



Together forever? Hummingbird-plant relationships in the face of climate warming

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Abstract

Identifying species' extinction risks and understanding their ecological associations are considered critical steps for achieving long-term conservation of biodiversity in the face of global changes. We evaluated the potential impact of global climate change (GCC) on the co-distribution patterns of 12 Mexican endemic hummingbirds and 118 plants they used as nectar resources. Using ecological niche modeling, we estimated the species' potential distribution areas and their degree of range overlap at present and under future scenarios (2040's–2080's). We then performed temporal beta diversity analyses (based on Sorensen's index) to assess changes in community assembly over time. To determine the potential impacts of GCC on the organization of hummingbird-plant relationships, we calculated niche overlap and network size metrics. Our results showed that even if we assume that species can disperse to novel habitat areas, at least 46.2% of hummingbirds and 45.8% of plant species will face range reductions due to changes in their climate-suitability areas, which will in turn result in an increased mismatch of their co-distribution patterns. Additionally, temporal beta analyses suggested species turnover between the present and future, as well as changes in niche size and overlap for hummingbird-plant co-occurrence networks. These changes could lead to the formation of novel assemblages through species reshuffling, with a tendency to the specialization of networks. These results emphasize that we should not expect uniform or matched responses among species and regions into the future. Therefore, analyses of species' co-occurrence are needed to accomplish the long-term protection of important ecosystem services such as pollination.

Keywords Global changes · Biotic interactions · Ecological niche modeling · Co-occurrence networks · Pollination networks

1 Introduction

Biotic interactions are considered an essential component of biodiversity because of their important role in maintaining communities' ecological dynamics (Thompson 2009; Simmons et al. 2018) and key ecosystem properties (i.e., stability, resilience, and

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resistance; Bascompte and Jordano 2013). Also, by maintaining ecosystem functions, biotic interactions mediate species' responses to global environmental change (Tylianakis et al. 2008). Species can only interact if they are simultaneously present. Unraveling species' co-occurrence patterns (i.e., range overlap) is a crucial first step toward understanding how global change may impact the interactions between species and throughout the community assembly (including species interactions). However, there are still large literature gaps in this area (Heinen et al. 2020).

Synergistic and individual effects of land use and global climate changes (GCC) may intensify extinction risk and redistribute biodiversity (Ceballos and Ehrlich 2018; Lovejoy and Hannah 2019). In this sense, landscape homogenization is expected to lead to large-scale compositional shifts (i.e., local extinction of species and/or replacement by newcomers) as well as the modification (i.e., novel, altered, or lost) of ecological interactions (Blois et al. 2013), ecosystem functioning, and the services provided by them (Senapathi et al. 2015; Kovács-Hostyánszki et al. 2017). Loss of key ecological interactions such as pollination and seed dispersal can have detrimental impacts on ecosystems and even cause their collapse, mainly because many species cannot complete their life cycles without their interaction partners (Jordano 2016a). In fact, several studies have documented pollinator declines and the threats behind them (e.g., Potts et al. 2016; Kovács-Hostyánszki et al. 2017), which has led to pollinators becoming the focus of current international concern. Hence, accounting for the complex interplay between climate and habitat change and the organization of biotic interactions is considered a research priority in order to achieve long-term conservation targets (García-Callejas et al. 2018; Pearson et al. 2019; García-Callejas et al. 2019; Regolin et al. 2020).

To address these challenges, methodological frameworks such as ecological niche and species distribution models have been increasingly used to explain, understand, and predict the spatio-temporal distribution of biodiversity (see Peterson et al. 2011). The use of these methodologies has exploded over the past 2 decades, with more than 6000 studies on biodiversity assessments in the past 20 years (Araújo et al. 2019). However, despite the extensive use of tools that are well suited to describing species' co-occurrence patterns, community assembly and potential species interactions are often overlooked in the literature and when designing specific management efforts (Palacio and Girini 2018; Ramírez-Ortiz et al. 2020; Heinen et al. 2020). This is an important information gap because changes in biotic associations can be as relevant as changes in temperature and precipitation, if not more so (Araújo and Luoto 2007; Şekercioğlu et al. 2012; Luna et al. 2022).

Currently, an approach to deal with this problem is the use of co-occurrence networks, in which species are treated as nodes and their co-occurrences as links. These are helpful for inferring potential broad-scale interactions between species and for understanding the organization of biotic associations across time and space (Araújo et al. 2011; Corro et al. 2019; Antoniazzi et al. 2020). In fact, network size (i.e., number of species in the network) and niche overlap (i.e., mean similarity in interaction pattern between species of the same trophic level) are two network descriptors that could be suitable for evaluating co-occurrence networks (Dormann et al. 2009). Although this approach has its limitations (see Blanchet et al. 2020), it is an important first step to improve our knowledge of species assembly in the face of rapid global change (Morueta-Holme et al. 2016).

Hummingbirds (Aves: Trochilidae) are an ideal model to explore the relationships between the spatio-temporal distribution of biodiversity and biotic interactions. These specialized nectarivorous birds play an important role in ecosystem functioning by pollinating

nearly 15% of the plant species in North and South America (Buzato et al. 2000; Able 2000). At the same time, they are considered one of the most threatened groups in the world (<https://www.iucnredlist.org/>). Predictions of extinction risk in hummingbirds are not optimistic, since population declines and important habitat reductions are expected as a consequence of global environmental changes (e.g., Infante et al. 2020b; Chávez-González et al. 2020; Prieto-Torres et al. 2021). Moreover, the spatio-temporal distribution patterns of hummingbirds could also vary due to the flowering phenology of the plants they use as nectar resources (Correa-Lima et al. 2019; Infante et al. 2020a; Chávez-González et al. 2020). Such changes in floristic composition and phenological overlap represent further challenges for plant–hummingbird interactions in the future. Given that a reduction in these pollinators could create a feedback loop with biodiversity loss and degradation of ecosystem services (e.g., Ollerton et al. 2011), it is imperative to evaluate the susceptibility of these interactions to GCC.

The hummingbird species of Mexico are no exception to these future critical-reduction scenarios, including both currently threatened and non-threatened species. Recent studies have shown that climate warming could have a serious negative impact on individual species by decreasing their abundance, increasing their extinction risk, and even reorganizing entire communities throughout the country in the coming decades (e.g., Correa-Lima et al. 2019; Chávez-González et al. 2020; Prieto-Torres et al. 2021). More importantly, results reinforce the idea that current protected areas are not effective for safeguarding these species at present, nor will they be in the future (Prieto-Torres et al. 2021). However, an important drawback of that study is that only climate-suitability effects were considered when modeling the hummingbirds' distribution under future GCC scenarios. Biotic effects, such as changes in the floristic composition or in hummingbird-plant co-occurrence patterns, were not evaluated. So, the impacts and extinction risks may be even more drastic, especially for globally threatened and endemic species. Furthermore, a recent study assessing hummingbird-plant communities' vulnerability to GCC suggests that in North America, species in the network periphery will be more impacted than those core (generalist) taxa with the ability to connect to many mutualistic partners distributed throughout the network (Sonne et al. 2022). These predicted impacts on network roles could have important consequences in network structure, favoring the generalization of hummingbird communities. Therefore, future conservation efforts should consider both biotic and abiotic information to detect which species and regions are most resilient to biodiversity loss (see Pearson et al. 2019).

In this work, we sought to answer the following questions: (1) how could predicted GCC impact niche overlap and the size of co-occurrence networks of Mexican endemic hummingbirds and the plants they pollinate? And (2) does climate-driven redistribution of birds and plants indicate the uneven replacement of specialists by generalists across the region? We assumed that because future environmental change will potentially produce species-specific responses—such as distributional shifts (e.g., elevational ranges and local abundance) and migration patterns—it may lead to uneven modifications of the species co-occurrence patterns and, consequently, alter the interspecific dynamics that control interactions (McConkey and O'Farrill 2015; García-Callejas et al. 2018, 2019). An understanding of this information will facilitate decision-making to support rational biodiversity protection. This is especially critical because the conservation possibilities for hummingbirds and other pollinator communities will drastically decrease over time (see Dicks et al. 2016; Potts et al. 2016).

2 Methods

2.1 Species selection and historical records

Species selection was based on the diversity within the interaction networks of 12 hummingbird species that are endemic to Mexico (Arizmendi and Berlanga 2014) and the availability of biological information and occurrence data of the plants pollinated by them. The plant list was compiled from two sources: (a) specialized literature (see Online Resource 1) and (b) the taxonomic identification of specimens that were recorded as nectar resources and photographed in online databases (EncicloVida [<https://enciclovida.mx/>], eBird [<https://ebird.org/explore>] and iNaturalista [<https://www.naturalista.mx/>]). In sum, occurrence records for 118 plant species were assembled, excluding plants that are exotic in Mexico. All hummingbird species' names followed Chesser et al. (2020) and plant names followed the *Linear Angiosperm Phylogeny Group* taxonomy (The Angiosperm Phylogeny Group et al. 2016).

For each species, occurrence records were obtained from different scientific collections and online collaborative public databases (Global Biodiversity Information Facility [GBIF; <https://www.gbif.org/>], SNIB [<https://www.snib.mx/>], eBird, SiB-Colombia [<https://sibco.lombia.net/>]). The information from GBIF was downloaded directly using the "rgbif" library of R software (Chamberlain et al. 2021). To avoid uncertainties related to geocoding errors that affect model performance (Beck et al. 2014), a data cleaning process was performed for each species. This process consisted of four steps: (a) the removal of records without latitude–longitude coordinates or that had data transcription errors (e.g., reversed latitude and longitude fields), (b) the exclusion of records that did not have data for the bioclimatic variables used, (c) removal of data falling outside the year interval from 1970 to 2021, and (d) elimination of occurrences that were repeated among sources and retaining only information corresponding to unique localities within a vicinity of ~5 km² (i.e., same to spatial resolution of bioclimate variables).

We decided to exclude records from years prior to 1970 because important climate changes have been recorded over the past 4 decades (Fick & Hijmans 2017; Karger et al. 2017), such that the climates at those localities may have changed substantially since the time of collection, which could affect the reliability of our models. Moreover, for records from 2001 to 2021, an outlier exclusion procedure was performed in the environmental space by removing localities where temperature and precipitation values (based on annual mean temperature [Bio 01], annual precipitation [Bio 12] and precipitation seasonality [Bio 15]) were outside of the limits (considered at the upper and lower quartiles) defined by occurrence data within the time range (1970–2000) of bioclimatic variables (Robertson et al. 2016; Prieto-Torres et al. 2020). This latter step was important for identifying problematic or imprecise occurrences with incorrect climate values (Roubicek et al. 2010; Pérez-Navarro et al. 2021).

Additionally, to avoid biases derived from spatial autocorrelation in areas that were heavily represented in the data, we only retained localities that were farther from each other than the mean distance between occurrence records for each species (e.g., Aiello-Lammens et al., 2015; Prieto-Torres et al., 2021). All data were transformed to decimal degrees based on the WGS84 datum. Species with unbiased distributions (i.e., with a good representation of their known geographic distribution) and with a minimum of 10 records were selected. After all of these steps, there were a total of 71,285 unique occurrence records for all hummingbirds and plant species (see Online Resource 2).

2.2 Ecological niche modeling and validation

The maximum entropy algorithm implemented in MaxEnt ver. 3.4.3 (Phillips et al. 2017) was used to model climatic suitability for the potential distributional areas per species. This algorithm estimates the probability of suitability, ranging from 0 [unsuitable] to 1 [perfectly suitable], for each pixel given a sample of the background, following the idea that the expected value for each feature (i.e., climatic variables) must be equal to the empirical average value of presence points of the species (Phillips et al. 2006; Elith et al. 2006, 2011). This algorithm was selected for its good performance using presence-only data (Elith et al. 2011) and because it allows a calibration protocol to assess model complexity by selecting the best modeling parameters (see Muscarella et al. 2014; Cobos et al. 2019).

To characterize the species' ecological niches, environmental data from WorldClim 2.1 (at $\sim 5 \text{ km}^2$ cell size resolution; Fick and Hijmans 2017) was used. Four bioclimatic variables were excluded (bio 8, bio 9, bio 18, and bio 19) because they showed spatial anomalies in the form of odd discontinuities between neighboring pixels (Escobar et al. 2014). Furthermore, to avoid the overfitting and overestimation of model accuracy that can occur with an overly dimensional environmental space and collinearity among variables, two approaches were applied: (1) selection of a subset of uncorrelated variables based on a Pearson's correlation coefficient ($r < 0.8$) and variance inflation factor ($\text{VIF} < 10$) and (2) derivation of a set of four variables that explained up to 95% of the total variance using a principal component analysis (PCA; see Hanspach et al. 2011). The selection of the variables set was performed using the statistical software R 3.4.1 (R-Core Team, 2018) and the packages "*usdm*" (Naimi, 2015) and "*ENMGadgets*" (Barve and Barve, 2016). In addition to climate variables, we included elevation (USGS 2001), which has been used in numerous studies as a proxy for variables (e.g., microclimate or edaphic conditions) that are correlated with the physiological requirements of species (e.g., Rheingantz et al. 2014; Kübler et al. 2016).

On the other hand, given that dispersal plays a crucial role in the distribution of organisms and must be considered in the development of such models (Barve et al. 2011), an area for model calibration, known as "M," was created (Soberón and Peterson 2005). For each species, this area (a GIS mask) was defined by intersecting the occurrence records with the terrestrial ecoregions (Dinerstein et al. 2017) and the biogeographical provinces of the Neotropics (Morrone 2014) and excluding any grid cells outside these regions. This consideration was based on the assumption that these regions may define the historically accessible areas (because there are no ecological or geographical barriers that prevent access) for each species in geographical space (Soberón and Peterson 2005).

For all cases, models were generated using a randomly selected subset of 75% of the records as training data and the remaining 25% for model evaluation (testing data). To reduce model overfitting, models were first calibrated by creating 1080 candidate models (per species), with parameterizations resulting from the combinations of 18 regularization multipliers (β : 0.5–8.0), 15 feature classes (i.e., combinations of linear, quadratic, product, and threshold responses), and the four distinct sets of variables (un-correlated variables, with and without elevation vs. principal component analysis, with and without elevation). The models for each species were selected based on their significance according to the following parameters: partial ROC test (with $E = 5\%$, 500 iterations, and 50% of data for bootstrapping; see Peterson et al. 2008), omission rates lower than a previously defined error rate ($E = 5\%$; Anderson et al. 2003), and the lowest Akaike information criterion value (Muscarella et al. 2014; Merow et al. 2014), in that order. The chosen predictors and parameter

settings were used to create final models with 10 replicates by bootstrap, *cloglog* outputs (Phillips et al. 2017), and transferred to present and future global environmental scenarios (see below). Final model projections were created allowing “unconstrained extrapolation” and “extrapolation by clamping” in Maxent (Elith et al. 2011; Merow et al. 2014). All modeling processes were performed using the “*kuenm*” R package (Cobos et al. 2019).

After all, models were generated; the distribution maps for each species under each climate scenario (current vs. future [see below]) were created. To do that, median values across replicates were calculated to summarize model predictions (Campbell et al. 2015). Then, the logistic values of suitability were converted from each model into a presence-absence map by setting a decision threshold equal to the tenth percentile training presence, which reduces commission errors (areas of over-prediction; Liu et al. 2013). For all plant species, models were calibrated using the available data for their entire current range and then cropped to the approximate geographic extent of Mexico.

2.3 Future climate change and dispersal scenarios

The potential distribution areas for individual species and hummingbird-plant assemblages were predicted for the years 2040, 2060, and 2080. Variables for future climate projections were based on the Coupled Model Intercomparison Project 6 (CMIP6; Stoerk et al. 2018). From the CMIP6, five general circulation models (CanESM5, MIROC6, BCC-CSM2-MR, CNRM-CM6-1, and IPSL-CM6A-LR) and an intermediate Shared Socio-economic Pathway scenario (i.e., SSP3 7.0) that assumes a high greenhouse gas emission and low climate change mitigation policies (Riahi et al. 2017) were selected. These general circulation models were selected based on: (1) the results obtained from GCM compareR’s web application (Fajardo et al. 2020) adopting the “storyline” approach (Shepherd et al. 2018), as implemented by Prieto-Torres et al. (2021), and (2) the demonstrated improvements in the estimation of zonal-mean atmospheric fields, equatorial ocean subsurface fields, precipitation values, and the simulation of El Niño-Southern Oscillation in the Americas (e.g., Zelinka et al. 2020; Boucher et al. 2020).

For each species, the future (years 2040, 2060, and 2080) geographic distribution was obtained by manually overlaying the binary projections from the five global climate models, allotting “presence” to a pixel where most of the predictive models coincided (i.e., suitable in three or more general circulation models). Then, the loss and gain of suitable habitats were calculated by comparing the geographic projections of niche models in current and future scenarios. The comparisons were categorized as follows: (a) when current and future areas were suitable, these were defined as stable suitable areas; (b) when the current was suitable and the future not suitable, loss of suitable areas was defined; and (c) when the current was not suitable and the future was suitable, gains of suitable areas were identified. These areas of stability, gain, and loss were calculated (in km²) for all species under two different dispersion scenarios: “contiguous dispersion” vs. “non-dispersion.” In the contiguous dispersion scenario, it is assumed that species would be able to disperse through continuous habitat but not jump over barriers (i.e., all the cells with suitable conditions within “M” in the future are considered part of its future distribution range). In the non-dispersion scenario, species are assumed to be unable to disperse at all (i.e., only cells that are occupied in the present can be occupied in the future). The “non-dispersion” scenario only allows for decreases in the distributional range in response to GCC; therefore, it is the most “unfavorable” for the species (see Prieto-Torres et al. 2021). All Ecological Niche Modelling processing was performed using the “*maptools*” (Bivand et al. 2016),

“*raster*” (Hijmans et al. 2015), and “*LetsR*” (Vilela and Villalobos 2016) R packages. For each dispersal assumption scenario, a Kruskal–Wallis test was performed to determine whether species’ vulnerability to GCC (change in range size) differed between habitat generalists and habitat specialists (see Online Resource 2).

2.4 Model uncertainty

Mobility-oriented parity was implemented using the “*ntbox*” R package (Osorio-Olvera et al. 2020) to measure the risk of strict extrapolation into future species’ models resulting from projections to non-analogous conditions. The MOP consists of measuring the similarity between the closest 10% of the environmental conditions of the calibration area to each environmental condition in the area of transference (see Owens et al. 2013; Alkische et al. 2017). Areas of projection with values of similarity of zero indicate higher uncertainty, as suitability in those regions derives from model extrapolation only, and caution is required when interpreting the likelihood of species presence in such areas (Alkische et al. 2017). Binary maps of MOP results were generated considering only areas with zero similarity as strict extrapolation areas.

2.5 Spatio-temporal patterns of species co-distribution

To identify the spatial patterns for hummingbird-plant assemblages, we first constructed a site \times species presence–absence matrix (PAM) for each climate scenario and dispersal ability assumption by overlaying the estimated distribution of each species on an equal-area grid of 5×5 km² spatial resolution. Then, the areas of high/low expected hummingbird-plant richness were identified employing a color gradient with four equal intervals overlapping the two PAMs (hummingbirds vs. plants). Using “*tempbetagrid*” functions for R (kindly provided by José Hidasí-Neto; available at: <http://rfunctions.blogspot.com/>), the temporal beta diversities between the present and future scenarios of each cell (i.e., species turnover from present to future) were calculated. Subsequently, to assess the potential modification in co-occurrence patterns across time, the geographic patterns between each endemic hummingbird and the plants it feeds on were compared, considering only the species that are known to interact in the present. This allows the identification of potential disruptions of important ecological associations between taxa under future climate scenarios.

2.6 Ecological co-occurrence networks

To analyze the impacts of GCC on the structure of hummingbird-plant co-occurrence networks in Mexico, we built additional PAMs of co-occurrences between endemic hummingbirds and the plants they use as nectar resources for each of the biogeographical provinces identified across the country (Morrone 2014) based on information gathered from specialized literature and online databases. To avoid statistical problems due to low sample size, all provinces where less than three hummingbird species and three plant species occurred in the current scenario were eliminated from the analyses. This resulted in comparisons in eight biogeographical provinces: Costa del Pacífico, Depresión del Balsas, Eje Volcánico, Golfo de México, Oaxaca, Sierra Madre del Sur, Sierra Madre Occidental, and Sierra Madre Oriental (Fig. 1).

In sum, we built 56 binary co-occurrence networks for current and future scenarios ($A = i \times j$), where hummingbirds (i) were represented as rows and plants (j) as columns.

All interactions between the i hummingbird species and the j plant species were defined by $A_{ij} = 1$, while the interactions that did not occur were coded as zero. Then, using the package *bipartite* implemented in R (Dormann et al. 2021), two network descriptors (network size and niche overlap) for each hummingbird-plant co-occurrence network per province and climate scenario were calculated. The network size was calculated by multiplying the number of hummingbird species (i.e., rows) by the number of plant species (i.e., columns). Higher network size values indicate more species-rich networks. Niche overlap, based on Horn's similarity index, estimates the degree of similarity among potential hummingbird-plant interactions; high values indicate high similarity between species trophic niches (i.e., low trophic specialization; see Dormann et al. 2009). Finally, generalized linear models (GLMs) using Gaussian distribution were fit to test whether the percentage of change in the network size and niche overlap values differed among climate and dispersal scenarios. When significant differences were observed, contrast analyses were performed using the "RT4Bio" R package (Tylianakis et al. 2008; Reis et al. 2015).

3 Results

3.1 Model statistics

All models were statistically significant, meeting AIC criteria, exhibiting significant values for the partial ROC test (mean AUC ratio of 1.50; $P < 0.05$), and low omission error values (average $3.42 \pm 4.20\%$) for the 10% training presence threshold. Based on these performance estimates, our models were better than random and had good discrimination capacity

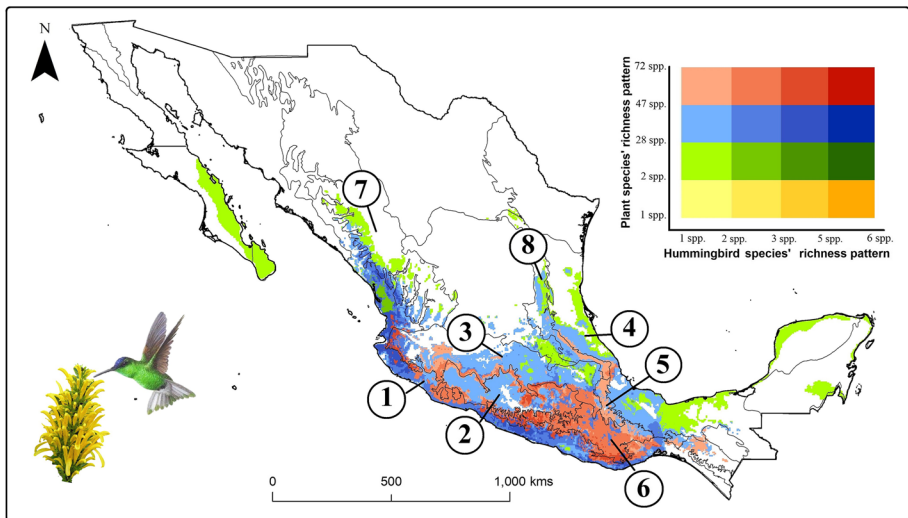


Fig. 1 Map of the current endemic hummingbird-plant richness co-occurrence patterns across Mexico. The color gradient represents species richness patterns, with areas in dark red showing overlap of the maximum richness values for both hummingbird and plant species. Numbers in the map correspond to biogeographical provinces considered in this study: (1) Costa del Pacífico, (2) Depresión del Balsas, (3) Eje Volcánico, (4) Golfo de México, (5) Oaxaca, (6) Sierra Madre del Sur, (7) Sierra Madre Occidental, and (8) Sierra Madre Oriental. The picture in the map depicts the interaction between the hummingbird *Eupherusa cyano-phrys* and the plant *Justicia aurea* (Source: Arizmendi and Berlanga 2014)

in recovering the ecological niches for each species. The environmental variables that were most frequently used ($\geq 55\%$ of the cases) for model construction were Bio 15, Bio 03 (isothermality), and Bio 02 (mean diurnal range). However, according to the Jackknife test and contributing variables test by MaxEnt, the most important variables on average for hummingbirds were bio 12 (35.8%) and bio 14 (precipitation of driest month; 36.53%); while for plant species, the variables bio 01 (28.13%), bio 04 (temperature seasonality; 24.53%), and elevation (24.15%) were the ones that most contributed into the model. For performance values and parameter settings chosen for each species, see Online Resource 2.

3.2 Current species richness and co-distribution patterns in Mexico

Overall, the number of hummingbirds per site (pixel) varied from 1 to 6 species (mean values of 1.86 ± 1.09 spp.), and plant species richness varied from 1 to 72 species (mean 18.72 ± 15.88 spp.). For both hummingbirds and plants, current hotspots (i.e., sites [pixels] whose species richness exceeded half of the maximum values observed) are located mainly in the states of Oaxaca, Guerrero, and Chiapas (Fig. 1). Hummingbird species were associated with between six (*Pampa excellens*) and 42 plant species (for *Phaeoptila sordida*), with an average of 13 ± 10.33 plant species per hummingbird. Plant species interacted with an average of 1.32 ± 0.74 hummingbird species. Our distributional model estimates showed hummingbird-plant spatial coincidence values averaging $62.1 \pm 28.9\%$ km² under the current scenario, ranging from $44.3 \pm 38.5\%$ (*Basilinna xantusii*) to $84.3 \pm 12.9\%$ (*P. excellens*). The hummingbird-plant network analysis showed values, on average, of 0.32 ± 0.10 and 397.13 ± 331.04 for the niche overlap and network size, respectively.

3.3 Impacts of future climate change on species range patterns

Our results suggest that GCC will potentially lead to an important modification in both individual species' ranges and overall species richness patterns for Mexican endemic hummingbirds and their associated plants in the future (see Online Resource 3). In general, future scenarios were similar in their qualitative predictive patterns, although the pessimistic and unfavorable scenarios (i.e., SSP3 7.0 and non-dispersal ability) predicted larger decreases. When assuming a contiguous dispersion scenario, GCC could produce a range expansion for 53.9% of hummingbird species (on average from $33.8 \pm 23.5\%$ [2040's] to $83.8 \pm 65.6\%$ [2080's]) and 45.7% of plants ($25.5 \pm 29.3\%$ [2040's] to $70.5 \pm 87.9\%$ [2080's]). Under the non-dispersal scenario, range reductions were the most plausible response for both hummingbird species (on average from $-11.8 \pm 11.8\%$ [2040's] to $-32.9 \pm 26.9\%$ [2080's]) and plants (from $-17.6 \pm 16.4\%$ [2040's] to $-23.7 \pm 23.5\%$ [2080's]). These unfavorable scenarios predict that 69.2% of hummingbirds and 62.0% of plants might undergo range size reductions of $\geq 10\%$ in future scenarios. This general reduction in the species' distributional ranges is related to changes in climate-suitability (on average 0.02 [2040's]– 0.10 [2080's]) that are currently available. Species' vulnerability to climate change was significantly different across years ($\chi^2 = 47.35$; $df = 5$; $P < 0.01$) and dispersion and non-dispersal scenarios ($\chi^2 = 54.44$; $df = 5$; $P < 0.01$) when comparing between generalist and specialist taxa (Table 1). Moreover, MOP results indicated that strict extrapolative areas occur mostly beyond the potential distributional areas predicted by models in the future climates across Mexico (on average $< 5\%$ of predicted suitable areas match future novel conditions). This shows that non-analogous climate areas were not responsible for our results.

Table 1 Predictions of range change for 12 Mexican endemic hummingbirds and their 118 plants used as nectar resources considered in this study based on their habitat specificity (generalists vs. specialists). For hummingbirds, the species' ecosystem specificity was determined from Rodríguez-Flores et al. (2019), while for plants information was obtained using the published endemicity indexes by Linder (2001; i.e. number of ecosystems in which a given species was reported as present by our models)

Mean and standard deviation for observed range change		
	Dispersion scenario	Non-dispersion scenario
Hummingbirds		
2040's		
Generalists	20.65 ± 34.59%	− 13.51 ± 12.18%
Specialists	17.94 ± 19.92%	− 3.42 ± 4.83%
2060's		
Generalists	16.91 ± 57.02%	− 23.53 ± 19.69%
Specialists	− 4.79 ± 2.15%	− 10.77 ± 3.21%
2080's		
Generalists	14.79 ± 85.53%	− 35.08 ± 28.66%
Specialists	− 18.57 ± 21.64%	− 22.31 ± 18.61%
Plants		
2040's		
Generalists	12.41 ± 20.85%	− 20.6 ± 16.62%
Specialists	20.73 ± 40.62%	− 7.93 ± 11.40%
2060's		
Generalists	2.25 ± 33.84%	− 18.95 ± 17.32%
Specialists	28.28 ± 63.16%	− 12.13 ± 16.89%
2080's		
Generalists	1.95 ± 49.96%	− 26.33 ± 23.42%
Specialists	68.52 ± 132.46%	− 15.40 ± 22.08%

These individual modifications of the species' distributional ranges could thus lead to changes in the spatial patterns of the assemblages across the country (Fig. 2). Overall, the temporal beta diversity values ranged from 0.09 (non-dispersion scenarios) to 0.15 (dispersion scenarios). On average, richness patterns tended to decrease for both hummingbirds (from − 10.5% [dispersion assumption] to − 13.8% [non-dispersion assumption]) and plants (from − 2.8% [dispersion] to − 14.3% [non-dispersion]) in the future (see Online Resource 3). Similarly, hotspot areas were also predicted to decrease in size for hummingbirds (ranging from 19.6% [2040's dispersion] to 72.6% [2080's non-dispersion]) and plants (from 6.8% [2040's dispersion] to 44.6% [2080's non-dispersion]). Furthermore, these hotspot areas for taxa were predicted to have less overlap in the future scenarios (from 24.2% [2040's dispersion] to 12.4% [2080's non-dispersion]) than at present (27.3%).

3.4 Hummingbird-plant co-occurrence networks

The average number of plant species associated with each hummingbird species (13 ± 10.3 spp.) and hummingbird species associated with each plant species (1.3 ± 0.74 spp.) were predicted to remain similar in the future scenarios. However, the hummingbird *Eupherusa cyanophrys* will no longer share distribution with the plant *Justicia aurea* by the 2080's, even under the favorable dispersion scenarios. Moreover, reductions of 5.9% [dispersion scenario] to 6.8% [non-dispersion scenario] in the area of co-occurrence between hummingbirds' and plants' geographic were also predicted. Two hummingbird species—*Eupherusa ridgwayi* and *Pampa excellens*—are expected to be

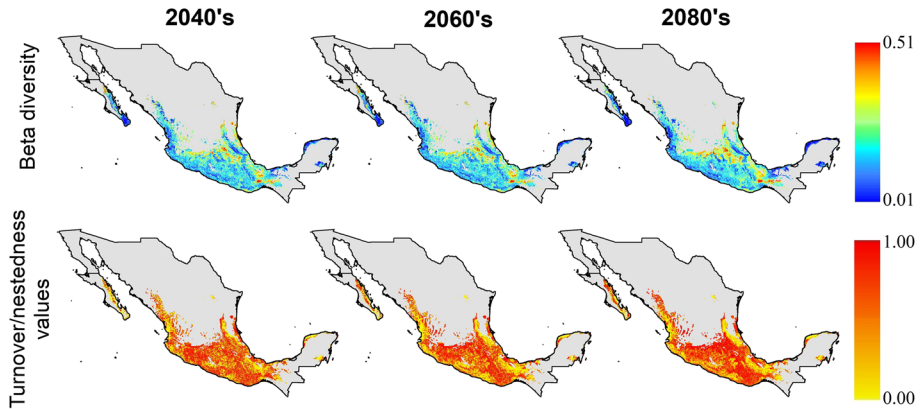


Fig. 2 Spatio-temporal patterns for beta diversities of Mexican endemic hummingbird and plant species projected onto future climate scenarios (years 2040, 2060, and 2080) under an intermediate Shared Socio-economic Pathway scenario (i.e., SSP3 7.0) and assumption of dispersion for taxa. Maps of temporal beta diversity show the dissimilarity/similarity values for communities between the current and future scenarios within each cell; maps of turnover/nestedness indicate whether estimated temporal beta diversity values are more related to changes in species composition or to species losses/gains

the most strongly affected, with reductions of > 18% of the spatial coincidence with their associated plants under either dispersion scenario. On the contrary, *Selasphorus heloisa* will potentially increase (on average > 4%) the proportional area of co-occurrence with its associated plants.

We observed differences between the current and future scenarios when analyzing the percentage change in niche overlap and network size (Fig. 3; GLM: all P -values < 0.05). The hummingbird-plant co-occurrence network analyses for the future showed an increase in size values under both dispersion scenarios (410.4 ± 368.7 [non-dispersion scenario] and 604 ± 308.1 [dispersion scenario]). On the contrary, niche overlap values did not change in the non-dispersion scenarios (Horn's index: 0.32 ± 0.1) but decreased (Horn's index: 0.27 ± 0.07) under the dispersion scenario. Overall, the following patterns emerged from our projections: (1) changes in network size will be largest in the year 2040 under the dispersion scenarios ($F = 2.97$, $P = 0.02$); (2) changes to niche overlap were higher under all future scenarios that assumed dispersion ($F = 4.20$, $P < 0.01$); and (3) the provinces most affected by this change will be Oaxaca (for both niche overlap [21.8% of change observed] and network size [147.0% of change]), Sierra Madre del Sur (niche overlap [20.6% of change] and network size [32.6% of change]), and Sierra Madre Oriental (for network size [111.9% of change]) (Table 2).

4 Discussion

Several studies have investigated the potential impacts of climate variations on animal-plant networks, mainly for insects and host species or plants (see Schweiger et al. 2008; Gorostiague et al. 2018). Fewer studies have addressed how GCC could affect interspecific relationships among vertebrates, with the exception of frugivorous birds, carnivorous mammals, and pollinator-bats (e.g., Pandey and Papeş 2018; Scully et al. 2018; Nowak et al. 2019; Corro et al.

2021). Although there is still debate about the link between co-occurrence data and species' interactions (see Jordano 2016b; Blanchet et al. 2020; Chávez-González et al. 2020), it is a truism of ecology that species must co-occur to directly interact. From this perspective, changes in the co-occurrence networks will probably have variable effects depending on the species, but for hummingbirds and their plants, important negative effects seem likely in the future. Our results show that endemic hummingbirds and plants are likely to undergo changes that are not uniform and differ among groups of species across Mexico in the future.

These results are in agreement with other studies in Mexico, suggesting that the estimated patterns of change for biota are attributed to the expected increase in the average temperature and decrease in annual precipitation (see Cuervo-Robayo et al. 2020). This is of major concern since range reductions will probably affect the physiological responses and activity patterns of individual species and population dynamics, increasing the species' vulnerability to global extinction (Tylianakis et al. 2008; Sonne et al. 2022), especially if species are not capable of quickly adapting to new environmental conditions. In fact, although upslope shifts have been predicted for hummingbird and plant species in the future (Buermann et al. 2011; Crimmins et al. 2011; Graham et al. 2017; Correa-Lima et al. 2019), many studies reported declines in wing-loading capacity and flight-limited performance traits for hummingbirds at higher altitudes along elevational gradients (Altshuler et al. 2004; Correa-Lima et al. 2019). From this perspective, more studies analyzing the ability of these taxa to rapidly adapt or move into new areas are encouraged (see Sousa et al. 2021).

On the other hand, climate-driven range shifts may cause modifications in the co-occurrence patterns of taxa and on communities' structure through species' reshuffling

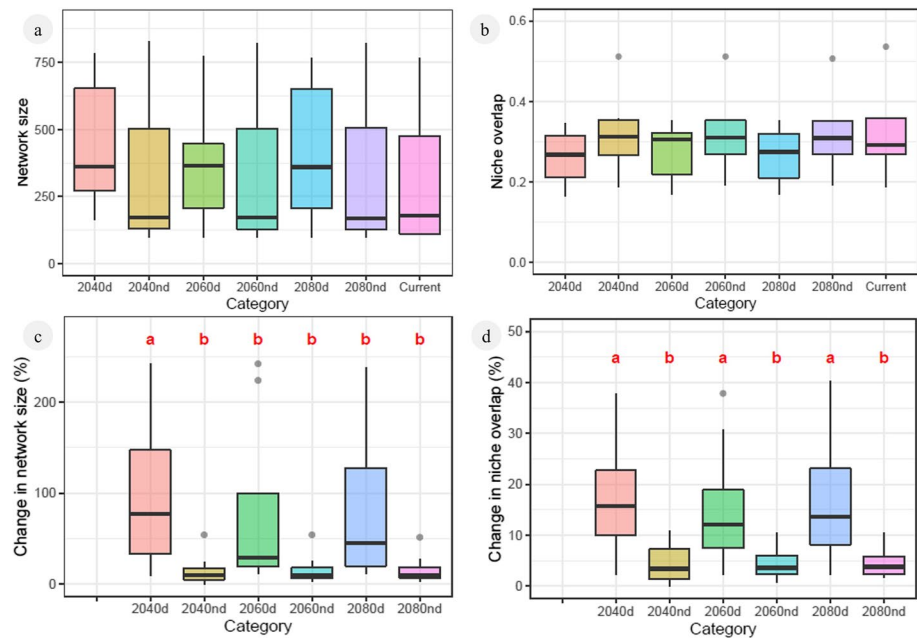


Fig. 3 Summary of patterns of change observed in network size **a, c** and niche overlap **b, d** in the hummingbird-plant co-occurrence network under future climates, considering an intermediate Shared Socio-economic Pathway scenario (i.e., SSP3 7.0) and two assumptions of dispersion for taxa: contiguous dispersion **d** vs. non-dispersion scenarios (nd). Red letters indicate statistical differences (GLM: all P-values < 0.05) between scenarios

Table 2 Summary of niche overlap and network size metrics for the hummingbird-plant co-occurrence patterns across eight Mexican biogeographical provinces under future climate scenarios (years 2040, 2060, and 2080) based on intermediate Shared Socio-economic Pathway scenario (i.e., SSP3 7.0) and two dispersion assumptions

	Costa del Pacífico	Depresión del Balsas	Eje Volcánico	Golfo de México	Oaxaca	Sierra Madre del Sur	Sierra Madre Occidental	Sierra Madre Oriental
Niche overlap								
Current	0.19	0.28	0.28	0.36	0.54	0.24	0.30	0.36
Dispersion scenario								
2040's	0.17	0.23	0.23	0.35	0.33	0.17	0.31	0.30
2060's	0.17	0.24	0.30	0.35	0.33	0.17	0.32	0.31
2080's	0.17	0.24	0.22	0.35	0.32	0.17	0.32	0.31
Non-dispersion scenario								
2040's	0.19	0.28	0.30	0.35	0.51	0.22	0.32	0.36
2060's	0.19	0.29	0.30	0.35	0.51	0.22	0.32	0.35
2080's	0.19	0.29	0.30	0.35	0.51	0.22	0.32	0.35
Network size								
Current	950	574	378	111	111	765	180	108
Dispersion scenario								
2040's	1177	783	744	248	380	1210	164	345
2060's	1155	774	468	99	380	1210	160	350
2080's	1166	765	744	99	375	1199	160	345
Non-dispersion scenario								
2040's	940	539	468	99	171	828	152	108
2060's	920	532	474	99	171	819	152	105
2080's	920	532	480	99	168	819	152	102

(see Lovejoy and Hannah 2019; Sonne et al. 2022). The spatial mismatches between taxa observed here suggest potential changes in the availability of mutualist partners that could lead to the decoupling of the pollination interaction, with detrimental effects for ecosystems functioning (Visser and Both 2005; Hegland et al. 2009; Correa-Lima et al. 2019).

Moreover, estimations could be more pessimistic considering that plant phenology is frequently impacted by changes in climate (Ponti and Sannolo 2022), which could impact the animals that utilize them. For instance, desynchronization of the flowering period of plants with the activity patterns of pollinators can affect population dynamics and reproductive success for both hummingbirds and plants (e.g., Correa-Lima et al. 2019; Ponti and Sannolo 2022). In fact, it is well known that the flowering times of early-flowering plants appear to be changing more quickly in response to warming temperatures than late-flowering plants, while late-flowering plants are more susceptible to frost at high elevations (Phillips et al. 2018; Powers et al. 2022). Such changes might impact survivorship and nesting success in hummingbirds, particularly for altitudinal and latitudinal migratory species that depend on the availability of floral resources along their migratory route and will not be able to adjust their arrival to their breeding grounds (McKinney et al. 2012; López-Segoviano et al. 2018; Ponti and Sannolo 2022).

Reduced floral resources for pollinators could have detrimental impacts on ecosystems because many species will not be able to complete their life cycles in the future (Scaven and Rafferty 2013; Takkis et al. 2018). In the case of highly specialized hummingbird-plant relationships, it is unlikely that other animals would take over pollination if hummingbirds are absent (Linhart and Feinsinger 1980), increasing the co-extinction risk for species (see Sonne et al. 2022). Nonetheless, hummingbird-plant networks are known to be highly dynamic, with species turnover and rewiring (not evaluated here) acting as the primary drivers of spatio-temporal changes in the composition of interactions. It is therefore possible that network plasticity could mitigate the effects of GCC scenarios on plant reproduction and hummingbirds' food resources (Poisot et al. 2012; CaraDonna et al. 2017; Correa-Lima et al. 2019; Chávez-González et al. 2020). However, this issue remains poorly studied.

Here, predicted species turnover patterns and changes of network size/niche overlap values suggest that several species will probably not be able to colonize novel areas in the future. The factors that influence a species' potential to establish and survive in new areas are difficult to predict, so these results should be interpreted with caution. However, there is evidence that new assemblages could form in locations that are currently at the extreme ends of the environmental gradient, like dry regions and high-elevation zones (Graham et al. 2017). The formation of new assemblages could change not only the identity of species in the network but also network properties such as nestedness and specialization (see Dormann et al. 2009). This is relevant because small-range species are typically habitat specialists (Sonne et al. 2016), so they may not be able to colonize new areas or persist in novel conditions in the near future (Broennimann et al. 2006).

Past and contemporary climates play an important role in determining specialization on mutualistic systems (Dalsgaard et al. 2011). Temperate hummingbird-plant networks were less specialized than tropical networks (measured with network-level contemporary specialization, Blüthgen et al. 2006), and this pattern was tightly linked to species-poor networks, low contemporary precipitation, and high quaternary climate-change velocity. This climatic scenario favored low biotic specialization and local adaptations in North American hummingbird-plant communities (Dalsgaard et al. 2011). Due to the predominance of generalist hummingbird clades (Bees and Emeralds) in North America and hummingbird

communities' ability to colonize new areas and access different floral resources (Rodríguez-Flores et al. 2019), we initially expected an uneven replacement of specialists by generalists under future climate change. However, we found lower values of niche overlap in future scenarios that assume species will be able to disperse, suggesting a tendency toward network specialization rather than generalization. Specialized network structures may mitigate the effect of coextinctions, as there is little overlap between species' foraging niches, so species are more vulnerable to the loss of their mutualistic partners than to the loss of other species' partners (Sonne et al. 2022). Although changes in community structures due to climate change might favor these patterns, it is important to highlight that this work includes only a small subset of co-occurrence networks, since only endemic hummingbird species were studied. Thus, future research incorporating all Mexican hummingbirds and their associated plants is needed.

Whether GCC will affect ecosystem functioning depends on how interactions among species are affected (Hegland et al. 2009), it is important to highlight that communities, where niche overlap and competition are high, tend to be more unstable and less resilient to change (Pastore et al. 2021; Sonne et al. 2022), though colonization by generalist species could compensate for local extinctions to some extent. From this perspective, special attention must be paid to the provinces of Oaxaca, Sierra Madre del Sur, and Sierra Madre Oriental (Table 2). According to our results, they are expected to be the most affected provinces in the future by GCC. However, these regions are considered hotspot areas for both hummingbird and plant species, at the same time as being high-priority conservation areas for hummingbirds under climate and land-use changes (see Prieto-Torres et al. 2021). We therefore argue that it is important to include relevant biotic interactions in the prediction of GCC impacts in order to increase the accuracy of model forecasts. We also recommend additional fieldwork to test the projections based on our results to obtain reliable knowledge of both species and assemblage responses to future environmental scenarios.

While this study is the first approach for understanding hummingbird-plant co-occurrence patterns in the face of global changes, future research incorporating more network metrics and relevant ecological information such as phenology, morphology (body size, beak length, and curvature, corolla length and curvature) and a hummingbird and floral abundances is needed. Also, further analyses incorporating other factors that influence species co-occurrences at fine scales, such as land-use change, are critical, because circumstantial evidence suggests that hummingbird-pollinator losses due to deforestation intensification are already happening (Infante et al. 2020b). In sum, the main lesson from this study is that dedicating more land per se to conservation will not guarantee the medium and long-term conservation of biodiversity and important ecosystem services like pollination. It is imperative that policy makers promote new policies that take into account species interactions, and our results constitute a valuable guide for using scientific evidence of which species and areas require attention to achieve more efficient conservation planning in Mexico.

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