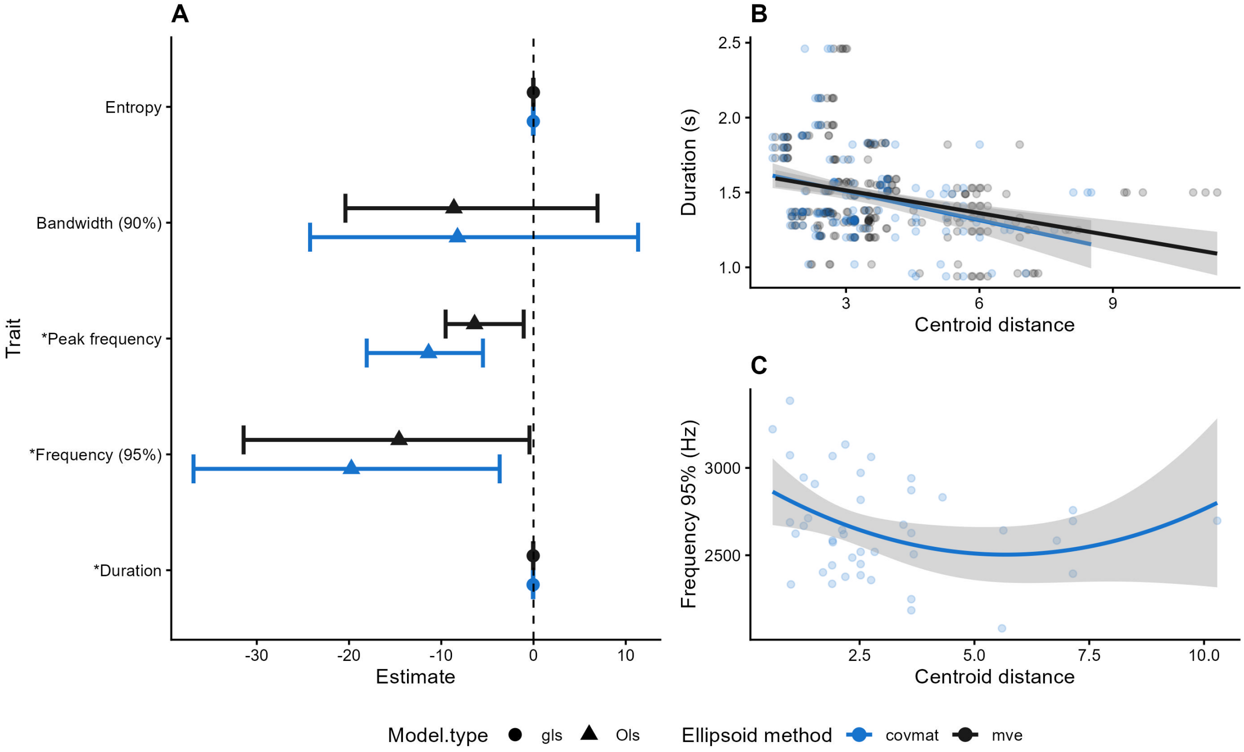

Figure 7. Relationship between acoustic traits and the centroid distance for each of the 56 niche models. A) Mean estimates of regressions and their 95% confidence interval for linear regressions. B) Relationship between song duration and niche centroid; C) Relationship between 95% frequency and niche centroid. The points in each panel represents statistically significant models. No statistically significant models were found for peak frequency. *Traits that presented a consistent relationship (all negative or positive).

with the centroid distance (Fig. 7A), but not all regressions were statistically significant (duration: 14.3%; 95% frequency: 1.8%). Individuals that exhibited higher song duration were more likely to be found near the niche centroid (negative relationship; Fig. 7B). Likewise, individuals close to and far from the niche centroid displayed songs with high 95% frequency but low values in middle distances (concave quadratic relationship; Fig. 7C). Conversely, we found a lack of consistency in the relationship between the niche centroid distances and both the entropy and bandwidth (90%) (Fig. 7A). Further, the relationship between the centroid distance and traits was weak (i.e. $R^2<0.1$).

Power test

The frequency distribution of the power test for each trait dataset showed substantial variation among them (Fig. S4). The histogram showed that morphological (44.5%), genetic (60.7%), color (24.2%), and acoustic (53.6%) regression models exhibited low power values (i.e., <0.1), indicating limited sensitivity to detect significant effects for each trait relative to the niche centroid distance. Furthermore, we noted that in some cases the regression model had moderate power values (i.e., 0.2-0.7; morphological – 46.9%; genetic – 39.3%; color – 56.4%; acoustic – 46.1%), while high power values (i.e., 0.8–1.0) were comparatively rare (morphological – 8.6%; color – 19.4%, acoustic – 0.3%).

Discussion

The study of geographic variation in individual traits, including morphology, color, song frequency, and genetic diversity, has been extensively investigated across birds (e.g., Krebs and Kroodsma, 1980; González-Quevedo et al., 2015; Delhey et al., 2023; Mota-Vargas et al., 2023). The causes of such variations at the population or intraspecific level had been attributed to biotic (e.g., food availability; Miller et al., 2021) and abiotic factors (e.g., climate, habitat, geographic barriers; Eeva et al., 2006; Tellería et al., 2013). In this study, we aimed to determine whether traits (i.e., morphological traits, genetic diversity, coloration, and acoustic metrics) exhibit niche structuring in the Antioquia Wren. Our findings indicate that three morphological traits, one color trait, and three acoustic traits exhibited consistent relationships with distance to the niche centroid, regardless of variation in environmental predictors or niche configurations. However, not all models for those traits that showed consistent positive or negative relationships were statistically significant. For example, beak width and height showed consistent positive relationships, but only 17.1% and 91.1% of the relationships with the centroid distances were statistically significant respectively. Therefore, the inference about the trait-centroid distance relationship depends on the niche configuration. Conversely, we did not observe a consistent relationship for the remaining 13 traits. Our results suggest that not all traits are related in the same way to the environmental dimensions used to characterize the species' climatic niche.

Morphometry traits and niche structure

Our results suggest a positive and consistent relationship between centroid distances and beak width and height, contrary to our expectation based on Maguire's (1973) niche structure hypothesis, but negative with the longest primary and first secondary flight feathers (LP-FSF); however, such consistent relationships with the centroid distance on those traits in many cases are weak. This indicates that, despite the low power, the relationship is strong enough to show that Antioquia Wren individuals have thinner, narrower beaks and broader, rounder wings near the niche centroids than those at the margins. Such relationships imply that environmental variation might configure morphological attributes related to foraging ability (e.g., prey; Tellería et al., 2013; Carrascal et al., 1990) and the capacity to defend its territory (Duckworth, 2006). Consequently, we can hypothesize that these results might be related to biotic factors, such as the size of prey and territory quality in the marginal climatic niche (colder or wetter conditions) compared to near the species centroid (warm and dry).

Genetic diversity and niche structure

We did not find consistency or statistically significant regression models for the relationship between Internal Relatedness (IR) and the centroid distance. This suggests that for the Antioquia Wren, the genetic diversity is not related to the niche centroid distance. However, this result can be explained by the species' low levels of genetic diversity, which is common in species with restricted distributions and threatened status (Kleinhans and Willows-Munro, 2019; Peters et al., 2023; Gautschi et al., 2024). The low genetic diversity observed in the Antioquia Wren has also been reported in a study that assessed both neutral and adaptive genetic diversity, finding low heterozygosity and allelic richness indices overall (Zapata et al., 2020; Restrepo-Arias et al. 2025). Furthermore, Restrepo-Arias et al., (2025) found no genetic differentiation among the sampled individuals, suggesting a single population in the same sampled area. Conversely, it is possible that the four polymorphic microsatellites used to assess genetic diversity are not representative of the genome-wide diversity in this species. Although we are aware of the limitations of using microsatellites, individual heterozygosity has also been reported with few microsatellite markers (Velando and Moran, 2015). Future studies should use whole distribution range and more informative markers (e.g., Single-Nucleotide Polymorphism – SNPs) when estimating genetic diversity.

Color traits and niche structure

Our results indicate a consistent quadratic relationship between hue and the niche centroid distance, suggesting that individuals with higher hues are not in ”optimal” conditions (i.e., the niche centroid) but instead in conditions distanced from the centroid. This could be related to a trade-off in resource availability across the ecological niche, which could affect the individual's condition. For example, investment in pigmentation may decline under resource-poor or resource-rich conditions due to energetic or ecological trade-offs (Jawor and Breitwisch, 2003), a pattern common in species that exhibit rufous coloration, which is caused by pheomelanin production (Galván et al., 2019). Conversely, the lack of a relationship between the centroid distance and color saturation and brightness may also reflect the low genetic diversity within our data. It also aligns with previous observations that plumage coloration does not exhibit significant intraspecific variation, even across other plumage patches (e.g., breast and mantle; Chinome, 2025). Although Gloger´s rule posits that organisms are more melanic in more humid environments, the Antioquia Wren shows mostly brown hues and thus may not apply in this case (Chui and Doucet, 2009; Delhey, 2019).

Acoustic traits and niche structure

Despite the weak power of our analysis, our findings indicate that Antioquia Wren individuals deployed more energy for singing near and at the margin of the centroid niche, suggesting a middle effect on environmental variation. However, the absence of consistency in many traits (i.e., entropy, 90% bandwidth) suggest that variation in the duration and frequency of bird song tends to be related to other variables, such as the optimization of the sound propagation in space (Morton, 1975; Hansen, 1979) rather than environmental gradients (Snell-Rood, 2012) due to a degradation of the acoustic energy across the vegetation cover (Blumenrath and Dabelsteen, 2004). Also, it implies that the response to environmental variation might depend, in some cases, on the local processes instead of coarsescale ones (e.g., Mikula et al., 2021; Rivera-Gutierrez et al., 2010a; Sagar et al., 2024), such as intraspecific interactions (i.e., reproductive deployment) or territory defense.

Trait variation and the niche centrality hypothesis

The evaluation of intraspecific variation in different traits through climatic niche structure is an interesting approach because trait variation does not always follow the expected relationship proposed by the niche centrality hypothesis. While predictions are well-established, some other empirical evidence has revealed contrasting results (e.g., Dallas et al., 2017; Altamiranda-Saavedra et al., 2020) that have been attributed to methodological artifacts and ecological factors such as environmental coverage and survey effort (e.g., Santini et al., 2019; Fristoe et al., 2023). Nonetheless, we hypothesize that these differences depend on several factors, which can lead to patterns deviating from niche centrality expectations. However, another important element to consider is the centroid position in the environmental space. For example, the position of the niche centroid in environmental space might constrain the expected pattern. If the niche centroid is located at an extreme of the environmental space (e.g., high temperature and low precipitation), then trait variation may not follow the expected relationship, as is the case with the Antioquia Wren. Conversely, if the niche centroid is near the center of climatic space, trait variation follows niche centrality expectations and agrees with ecogeographic rules (e.g., Bergmann's, Allen's, and Gloger's rules).

It is possible that the centroid estimation could be biased due to niche truncation (i.e., incomplete niche characterization) due to the incomplete sampling of the species' climatic niche (Anderegg, 2023). However, we addressed this potential bias indirectly by creating distinct niche model configurations, which yielded distinct niche centroids and amplitudes. Hence, we believe that niche truncation is not a serious issue in our study. Nonetheless, the Cauca River canyon presents climatic variability, including precipitation (latitudinally) and temperature (altitudinally), which lead us to think that niche truncation is not the case for this species, at least not in the primary climatic dimensions. Conversely, biotic interactions (e.g., competition - Eltonian niche) may be limiting the species' distribution in some of its limits.

On the other hand, the restricted distribution of the Antioquia Wren could imply a narrow niche amplitude and a homogeneous environment, reflecting slight trait variation within the niche structure. Also, some trait variation may arise from nonadaptive processes, such as stress-driven phenotypic shifts that lower fitness or random genetic changes in small, isolated populations (Anderegg, 2023). Therefore, the absence of robust relationships does not imply that the traits do not accurately reflect individuals' condition. Rather, it suggests the potential for relationships to emerge that operate indirectly or through other niche dimensions, such as biotic interactions.

Our results highlight an interesting and important outcome of implementing several niche configurations: the relationship between some traits and centroid distances depends on the environmental variables used to estimate the species' niche. Therefore, according to functional trait ecology and the environmental filtering hypothesis, species traits may respond to environmental gradients (i.e., climatic niches) in different ways, at different rates, and at different scales. Furthermore, although the described patterns of trait variation may contribute to individual conditions, they do not necessarily enhance their fitness. At the intra-specific level, trait variation along environmental gradients may arise from phenotypic plasticity, local adaptation, or a combination of both, without necessarily reflecting differences in survival or reproductive success (Barnett et al., 2015). Therefore, some traits may improve energy storage or maintenance without directly affecting reproductive output or survival (Andersson and Iwasa 1996; Cotton et al., 2009). Consequently, demonstrating a causal link between trait variation and fitness is still a challenge.

This study focuses on trait–environment associations and within-species trait variability, rather than on individual fitness variation. For example, Ahmad et al. (2025) found that some traits such as beak dimensions (i.e., width, height and depth) change more dramatically across climatic gradients than other body traits (i.e., weight, tarsus length or wing length). This agrees with our results for beak width and height, which may suggest that beak-related traits are more associated with phenotypic plasticity or local adaptation rather than with the individual fitness. Then, while traits related to morphometry, color, and acoustics may influence ecological performance (e.g., feeding efficiency and reproductive success), inferring fitness consequences would require demographic or reproductive data, which were beyond the scope of our research, but necessary in future studies.

Methodological limitations and future perspectives

We acknowledge that sample sizes were imbalanced among trait datasets and that this can have implications for our results and interpretation. However, our results suggest that, even with this spatial and sample bias, the trait dataset covered the majority of environmental variation within the species geographic distribution. The power analysis indicated that some relationships between traits and the distance to the niche centroid are strong enough to not be considered artifacts, and that most results should be taken with caution since our limited sample size would only allow us to capture large effects. Therefore, even for a limited sample size, the degree of intrinsic variation within the evaluated traits could play a crucial role in testing the niche centrality hypothesis. Further, other factors such as climatic heterogeneity, the species' range (wide vs. restricted), niche size, and the degree of intrinsic variation within the trait, might be assessed in future studies.

The geographic scale and the degree of environmental variation within the species range are key to estimating the climatic niche. Thus, species with broader distributions and/or more heterogeneous climates could present greater variability in the traits than those with restricted range and climatically homogeneous distributions (e.g., Moran et al., 2016), as is the case with Antioquia Wren. Further, species that present more restricted niches (small amplitude) tend to present less variation in the traits than species with broad niches (Dallas and Kramer, 2022). To address this issue, the spatial and temporal resolution of the variables used to characterize climatic niches play a fundamental role, particularly for species with restricted distributions (Quintero and Wiens, 2013; Pérez-Navarro et al., 2021). Ultimately, future studies should explicitly consider elements that evaluate different niche compositions to address the multidimensionality of the ecological niche (Hutchinson, 1957; Soberón, 2007). Such a multifactorial approach would clarify the relative importance of biotic and abiotic pressures on species traits.

Data Availability

The data and complete supplementary material can be found at Figshare repository https://doi.org/10.6084/m9.figshare.30281851

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Competing Interests

The authors have declared that no competing interests exist.

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Does niche centrality predict trait variation in the Antioquia Wren?

Supplementary material

Table S1: PCR conditions and sequences of microsatellite primers used for *Thryophilus sernai*. Ta = Annealing temperature optimized (°C); Mg = Concentration (mM) of MgCl2 used for each locus; * = Size in bp reported in the reference; ** = Forward primers were added with a tail of 16 base pairs M13 (-16) at the 5’end: 5′-CACGACGTTGTAAAACGAC-3′.

Locus	Size (bp)*	Forward primer**	Reverse primer	Ta	MgCl2	Reference
Hle284	146-403	GAGATCCTGTAGTTTTGCC	CACATTGACCTTTCAAGATC	62	2	Bowie et al., 2012
Hle315	122-224	CTGACATTTCTGTATGGATC	CTCAATTCACTGCACATGG	62	2	Bowie et al., 2012
ThPl30	221-252	ATGCCAGCACTAAAGAATGACAA	CTACATAGCAGGCAGCAGAGGTT	62	2	Brar et al., 2007
TA-C6-7	199-203	TGCAGTAGAAGACAGAGAGTAGCA	GCACAGCTGAGGTGATCTTG	65	1	Cabe and Marshall, 2001

Table S2: Environmental variables included in the different sets for model calibration

Name	Variable
Bio 1	Annual mean temperature
Bio 2	Mean diurnal range [mean of monthly (max temp - min temp)]
Bio 3	Isothermality (Bio2/Bio7) (×100)
Bio 6	Min temperature of coldest month
Bio 7	Temperature annual range (Bio5-Bio6)
Bio 10	Mean temperature of warmest quarter
Bio 11	Mean temperature of coldest quarter
Bio 12	Annual precipitation
Bio 15	Precipitation seasonality (coefficient of variation)
Bio 18	Precipitation of warmest quarter
Bio 19	Precipitation of coldest quarter
npp	Net primary productivity

Table S3: Hardy-Weinberg equilibrium test for the four polymorphic microsatellites

Locus	Number of Alles	Allelic richness	Ho	He	EHW
Hle284	7	6.98	0.68	0.64	0.09053
Hle315	2	2.00	0.34	0.37	0.21669
ThPl30	5	4.99	0.87	0.66	0
TA-C6-7	2	2.00	0.49	0.49	1

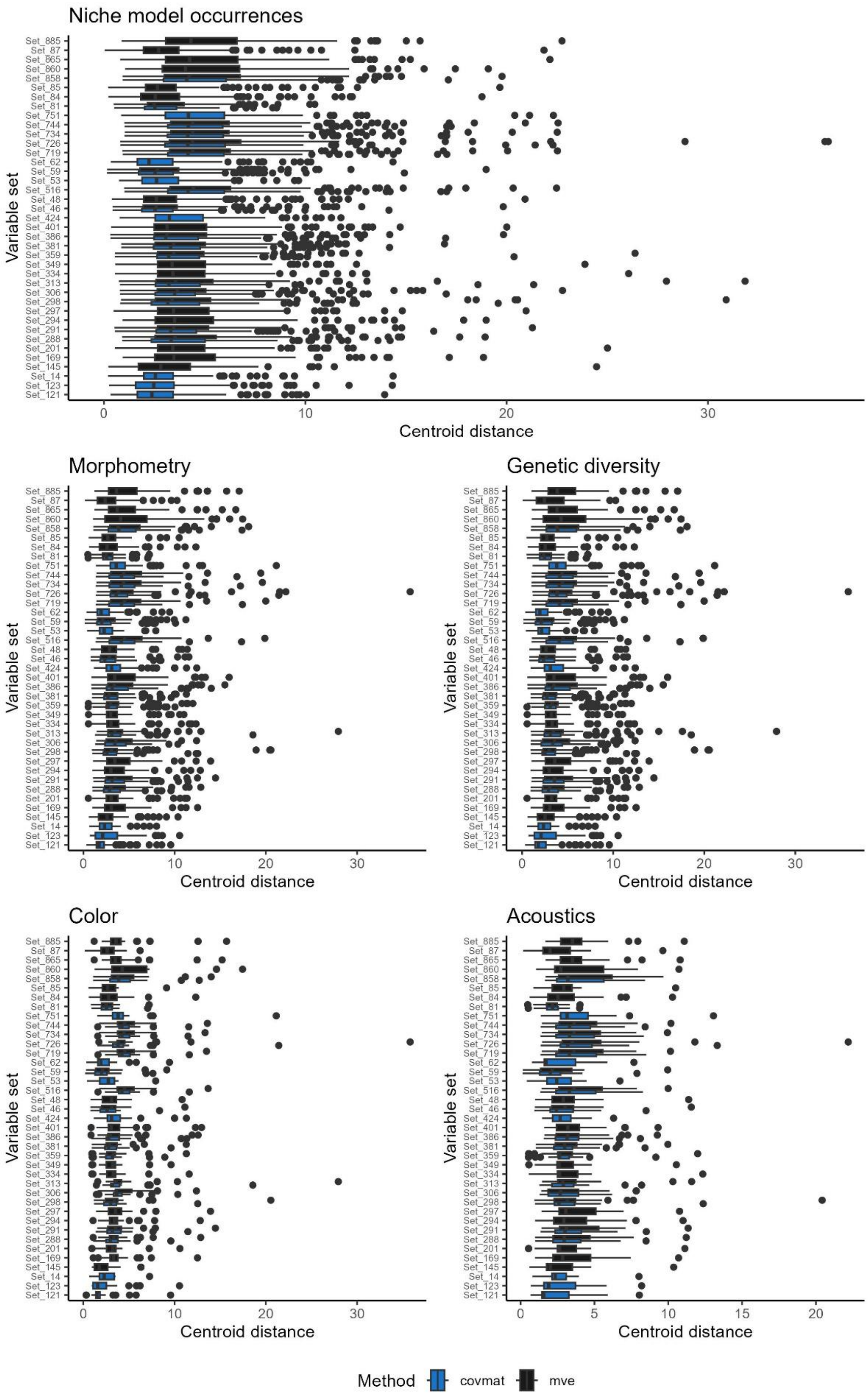


Fig. S1. Variation of centroid distances for the final species occurrences and for each trait dataset. Colors represent each method used to build the species niche model.

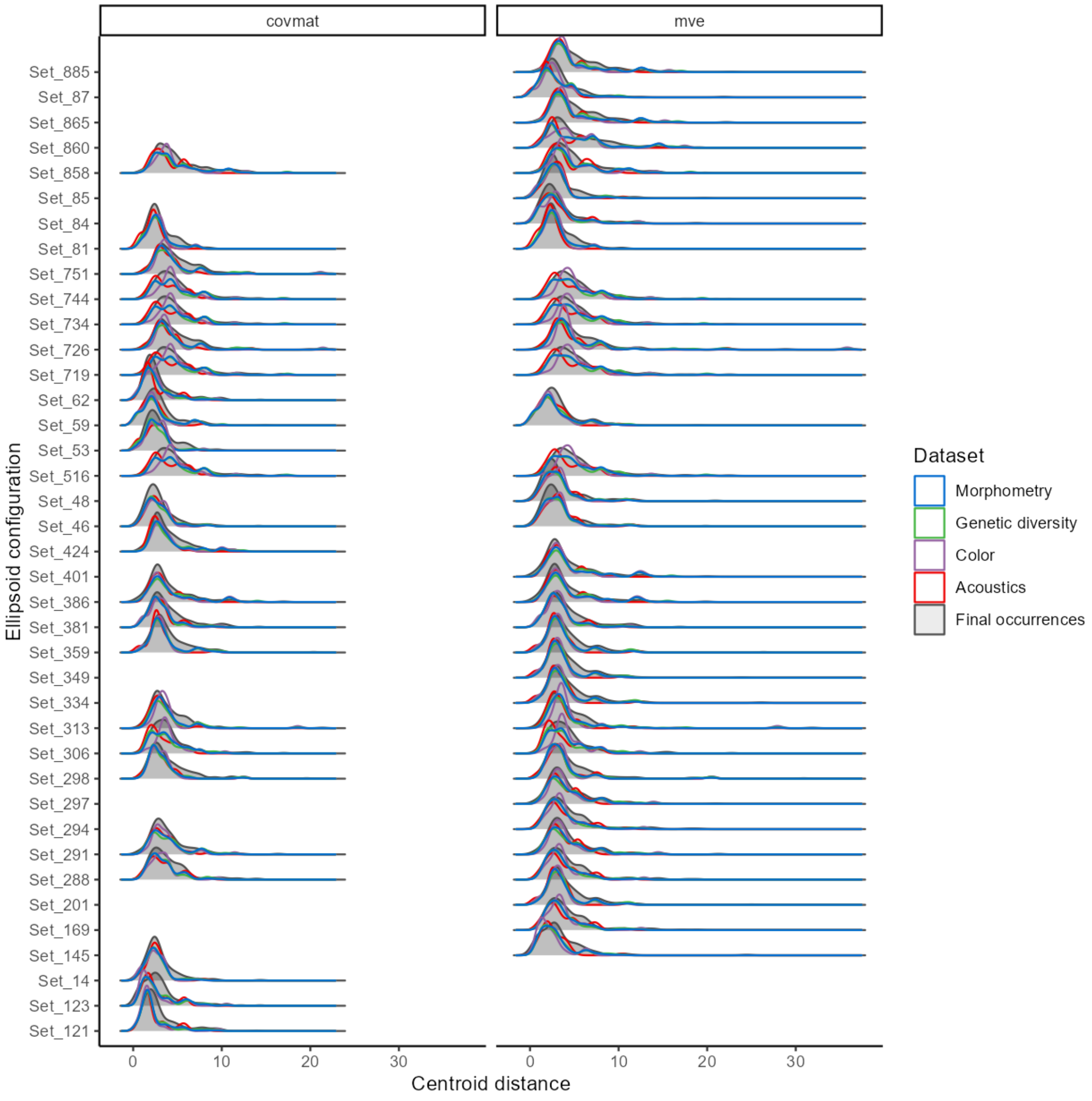


Fig. S2. Niche centroid distances density in each trait dataset per ellipsoid configuration. The black-shaded area shows the centroid distance covered by the final occurrences of the Antioquia Wren from GBIF used for the ecological niche model.

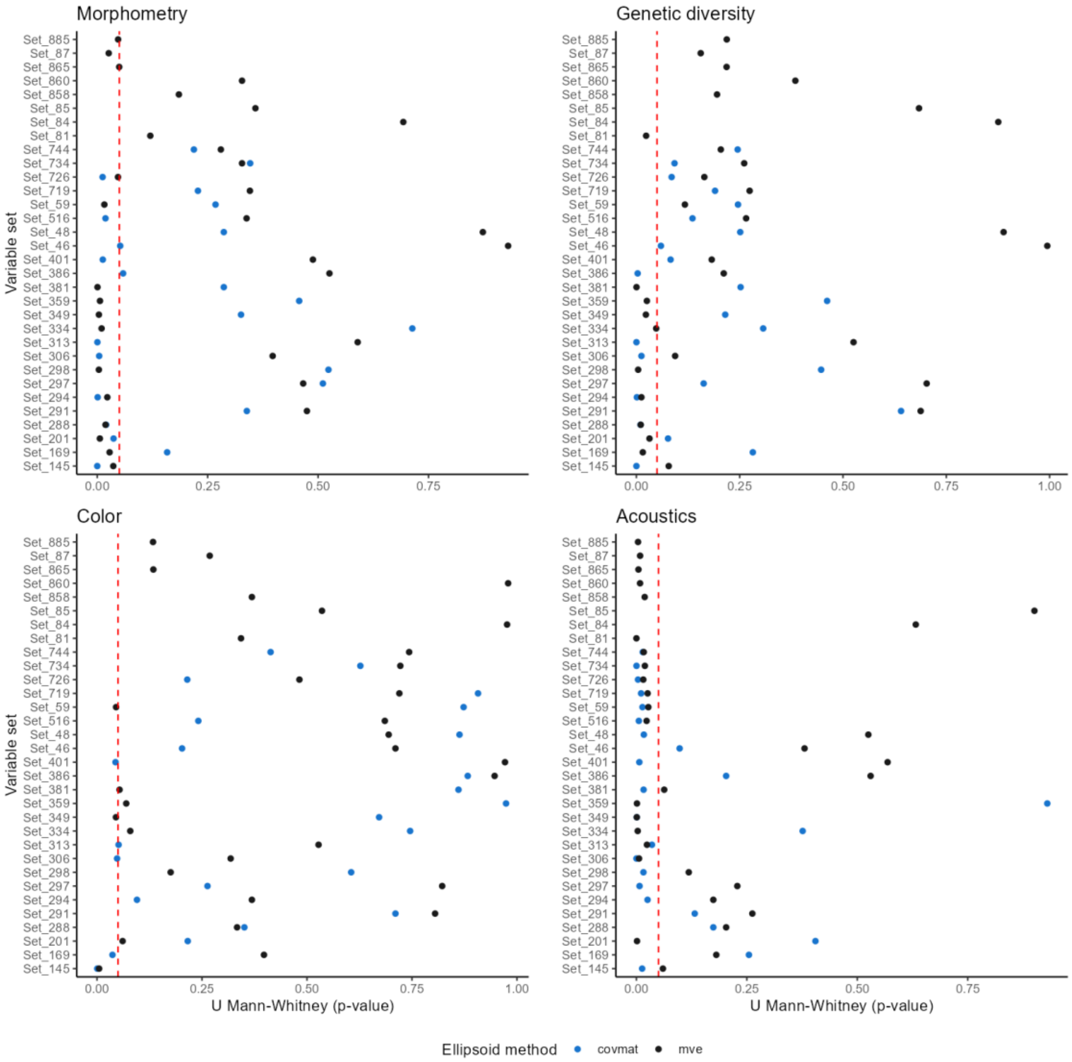
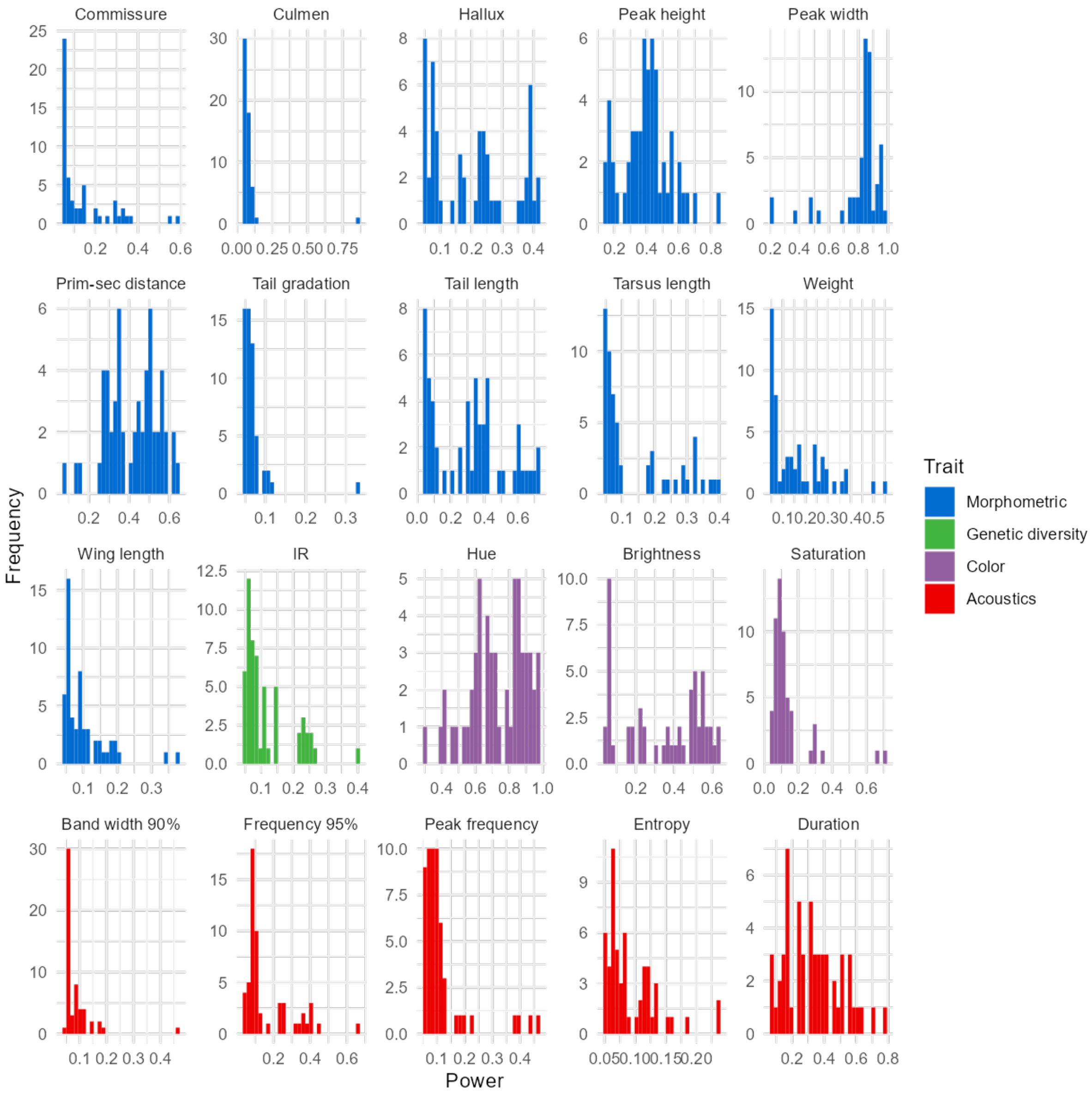


Fig. S3. U Mann-Whitney p-value test between the centroid distance of the final database and each trait data set per ellipsoid configuration. Blue dots: covmat method for ellipsoid configurations; black dots: MVE method for ellipsoid configurations. The red dotted line shows P=0.05; hence, the left dots represent the ellipsoid configuration for which the distance between the centroids of both final occurrences and traits is a statistically significant difference between the two groups.



47
48 **Fig. S4**. Frequency distribution of statistical power for the models for each trait.