

## Research Letters

## Most Mexican hummingbirds lose under climate and land-use change: Long-term conservation implications

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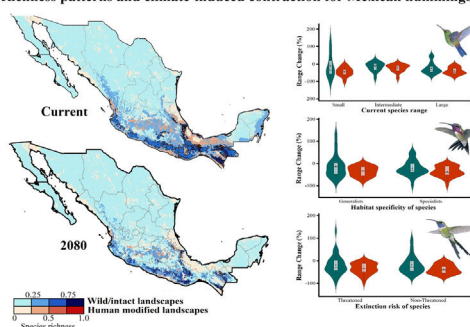


## HIGHLIGHTS

- Global climate and land-use changes will have a serious impact on individual species and communities of hummingbirds.
- Existing protected areas showed an important reduction of surface across the species distribution and hotspot areas for future.
- A large proportion of “safe places” does not match the areas targeted for agriculture expansion in future scenarios.
- It is imperative that policy-makers promote policies that are resilient to both threats as soon as possible.

## GRAPHICAL ABSTRACT

Richness patterns and climate-induced contraction for Mexican hummingbirds



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## ABSTRACT

Hummingbirds are one of the most threatened bird groups in the world. However, the extent to which global climate change (GCC) and habitat loss compromise their conservation status remains unclear. Herein, we proposed to: (1) assess how predicted GCC impacts the distribution of non-migratory hummingbirds according to their conservation status, degree of restriction and habitat specificity; and (2) delineate priority conservation areas where species could persist in the face of both threats. We estimated the potential distributions of 49 species under current and future climates (year 2040, 2060, and 2080), analyzing the effects of current habitat loss and the importance of existing Protected Areas (PAs) on the species' ranges and hummingbird hotspot areas in Mexico. Our projections were consistent in the identity of the species that are most vulnerable to GCC: while 10.2% of species will have potentially habitat gains/stability (“winners”), the remaining 89.8% of species (“losers”) will face habitat reductions under new climate conditions. These changes were mostly related to temperature increases (>2 °C) and rainfall decreases (<50 mm). The combined impacts of GCC and habitat loss may represent a higher risk, leading to an average reduction of 26–59% in species' ranges. Already-established Mexican PAs cover 12% of the hummingbirds' current ranges, but showed an important reduction of surface across the species distribution (on average >15%) and hotspot areas (>60%) for future. We identified highly resilient priority areas across southern Mexico, in Oaxaca and Guerrero. Ambitious conservation actions by decision-makers are now crucial to avoid losing these highly-vulnerable taxa.

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## Introduction

Hummingbirds (Aves: Trochilidae) are a New World bird family comprising ca. 330 species. This specialized nectarivorous taxon plays an important role in ecosystem functioning because they act as pollinators for nearly 15% of the plant species in North and South America (Schuchmann, 1999; Buzato et al., 2000). In addition, these small (2.5–24 g) birds have always been important in human culture (e.g., representing gods, soul carriers, love and fertility, good luck, and wellness) even in modern societies (Mazariegos, 2010). Therefore, they are often used by scientists and conservationists as ecological indicators and promoters of conservation policies. Unfortunately, these taxa are considered one of the most threatened groups in the world (<https://www.iucnredlist.org/>). Hence, there is a growing interest in understanding the effects of both anthropogenic disturbances (habitat loss and fragmentation) and global climate change (GCC) on the spatio-temporal distribution patterns of hummingbirds (e.g., Buermann et al. 2011; Infante et al., 2020), and in trying to identify priority sites for their conservation purposes.

All 58 of the hummingbird species distributed in North America are found in Mexico, a mega-diverse country; 49 species are resident and nine are Neotropical migrants (Arbeláez-Cortés and Navarro-Sigüenza, 2013; Arizmendi and Berlanga-García, 2014). For most of these species, current distribution patterns are relatively well known. In terms of species composition, six faunistic groups have been suggested across Mexico: the main mountain ranges, the Pacific tropical dry forests, the tropical dry forest of the Gulf of Mexico slopes, the humid tropical forest in southern Mexico, and the Yucatan and Baja California peninsulas (Arizmendi et al., 2016). In terms of conservation, at least six species are considered range-restricted and endangered at the global level (Berlanga et al., 2008; Arizmendi and Berlanga-García, 2014; IUCN, 2015). Also, most species of hummingbirds (all species except *Lophornis brachylophus*, *Eupherusa cyanophrys*, and *E. poliocerca*) have been reported in 85% of the National Protected Areas (PAs) network in Mexico (Arizmendi et al., 2016). However, despite this increase in the ecological and biogeographical information, details of hummingbirds' response to accelerated landscape transformation and global warming are poorly known and remain unclear (but see Lara et al., 2012; Mayani-Parás et al., 2020; Prieto-Torres et al. 2021b). This lack of information restricts our understanding of their vulnerability and extinction risk, and thus, potential impacts on natural ecosystems (see Pearson et al., 2019). Given that a reduction in pollination could create a feedback loop with biodiversity loss and degradation of ecosystem services (Ollerton et al., 2011), there is an urgent need to review future hummingbird conservation threats.

This latter is critical because Mexico continues to have high annual deforestation rates (over 1% nationwide; FAO, 2001), with more than 13.5 million ha of ecosystems lost over the last 50 years (see Mendoza-Ponce et al., 2020; Mayani-Parás et al., 2020). Moreover, recent studies have indicated a spatially heterogeneous increase in mean annual temperature over the last one hundred years (see Cuervo-Robayo et al., 2020). Indeed, the effects of GCC will likely outpace habitat destruction as a leading cause of loss in species richness and driver of species extinctions in the coming decades (e.g., Peterson et al., 2002, 2015; Zamora-Gutierrez et al., 2018; Esperon-Rodriguez et al., 2019; but also see Mayani-Parás et al., 2020). Hummingbirds (both threatened and non-threatened species) are not exempt from these critical scenarios (Lara et al., 2012; Prieto-Torres et al., 2020, 2021b). PAs network may be

less effective for conserving species under GCC, mainly because they may not cover species' modified future distributions (Jones et al., 2018; Esperon-Rodriguez et al., 2019; Maxwell et al., 2020). Therefore, future conservation efforts should take into account the combined effects of habitat loss and GCC in order to detect which species are most vulnerable versus resilient, and which regions are most stable versus susceptible to biodiversity loss (see Pecl et al., 2017; Pearson et al., 2019; Mendoza-Ponce et al., 2020).

Niche-based models (also called “ecological niche models” and “species distribution models”) are powerful tools that provide a conceptual and methodological approach for addressing the aforementioned challenges (see Peterson et al., 2011). These models rely on correlative relationships between field observations (species' occurrences) and environmental factors, allowing us to predict the areas that are currently suitable (i.e., Grinnellian niches; Rödder and Engler, 2011) for species and how environmental changes could impact their distribution (i.e., whether they will persist, increase, disappear or shift). This information can be used to test ecological hypotheses about species' dispersal ability and physiological performance under climate variations (e.g., Buermann et al. 2011; Esparza-Orozco et al., 2020; Cornejo-Páramo et al., 2020). The use of niche-based models by ecologists and conservation managers has exploded over the last two decades, with hundreds of papers published annually on conservation planning under GCC (see Araújo et al., 2019).

In this paper, we proposed to: (a) assess how predicted GCC could impact the distribution of 49 resident hummingbird species; (b) estimate the vulnerability of species in the face of GCC taking into account their conservation status, degree of restriction and habitat specificity; and (c) determine the effects of current habitat loss and the importance of the existing PAs network to safeguard both species ranges and hummingbird hotspots throughout Mexico. Based on this information, we provide new and more accurate evidence to guide the decision-making processes for the establishment of long-term and highly resilient priority conservation areas across Mexico. The priority areas identified here could help optimize the protection of these highly vulnerable taxa in the face of future environmental changes.

## Methods

### *Species occurrence and climatic input data*

We included the 49 resident hummingbird species inhabiting Mexico (Arbeláez-Cortés and Navarro-Sigüenza, 2013; Arizmendi and Berlanga-García, 2014). All species names followed Chesser et al. (2020). We downloaded occurrence data from: (a) online databases (Global Biodiversity Information Facility [GBIF; <https://www.gbif.org/>], SiB-Colombia [<https://sibcolombia.net/>], and EncicloVida [<https://enciclovida.mx/>]); and (b) the “Atlas de las Aves de México” (Navarro-Sigüenza et al., 2003). Access numbers for downloaded GBIF records are detailed in Appendix S1. In view of the shortcomings of GBIF data (Yesson et al., 2007) and the need for good quality data to avoid effecting model performance (Beck et al., 2014; Pérez-Navarro et al., 2021), we checked and vetted records carefully to remove erroneous and duplicate records. For each species, to avoid biases derived from spatial autocorrelation in areas that are heavily represented in the data, we applied a buffer distance (based on the mean distance among its occurrence records; Appendix S1) and retained only information corresponding to localities that were separated by at least this buffer distance. For those records from 2001 to 2020, we also performed an outlier exclusion procedure in the environmental space by removing points that fell outside the interquartile range of three environmental variables (annual mean temperature [bio

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01], annual precipitation [bio 12], and precipitation seasonality [bio 15]) for occurrences from 1970 to 2000 (e.g., Robertson et al., 2016, Prieto-Torres et al., 2020). Then, we removed spatially duplicate points near to each other by ca. 5 km<sup>2</sup> (i.e., the cell size resolution used for predictor variables). After these steps, we retained 30,468 unique occurrence records for all of the species.

Predictor variables were selected from bioclimatic variables (5 km<sup>2</sup> cell size resolution) from the WorldClim project 2.1 (Fick and Hijmans, 2017). We excluded the four variables (bio 8, bio 9, bio 18, and bio 19) that combine temperature and precipitation, owing to known artefacts (Escobar et al., 2014). To reduce dimensionality and collinearity of environmental layers, we applied two approaches: (1) selection of a subset of variables based on a Pearson's correlation coefficient ( $r < 0.8$ ) and Variance Inflation Factor (VIF  $< 10$ ), using the "usdm" R package (Naimi, 2015); and (2) derivation of a set of four variables (explaining up to 95% of the total variance) using a Principal Component Analysis (see Hanspach et al., 2011), as implemented in the "ENMGadgets" R library (Barve and Barve, 2016). We selected the best approach for models building based on the statistics estimated in the "kuenm" R package (Cobos et al., 2019).

For models based on future climate projections (year 2040, 2060, and 2080), we used climate data from the Coupled Model Inter-comparison Project 6 (CMIP6; Stoerk et al., 2018) available at the Worldclim web portal. Because predicted future species distributions can vary widely, we selected five global climate models based on results obtained from GCM compareR's web application (Fajardo et al., 2020). We adopted the "storyline" approach, where different GCM projections are classified into self-consistent narratives that represent specific future climate conditions (Zappa and Shepherd, 2017): (i) high temperature and low precipitation compared to the ensemble projection (CanESM5), (ii) low temperature and high precipitations compared to the ensemble projection (MIROC6) and, (iii) temperature and precipitations close to the average ensemble projection (BCC-CSM2-MR, CNRM-CM6-1, and IPSL-CM6A-LR). Additionally, it is important to note that these five models show improvements in the estimation of precipitation values, zonal-mean atmospheric fields, equatorial ocean subsurface fields, and the simulation of El Niño-Southern Oscillation in the Americas (Cook et al., 2020; Zelinka et al., 2020). All projections were performed using an intermediate Shared Socio-economic Pathways scenario (i.e., SSP 370), which assumes high greenhouse gas emission and low climate change mitigation policies (Riahi et al., 2017).

### Ecological niche and species distribution models

We modelled the potential distribution for each species using MaxEnt version 3.4.3 (Phillips et al., 2017). We decided to use this software given 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 modelling parameters (see Muscarella et al., 2014; Cobos et al., 2019). Although the choice of background data is an important step into modelling method using presence-only data (Phillips et al., 2009), we did not include a sampling bias variable because there is no existing sampling bias layer that covers our study region and group, and we do not have the necessary sampling effort data to generate such a layer. Moreover, following Barve et al. (2011), we created an area for model calibration (known as "M"; Soberon and Peterson, 2005) that reflects the accessible historical areas and restriction regions for each species. We established "M" based on the intersection of occurrence records with the Terrestrial Ecoregions (Dinerstein et al., 2017) and the Biogeographical Provinces of the Neotropics (Morrone, 2014). The hypothesized areas of accessibility for each species are provided in Appendix S2.

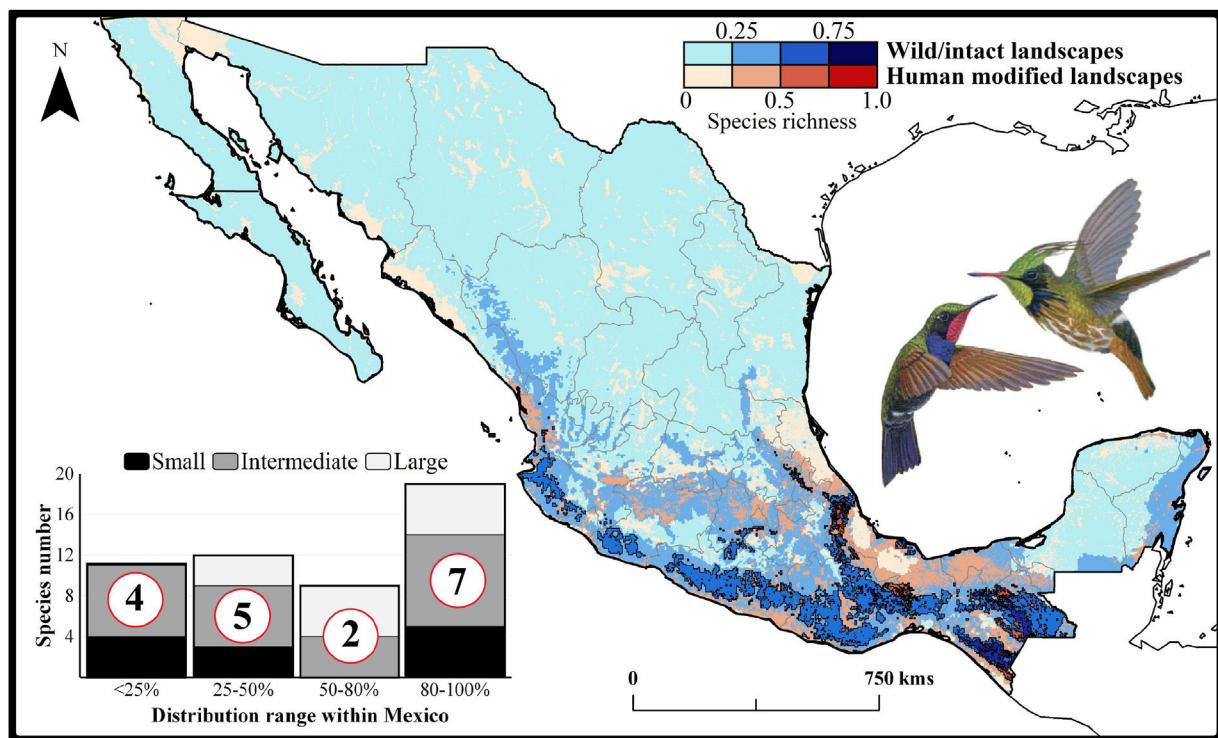
All models were run allowing "unconstrained extrapolation" and "extrapolation by clamping" in Maxent projections, which allowed us to identify potential novel conditions that could be considered suitable for each species in the future scenarios (Elith et al., 2011, Merow et al., 2014). Models for species with 9–14 records were developed using all presence data (using MaxEnt default parameters) and evaluated with a Jackknife test (Pearson et al., 2007). For species with  $\geq 15$  records, models were generated using the "kuenm" R package (Cobos et al., 2019; available at: <https://github.com/marloncobos/kuenm>) to perform a calibration protocol assessing model complexity (Merow et al., 2014). To do this, we created 570 candidate models by combining two distinct sets of environmental predictors, 19 regularization multiplier values (RM: 0.5 – 8.0) and 15 feature classes (i.e., combinations of linear, quadratic, product, and threshold). We used 30% random subsets of occurrence data for model evaluation (i.e., model testing and selection of best models). The best models were chosen based on the omission errors (Anderson et al., 2003), the partial ROC test (Peterson et al., 2008) and the Akaike Information Criterion (AIC; Merow et al., 2014; Muscarella et al., 2014). After model calibration, we created models with the selected parameter values, 500 iterations with 10 bootstrap replicates, and *cloglog* output (Phillips et al., 2017).

Then, to generate the distribution maps for each species under each climate scenario, we first calculated median values across replicates to summarize model predictions (Campbell et al., 2015). Then, we created presence-absence maps from the logistic values of suitability maps, using as the threshold value the "tenth percentile training presence" in order to reduce commission (i.e., the false-positive rate) errors (Liu et al., 2013). For each species, the future geographic distribution (year 2040, 2060, and 2080) were obtained manually by overlaying the binary projections from the five global climate models, allotting "presence" to a pixel where the majority of predictive models coincided (i.e., suitable in 3 or more models = 1). For all species, models were calibrated using the available data for their entire current range, and then cropped to the approximate geographic extent of Mexico (Fig. 1).

Finally, using the "ntbox" R package (Osorio-Olvera et al., 2020), we performed the Mobility-Oriented Parity (MOP; Owens et al., 2013) test to identify areas where strict or combinational extrapolation risks could be expected in model transfers, given the presence of non-analogous conditions (see Owens et al., 2013; Alkhishe et al., 2017). Areas in which extrapolation risks were detected were deleted from our binary results (suitable areas) for the subsequent analyses. This step is important for proposing conservation areas, as protecting areas are more advantageous where a species has low uncertainty values for predictions (i.e., one would rather fail to create PAs where a species occurs than to create PAs where it does not occur; see Velazco et al., 2020).

### Data analyses: impacts of climate changes and habitat loss

We measured the potential impacts of GCC on the geographic range of each species under two different dispersion scenarios (Peterson et al., 2002). The "contiguous dispersion" scenario assumes that species would be able to disperse through continuous habitat, but not jump over barriers (i.e., all the cells with suitable conditions within Min the future are considered part of its future distribution range). In the "non-dispersion" scenario, it is assumed that species are unable to disperse at all (i.e., only those cells that are occupied in the present can be occupied in the future). This non-dispersion scenario only allows for negative responses (decreases in distributional range) to GCC; therefore, it must be considered the most "unfavorable" for the species (Peterson et al., 2002; Atauchi et al., 2020; Prieto-Torres et al., 2020).



**Fig. 1.** Current patterns of species richness maps for non-migrant hummingbird species ( $n = 49$  spp.) across Mexico. The color gradient represents species richness: darker color indicates sites with higher species richness (i.e., hotspots) in both human-modified (red) and intact (blue) landscapes. The inset bar plot indicates the proportion of current distribution area within Mexico for hummingbirds, showing the number of species categorized as small, intermediate, and large distributional ranges. Circles in bars correspond to the number of threatened species (NOM-059-SEMARNAT-2010) in each range size category. The birds shown in the figure are *Lamprolaima rhami* (left), and *Lophornis helenae* (right). The bird pictures were taken from "Colibríes de México y Norteamérica" (Arizmendi and Berlanga-García, 2014)

For each species, losses and gains due to GCC were calculated from the binary maps by subtracting the future from current models (following Thuiller et al., 2005). Also, where a loss of suitable areas was predicted in future-projected models, we calculated the differences between current and future values for the environmental variables (Atauchi et al., 2020). In addition, for each dispersal assumption scenario, a Kruskal-Wallis test was performed to estimate the species' vulnerability (based on species' range changes) in the face of GCC as a function of their extinction risk in Mexico (NOM-059-SEMARNAT-2010 [available at: [https://dof.gob.mx/nota\\_detalle\\_popup.php?codigo=5173091](https://dof.gob.mx/nota_detalle_popup.php?codigo=5173091)], their degree of geographical restriction and their habitat specificity. We classified geographical restriction into three categories based on the number of occupied sites (pixels) in the current species range: large (in the upper quartile, 249,677 km<sup>2</sup>), intermediate, and small (in the lower quartile 25,067 km<sup>2</sup>). Habitat specificity was described as species generalists or specialists (Appendix S1) based on their habitat use (e.g., Stotz et al., 1996; Arizmendi and Berlanga-García, 2014; Schulenberg, 2019).

To assess the effects of current habitat loss (i.e., human modified areas that may be unsuitable for some species) in our models, we used the 2017 land cover and vegetation map generated by the Mexican Instituto Nacional de Estadística y Geografía (INEGI). This vectorial map (scale of 1:250 000) was generated from photointerpretation of Landsat TM5 satellite images from 2014 and 2015, validated in the field, and it included the information on location, distribution, and extent of different plant communities (including intact and modified areas) and agricultural uses (see metadata [available on: <https://www.inegi.org.mx/temas/usosuelo/>] for more information about the map). We reclassified this map using the "majority" resampling technique in ArcMap 10.2.2 (ESRI, 2010) to discriminate pixels representing extremely disturbed landscapes (i.e., areas occupied by crops, deforested areas, farming areas,

pastures, and urban settlements) in order to identify highly human-modified areas. We then calculated the average extent of species distribution (current vs. future) that had extremely disturbed landscapes in this current map. Because future habitat loss estimations are not available for the entire study area, this approach is useful for improving our knowledge of future threats to forest-dependent species that are unable to persist in an agricultural matrix (Bregman et al., 2014); thus it is commonly used in the literature.

We also identified hummingbird hotspots (i.e., sites whose species richness exceeded half of the maximum values observed) and determined their overlap with current highly human-modified areas. For this, we first obtained the species richness pattern by summing all binary species maps for each year, then converted them into a standardized raster (ranging 0 to 1) by dividing each raster by its maximum value. These maps were classified using a color key based on four equal intervals, and then overlapped with the human-modified areas map (following Bolocho et al., 2020). All of these post-modelling analyses and statistical calculations were performed in ArcMap using the "raster calculator" toolbox.

#### Protected Areas network and long-term hummingbird conservation

We estimated the importance of the existing PAs network for hummingbird protection by calculating the proportion of potential distributional areas within the current PA system. To do this, we overlapped the raster of current Mexican PAs with each species' distribution and the binary raster of hummingbird hotspots for each climate scenario (see above). Also, to test the efficiency of PAs, we compared the distribution of hummingbird species concentration values (based on the standardized raster ranging 0 to 1) for pixels with at least one species at present and ran a Kolmogorov-Smirnov (KS) test to verify whether

the curves within and outside PAs differ significantly between them (e.g., Ramírez-Albores et al., 2021). PA boundaries were obtained from a shapefile downloaded from the Mexican *Comisión Nacional de Áreas Naturales Protegidas* (CONANP; available on: [http://sig.conanp.gob.mx/website/pagsig/info\\_shape.htm](http://sig.conanp.gob.mx/website/pagsig/info_shape.htm)), selecting both terrestrial official PAs and voluntary conservation areas.

Also, following the criteria proposed by Rodrigues et al. (2004) and Goettsch et al. (2019), we identified covered (i.e., if a predetermined percentage of its distribution was included), partial gap and gap (i.e., if it was not included) species within current PAs. The percentage used is referred to as the conservation target for each species: for species with geographic ranges of  $\leq 1,000$  km<sup>2</sup> is required that entire range have been covered, whereas for species with ranges  $\geq 250,000$  km<sup>2</sup> only 10% of their distribution must be included in PAs. For species with intermediate geographic ranges, we determined conservation targets by interpolating between these two extremes (Rodrigues et al., 2004; Goettsch et al., 2019).

To determine key regions for Mexican hummingbirds' long-term conservation, we summed binary hotspot maps (current and future) to detect the consensus areas among them. Then, we calculated the area (in km<sup>2</sup>) and percentage of consensus areas that overlap with: (i) already-established Mexican PAs, and (ii) current human-modified areas. From this perspective, the consensus hotspots that did not match among maps correspond to "priority conservation sites" that will be protected in the near future because they represent the areas where a high species concentration could persist in face of both habitat loss and GCC impacts. To assess the degree of resilience of these priority areas to future land-use changes, we compared our results with a human-modified areas map for the 2050's (choosing the "Middle of the road" intermediate scenario from the application of CLUMondo application). This global map (available on: <https://www.environmentalgeography.nl/site/data-models/data/implementing-spps-in-clumondo/>) shows the future modified areas based on the projected demand for crop production, bovines, goats and sheep and urban area, as these were the exogenous productivity increase factors due to technological change per year (for a detailed explanation see Van Asselen and Verburg, 2013).

Finally, to assess the representation levels of species richness in these highly resilient priority areas, we performed a complementarity analysis as suggested by Margules and Sarkar (2009). To do this, we built a presence-absence matrix data based on each cell, analyzing them in Excel 2013 using an iterative process to choose the highest richness cells with more complementary species until completing all possible species (e.g., Humphries et al., 1991; Sánchez-Ramos et al., 2018). The complementarity was plotted in a species accumulation curve using the "BiodiversityR" R package (Kindt, 2016).

## Results

### *Species models and current hummingbird species richness pattern in Mexico*

All of our maxent models exhibited highly significant values for the partial ROC test (range = 1.16 – 1.94,  $P < 0.05$ ) for species with  $\geq 15$  occurrence records, while the Jackknife test showed statistically significant ( $P < 0.01$ ) values when the threshold was applied for species with nine occurrence records. On average, models had low omission errors, with values of  $4.6 \pm 5.1\%$ . Based on these performance estimates, we considered our models to be accurate (i.e., have good discrimination capacity) in recovering the ecological niches for each species. Parameter settings and performance values for each model are detailed in Appendix S1.

The current predicted distribution area for hummingbirds in Mexico ranged from 225 km<sup>2</sup> (*Cyananthus forficatus*) to 797,150 km<sup>2</sup> (*Cyananthus latirostris*). On average, 60.1% of species' whole distribution occurred within Mexico. About 38.8% ( $n = 19$ ) of the hummingbird species possess ranges that overlap at least 80% of Mexico's surface; while 42.9% ( $n = 21$ ) of species show overlap values of  $< 50\%$  of their distribution within Mexico. According to our range size categories, 49% of the species had intermediate sized ranges in Mexico, 26.5% of the taxa had large ranges, and 24.5% had small ranges (Fig. 1). Based on the Mexican list of extinction risk (Appendix S1), eight species are classified as threatened, one as endangered, nine as under special protection, and 31 are not included in any risk category.

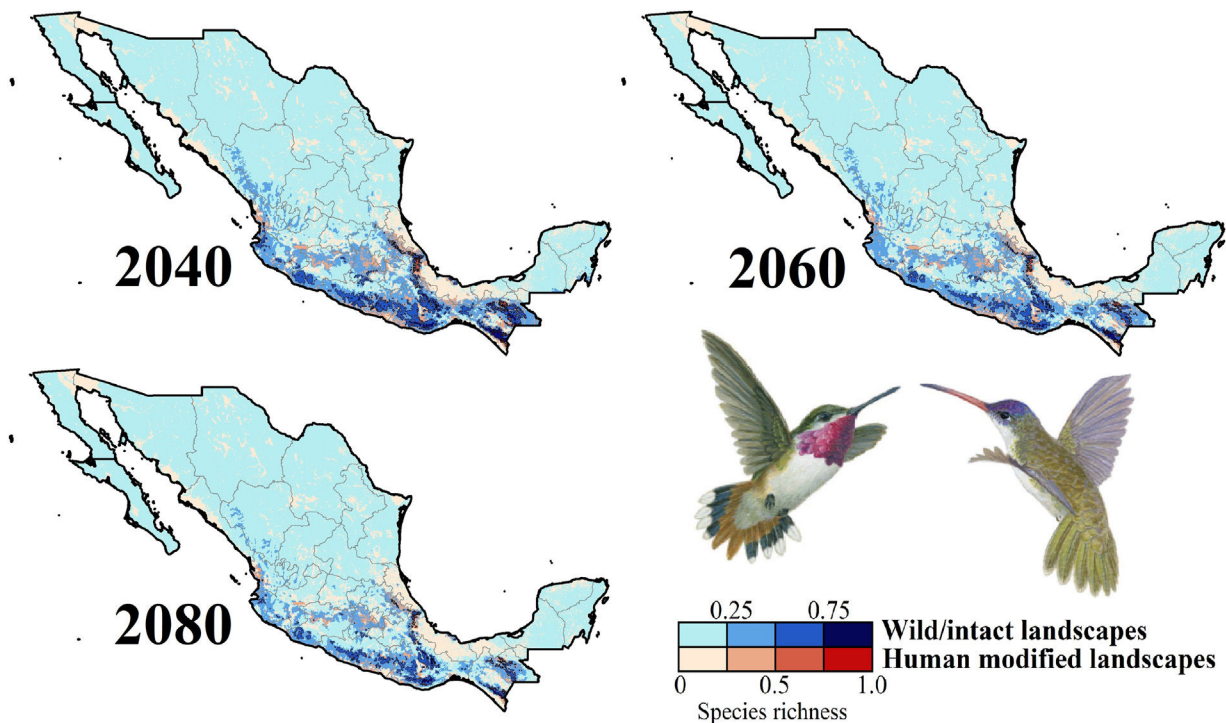
There was a variable number of total hummingbird species per site, ranging from 1 to 27 spp. (mean of  $5.8 \pm 4.7$ ). The current hotspots ( $> 0.5$ , dark colors in Fig. 1) covered an area of 108,562 km<sup>2</sup>, and are mainly located across southern Mexico, in the states of Oaxaca (33.7%), Chiapas (27.4%), Guerrero (18.4%), and Veracruz (6.9%).

### *Impacts of current habitat loss*

Our models showed an important degree of overlap between highly human-modified areas and estimated species ranges (mean of  $24.5 \pm 10.8\%$ ). The species with the highest proportions of suitability climate-areas within current human modified areas were *Saucerottia cyanura* (51.8%), *Pampa excellens* (49.8%), and *Phaethornis striigularis* (40.8%). We observed that the majority of species (57.1%) had between 20–40% of their distribution within highly human-modified areas, while 30.6% (15 spp.) showed overlap values of 10–20%. Only three species had less than 10% of their potential range in human-modified areas: *Eupherusa cyanophrys* (6.83%), *Lophornis brachylophus* (5.84%), and *Basilinna xantusii* (3.55%). Furthermore, 15.5% of current hummingbird hotspots areas in Mexico overlapped with these highly human-modified areas (see Fig. 1).

### *Impacts of future climate change*

Overall, the following patterns emerged from our projections (Fig. 2; Appendix S3): (i) climate change will lead to range reductions for hummingbirds in Mexico by an average of 4.6% [2040's] – 32.3% [2080's] if we assume contiguous dispersion scenarios and 23.6% [2040's] – 48.4% [2080's] if we assume the non-dispersion scenario; (ii) these distributional areas in the future showed a decrease in values of suitability for projections by an average of 0.05 [2040's] – 0.11 [2080's]; (iii) for those regions where suitable areas will likely decrease, temperature metrics—especially annual mean temperature, maximum temperature of the warmest month, and mean temperature of the coldest quarter—tended to increase by more than 2.0 °C; while (iv) the values for annual precipitation and wettest quarter tended to decrease on average 85.1 mm and 52.1 mm, respectively; (v) species richness of hummingbirds will decrease, on average, by 37.3% [dispersion scenario] – 40.6% [non-dispersion scenario] across 50% of Mexico; and (vi) the hotspots areas will also decrease in size (ranging from 34.3% [2040's dispersion scenario] to 53.8% [2080's non-dispersion scenario]), occupying higher elevation zones (at least 260 m; independently of dispersion scenarios) than their current average distribution ( $1,227 \pm 653$  m asl). Moreover, extinction (i.e., disappearance of suitable areas) is the most likely future for the insular *C. forficatus*. The MOP analysis indicated that, regardless of our dispersion assumption, areas where strict extrapolation occurs represent a low proportion (on average  $< 5\%$ ) of predictions by models in the future climates across Mexico (Appendix S4). This pattern suggests that there is scarce or null proportion of novel conditions that could be considered suitable for each species in the future. In this sense, the general



**Fig. 2.** Species richness patterns for non-migrant hummingbird species ( $n = 49$  spp.) across Mexico projected for years 2040, 2060, and 2080 assuming contiguous dispersion. The color gradient represents species richness for each scenario analyzed. Darker color in maps indicates the higher hummingbird hotspots areas (i.e., higher species richness) in both human-modified (red) and intact (blue) landscapes. Detailed results for the no dispersal ability scenarios are available in the Appendix 2. The birds shown in the figure are *Selasphorus heloisa* (left), and *Leucolia violiceps* (right). The bird pictures were taken from “Colibríes de México y Norteamérica” (Arizmendi and Berlanga-García, 2014)

reduction in species ranges corresponded to changes in climate-suitability available currently.

The Kruskal–Wallis tests showed that species’ sensitivity to climate change was not significantly different across years under dispersion and non-dispersion scenarios, among the categories of extinction risk ( $\chi^2 = 4.4$ ;  $df = 3$ ;  $P = 0.23$ ) or habitat specificity ( $\chi^2 = 4.4$ ;  $df = 3$ ;  $P = 0.22$ ). There was, however, a statistically significant difference ( $\chi^2 = 11.9$ ,  $df = 5$ ;  $P = 0.03$ ) in climate-induced range contraction among the three geographical restriction categories (Fig. 3). Both of the dispersion scenarios yielded the same patterns; although the no dispersal scenario led to larger decreases in species’ predicted range (Fig. 3; Table 1). Under the full GCC scenarios, we observed that 89.8% of the species showed large habitat reductions (“losers”), while the remaining 10.2% (five species) were predicted to have large potential habitat gains/stability (“winners”) under future climate conditions. These five species —*Cynanthus canivetii*, *C. latirostris*, *Eupherusa ridgwayi*, *Leucolia viridifrons*, and *Amazilia rutila*— showed range stabilities of >95%, even under the non-dispersion scenario.

#### Combined effects of climate change and current habitat loss

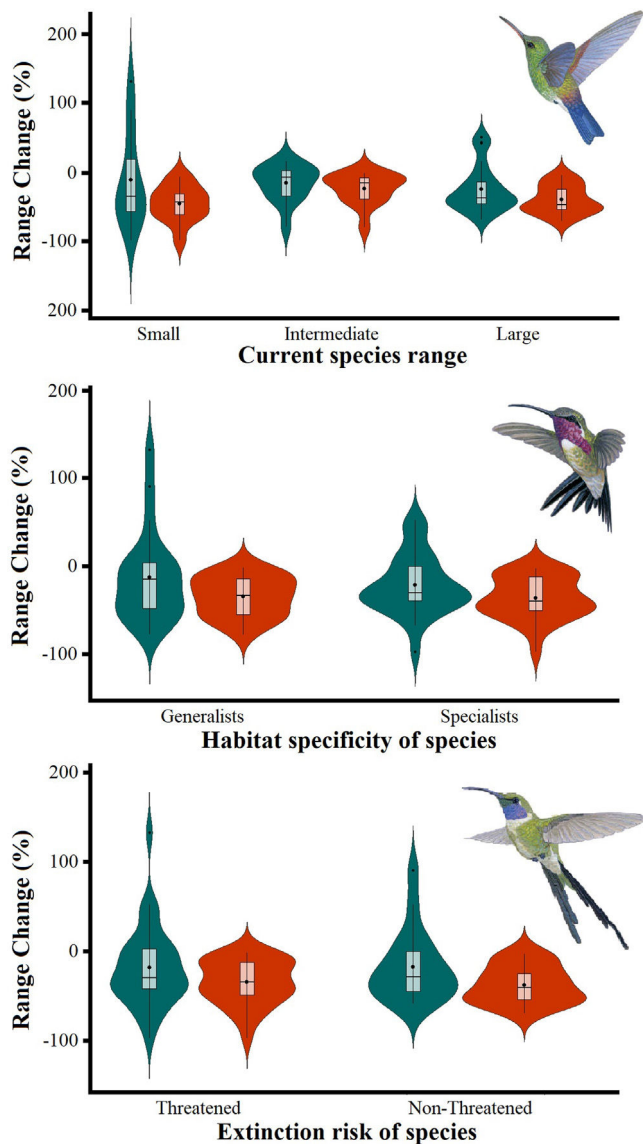
We observed that the combined effects of GCC and current human-modified areas would reduce species distribution by an average of 26.1% [2040’s] – 45.9% [2080’s] assuming a dispersion scenario, and 39.9% [2040’s]–59.1% [2080’s] if they cannot disperse. Overall, in both dispersion scenarios, 22.1% of potential distribution for species in the future overlapped with the currently highly human-modified areas (i.e., likely unsuitable for some species). This fact is particularly important for five species (*Hylocharis eliciae*, *P. excellens*, *Phaethornis longirostris*, *P. strigularis*, and *S. cyanura*), for which more than 43% of their remnant distribution in the future fell within these human-modified areas. Furthermore, on average

12.2% of remnant hummingbird hotspots in the future overlapped within current highly human-modified areas.

#### Protected Areas network and long-term hummingbirds’ conservation

Already-established Mexican PAs cover, on average,  $11.6 \pm 7.8\%$  of the distribution area of all of the hummingbird species, and  $13.3 \pm 11.1\%$  of the distribution of threatened species. Currently, the best represented species within the PAs were: *Phaechroa cuvierii* (47.3%), *Heliothryx barroti* (25.9%), and *Pampa rufa* (25.5%). However, a large number of hummingbird species ( $n = 25$ ) had less than 10% of their range protected. In fact, according to the species’ conservation targets, six species (12.25%) were considered fully covered, while 41 (83.67%) species were partial gap species, and two (*L. brachylophus* and *C. forficatus*) were identified as gap species. Overall, we observed no significant differences for species richness values ( $P > 0.05$ ) between areas within the existing PAs network ( $6.4 \pm 4.7$  spp.) and outside the PAs ( $6.0 \pm 4.7$  spp.). Moreover, we observed that only 8.9% of current hummingbird hotspots were included within some PAs category.

Our models predicted a critical reduction (on average 14.9% [dispersion scenario] – 31.8% [non-dispersion scenario]) in suitable areas for hummingbirds within the limits of several PAs in the future. We also noted a significant reduction in mean species richness ( $P < 0.05$ ) within PAs under the climate change scenarios for the 2040’s ( $6.3 \pm 4.4$  [dispersion scenario] and  $5.6 \pm 4.1$  [non-dispersion scenario] spp.), 2060’s ( $5.7 \pm 4.1$  and  $5.1 \pm 3.7$  spp.), and 2080’s ( $4.9 \pm 3.5$  and  $4.5 \pm 3.2$  spp.). Likewise, we observed that existing Mexican PAs had on average and regardless of the dispersal scenarios, only 6.8% overlap with the potential hotspot areas identified in the future. This represents an important reduction (>60%) of protected surface across the hotspot areas in the future.



**Fig. 3.** Differences in the proportion of range change (%) due to climate-induced contraction for the non-migrant hummingbird species ( $n = 49$  spp.) in Mexico, under the two considered dispersion assumptions (contiguous dispersion in green, no dispersion in red), considering the species extinction risk, degree of geographical restriction, and habitat specificity. The Kruskal–Wallis tests only showed statistically significant differences ( $\chi^2 = 11.9$ ,  $df = 5$ ;  $P = 0.03$ ) for species vulnerability among the range size categories. Birds shown in the figure are *Saucerottia cyanura* (small range; upper panel), *Calothorax pulcher* (specialist; in the middle panel), and *Doricha enicura* (Threatened; lower panel). The bird pictures were taken from “Colibríes de México y Norteamérica” (Arizmendi and Berlanga-García, 2014)

The consensus hummingbird hotspot areas under both dispersion scenarios for future climates showed high (62%; i.e., 26,689 km<sup>2</sup>) overlap values. Approximately 10.8% of the area of these long-term climate-resilient sites overlapped within current highly human-modified areas, while only 6% were including within existing PAs. Our analyses showed a high proportion (84.3%; 22,488 km<sup>2</sup>) of long-term hummingbird hotspots areas with good-quality forests outside the PAs limits (Fig. 4). These priority conservation and highly-climate resilient areas in the future cover mostly wide areas in Oaxaca (44.8%), Guerrero (23.8%), Chiapas (17.8%), and Michoacán (7.9%). The complementarity analysis showed that 219 cells of these resilient areas in the future contain 93.9% of hummingbird species richness (46 species, including 89% of endangered species; see Table 2). The species accumulation

curve reached its asymptote in a few cells (see Appendix S5). The three hummingbird species that were not included in these areas were *Basilinna xantusii*, *C. forficatus*, and *Doricha eliza*.

Moreover, according to the Mexican terrestrial ecosystem classification (INEGI-CONABIO-INE, 2008), we observed that these long-term consensus priority areas were distributed in four ecosystems (Table 3): pine-oak forests (17,330 km<sup>2</sup>; 77.06%), cloud forests (2,639 km<sup>2</sup>; 11.74%), seasonally dry tropical forests (1,384 km<sup>2</sup>; 6.15%), and low tropical rainforests (1,135 km<sup>2</sup>; 5.05%). Finally, it is important to note that our priority consensus conservation areas have 14.6% (3,288 km<sup>2</sup>) overlap with areas expected to be highly human-modified by the 2050's (Fig. 4).

## Discussion

Undoubtedly, the both climate warming and land-use change will have a serious impact on individual species and communities of hummingbirds throughout Mexico in the coming decades, even under the more optimistic change scenarios (e.g., Lara et al., 2012; Correa-Lima et al., 2019; Chávez-González et al., 2020; Prieto-Torres et al., 2021b). More importantly, our results reinforce the widely accepted idea (see Jones et al., 2018; Maxwell et al., 2020) that current PAs are not now effective for safeguarding these species, nor will they be into the future (see also Esperon-Rodriguez et al., 2019). This bleak scenario will lead to most species being highly vulnerable to extinction due to the reduction of range size and the increase in fragmentation (Zamora-Gutierrez et al., 2018; Lovejoy and Hannah, 2019; Mayani-Parás et al., 2020). It is imperative that policy-makers promote policies that are resilient to both threats as soon as possible. From this perspective, our results represent a valuable guide using scientific evidence on which species and areas require attention to establish new efforts for efficient long-term conservation planning in Mexico for these highly vulnerable and ecologically specialized Neotropical bird taxa.

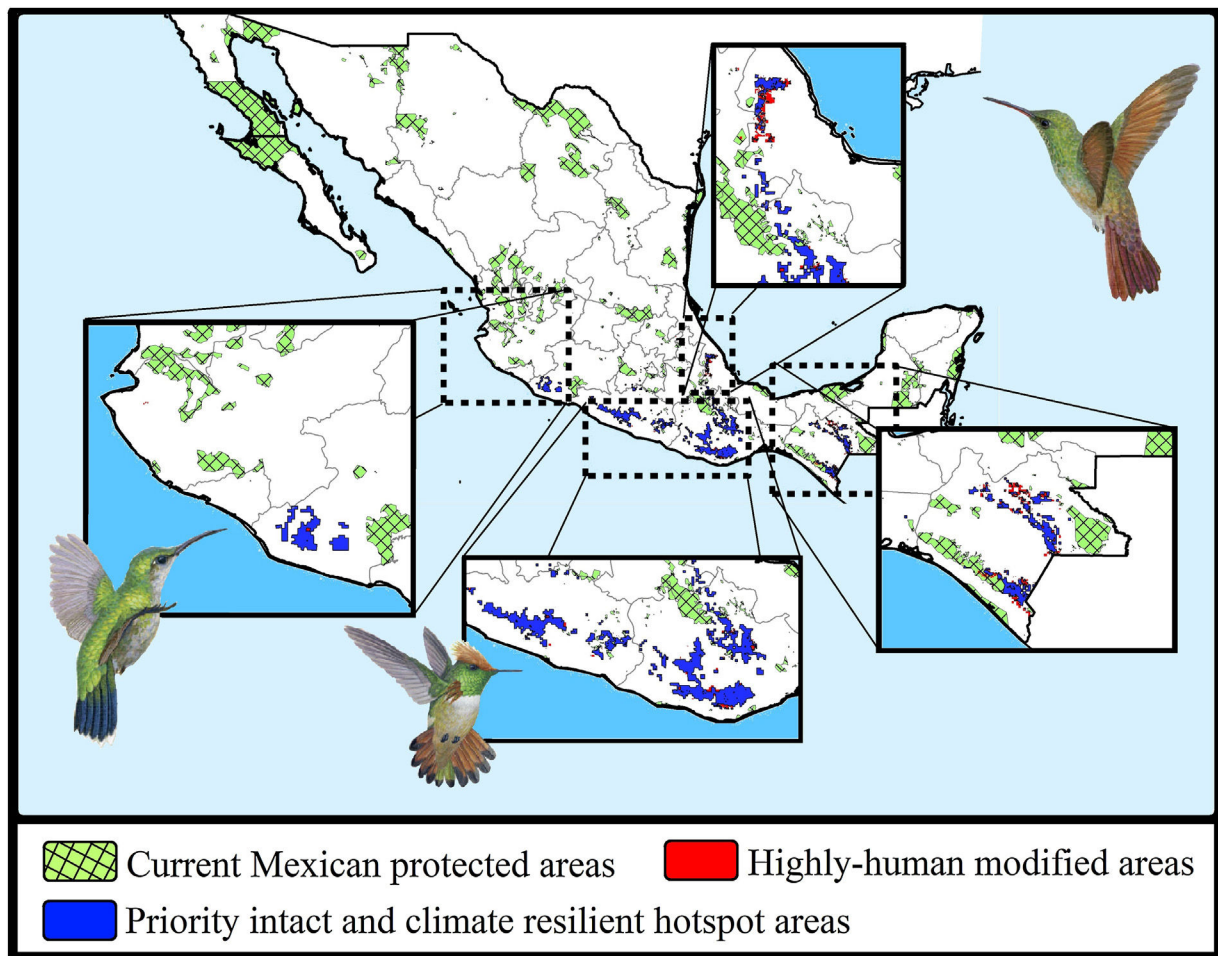
This latter is noteworthy considering that more than three quarters of species showed a reduction of suitable habitat areas as a consequence of GCC. These results are in agreement with other studies in Mexico, not just for birds (Lara et al., 2012; Prieto-Torres et al., 2020, 2021a, 2021b) but for a wide variety of organisms, including mammals, amphibians, reptiles and plants (e.g., Ochoa-Ochoa et al., 2012; Sinervo et al., 2017; Mason-Romo et al., 2018; Ureta et al., 2018; Arenas-Navarro et al., 2020). These patterns of change are attributed to the expected increase in the average global temperature and decrease in the annual precipitation across the region (Cuervo-Robayo et al., 2020; Esperon-Rodriguez et al., 2019; Hidalgo, 2021), which could promote changes in the physiological responses and activity patterns of the biota. Therefore, as our results show, under future climates it is likely that species will be pushed toward higher elevations (even losing geographical ranges), where future humidity will be a key limiting factor for the biota (Buermann et al., 2011; Harsch and HilleRisLambers, 2016). In fact, we observed that the overall patterns of geographic change were consistent among all of the climate and dispersal scenarios we considered, reducing uncertainties in our forecasting models (see Peterson et al., 2018; Araújo et al., 2019). Nevertheless, our results should be taken with caution because species' potential to adapt to future conditions is very difficult to predict, since their adaptive potential is influenced by many additional factors that we did not evaluate here, such as reproductive rates, physiological capacity, and habitat requirements (Peterson et al., 2002; Ortega et al., 2019).

When changes in local climates exceed the range of natural climate variation, species may acclimate by adjusting physiologically (through phenotypic plasticity) within individual's lifetimes (Urban et al., 2014) and/or shift their distribution to avoid dying

**Table 1**

Predictions of range change (in percentage) for non-migrant hummingbird species (n = 49 spp.) across Mexico considering the national extinction risk, degree of geographical restriction, and habitat specificity of species.

	Mean ± SD (min. / max) range change (%)	
	Dispersion scenario	Non-dispersion scenario
<b>Geographical restriction</b>		
# species increasing/decreasing range	14 / 35	0 / 49
Small	-10.28 ± 69.05 (132.35 / -97.62)	-44.25 ± 26.22 (-5.88 / -97.62)
Intermediate	-23.69 ± 33.45 (51.91 / -67.78)	-38.87 ± 20.39 (-3.48 / -69.59)
Large	-15.03 ± 26.12 (16.66 / -77.80)	-22.82 ± 22.33 (-1.76 / -78.64)
<b>Habitat specificity</b>		
# species increasing/decreasing range	14 / 35	0 / 49
Generalists	-12.98 ± 52.51 (132.35 / -77.80)	-34.52 ± 22.91 (-1.76 / -78.64)
Specialists	-21.95 ± 34.35 (52.32 / -97.62)	-36.55 ± 24.23 (-3.21 / -97.62)
<b>Extinction risk</b>		
# species increasing/decreasing range	14 / 35	0 / 49
Threatened	-17.60 ± 39.73 (90.23 / -58.70)	-37.86 ± 21.01 (-3.48 / -69.59)
Non-Threatened	-18.41 ± 45.14 (132.35 / -97.62)	-34.81 ± 25.01 (-1.76 / -97.62)



**Fig. 4.** Maps showing the current Mexican protected areas (PAs), the priority and climate-resilient hummingbird hotspot areas identified in our study. For the proposed areas, we show the sites that coincided with highly human-modified areas (red) for both current and 2050 scenarios. Birds shown in the figure are *Thalaurania ridgwayi* (♀ endemic to western Mexico; left), *Lophornis brachylophus* (endemic to Guerrero state; middle), and *Saucerottia beryllina* (right). The bird pictures were taken from "Colibríes de México y Norteamérica" (Arizmendi and Berlanga-García, 2014)

**Table 2**

Number of complementary species per grid cell of the total species richness and richness of endangered species.

# of cells	Complementary species	Accumulated richness	% of species	Endangered complementary species	Accumulated richness	% of species
4	29	29	59.2	11	11	61.1
20	11	40	81.6	4	15	83.3
155	4	44	89.8	1	16	88.9
40	2	46	93.9	0	0	88.9



**Table 3**

Priority conservation and highly resilient areas identified for non-migrant hummingbird species throughout Mexico by terrestrial ecosystem. The total area (in km<sup>2</sup> and percentages) of existing PAs was obtained from maps produced by the *Comisión Nacional de Áreas Naturales Protegidas* (CONANP; available at: [http://sig.conanp.gob.mx/website/pagsig/info\\_shape.htm](http://sig.conanp.gob.mx/website/pagsig/info_shape.htm)).

Ecosystem	Current PAs by ecosystem		Priority conservation areas identified	
	Km <sup>2</sup>	%	Km <sup>2</sup>	%
Pine-oak forests	40,056	12.00	17,330	77.06
Cloud forests	1,253	8.20	2,639	11.74
Seasonally dry tropical forests	19,537	6.78	1,384	6.15
Low tropical rainforests	16,662	10.03	1,135	5.05

(Peterson et al., 2002; Lovejoy and Hannah, 2019). In the particular case of hummingbirds, their responses may be determined by performance of hovering flight and feeding across these challenging new environments (Buermann et al., 2011). Higher elevation locations have reduced air density and oxygen availability, and high-elevation hummingbirds exhibit flight adaptations (e.g., lower wing loadings, increase in the wing stroke amplitude and changes in flight kinematics, etc.) that compensate for these effects (Altshuler et al., 2004; Buermann et al., 2011). So, if low-elevation species are not able to quickly adapt to new environments at higher elevations, population sizes would be expected to decrease, and their future survival may be threatened. Therefore, the impacts and extinction risks may be even more drastic than the results obtained here. More studies analyzing the ability of these taxa to rapidly adapt or move into new areas and environmental conditions are needed (see de Matos Sousa et al., 2021). For this, the implementation of monitoring programs is essential, especially for the species and zones that are predicted to suffer the most drastic decreases.

Clearly, the existing scenario of loser and (few) winner species for new climate conditions support the idea that a species' ecological generalization (including niche breadth and range size) is one of the key attributes affecting their extinction risk. In fact, our models show that most of the winner species do not have a particularly habitat affinity (e.g., *A. tzacatl*, *A. prevostii*, and *S. cyanura*), whereas species that have an arid/dry affinity (e.g., *B. xantusii*) are expected to be more negatively affected in the extent of their suitable areas. This is expected because small-range species are typically specialists with narrow ecological niches (e.g., Sonne et al., 2016), so they are less likely to be able to colonize novel conditions in the near future (e.g., Thuiller et al., 2005; Broennimann et al., 2006). This pattern could explain, in fact, the extinction scenario obtained for the insular *C. forficatus* in the future. Moreover, this is consistent with previous studies in Mexican seasonally dry forests which suggest higher vulnerability to GCC and habitat loss for these biota (Prieto-Torres et al., 2016, 2020, 2021b). Nevertheless, it is important to note that recent studies have shown hummingbird range expansion associated with urbanization, even under non-suitable climatic conditions (e.g., Greig et al., 2017; Battey, 2019). Therefore, we recommend further fieldworks testing the projections (i.e., hypothesis) from our results to obtain reliable knowledge about the species' dynamic responses to future environmental scenarios. Based on our results, the species *H. eliciae*, *P. excellens*, *P. longirostris*, *P. strigularis* and *S. cyanura* represent promising models for future studies addressing these questions.

Although hummingbird-pollinator losses due to deforestation and agricultural intensification have not yet been documented in Mexico, circumstantial evidence suggests this is already happening (e.g., Infante et al., 2020). Certainly, there are hummingbirds species that occur within transformed areas, but whether they successfully establish reproductive (e.g., subcanopy is an essential element for successful nesting) and permanent resident populations in these transformed habitats is unknown for most species (Smith et al., 2014). In this sense, further fieldwork is needed because niche modeling-based approaches have some limitations that could pre-

clude the identification of continuously changing trajectories and responses. First, there are uncertainties when forecasting species distributions depending on the algorithm used (see Qiao et al., 2015). Second, land uses should be used as environmental variables for distribution modelling, but temporal quality data reporting land uses change (on past, present and future) are hard to get. In addition, there are factors that influence species occurrence at fines scales that we could not include in our approach, such as species interactions, population processes, phenological acclimation, topographic and micro-climates (Araújo and Luoto, 2007; Araújo and Rozenfeld, 2014; Hannah et al., 2014).

Indeed, an important drawback of our study is that we only considered abiotic effects, but previous studies suggest that the spatio-temporal distribution patterns of hummingbirds could vary also due to the flowering phenology of the plants they pollinate (Correa-Lima et al., 2019; Chávez-González et al., 2020; Infante et al., 2020). Thus, it is likely that other factors such as interspecific competition (see Rodríguez-Flores et al., 2019) and changes in floristic composition represent further challenges for these species in the future. From this perspective, areas predicted to be climatically suitable but where essential hummingbird resources are lost (e.g., nesting sites, nectar sugar content from plants) may be in fact an unsuitable habitat for this specialized nectarivorous group. This issue remains poorly studied, but our intuitive hypothesis do not seem totally wrong (see Atauchi et al., 2018). More research is needed on these ideas (Hegland et al., 2009).

It is important to note that shifts in the regional structure of hummingbird-pollinated plant networks (see Chávez-González et al., 2020) may have significant consequences for ecosystem functioning, which could lead to negative cascade effects on animal-plant interactions (Pauw, 2019). In fact, it is also expected that the unprecedented redistribution of biodiversity at the level of taxonomic diversity will lead to an overall reduction in alpha phylogenetic and functional diversities within communities (Graham et al., 2017; Prieto-Torres et al., 2021b), affecting the responses, traits and resilience of ecosystems to disturbances (Weiss and Ray, 2019). In this sense, novel and disappearing hummingbird assemblages are likely to pose management challenges for future conservation (Graham et al., 2017). This is not a minor detail and, therefore, research to understand the susceptibility of pollinator-plant interactions to environmental changes (including different dimensions of diversity) must be considered a top-priority question (see Pearson et al., 2019). From a strategic point of view, this information provides critical context to make better decisions about biodiversity protection and avoid wasting valuable conservation resources (Jones et al., 2018). For developing countries such as Mexico where economic resources for conservation are limited, this is crucial for policy makers (Maxwell et al., 2020).

#### Conservation implications

Despite the increase in the extent of terrestrial PAs over the past 20 years, we detected some important gaps for hummingbirds conservation across Mexico (see Arizmendi et al., 2016). For instance, it

is likely that the proportion of species' ranges contained within PAs will decrease substantially in the future, and it is also important to note that most the priority areas that are highly resilient to GCC and land use change are located outside the current PAs (Fig. 4). Additionally, currently there are at least two globally threatened and endemic species without protection. This leaves the overall long-term conservation picture for hummingbirds quite weak in Mexico. Future efforts to maximize the performance of the PA network must be planned differently.

From this perspective, the priority conservation areas found here provide insights into where to focus future conservation expansion efforts to accomplish a representative and connected PA network in the long-term. This is important because to truly conserve biodiversity, we must ensure that PAs are not only designated in sufficient quantity, but also in locations that are suitable for imperiled species through time (Hannah et al., 2007; Carroll et al., 2010; Prieto-Torres et al. 2016, 2020). Thus, research like this study, focused on identifying these “safe places” (i.e., sites with high species richness where human induced changes in the near future are not expected) are of paramount importance. Given that these areas may remain well-preserved in the future, the necessary resources and efforts should be directed for their long-term maintenance and preservation. The areas we point out for prioritization here coincide strongly with sites previously identified as important in Mexico: 91.9% correspondence with priority areas for conservation and research of terrestrial vertebrates (mammals, birds and amphibians; Nori et al., 2020), 30% correspondence with extreme-priority attention sites for biodiversity conservation (CONABIO, 2016), and 45.1% correspondence with biological corridors across southeastern Mexico (Coordinación de Análisis Territorial, 2015). This suggests that in addition to their importance for hummingbirds, they are also important sites for entire biotas across the region, especially considering the role of hummingbirds as pollinators (see Buzato et al., 2000). In this sense, it is also advantageous that a large proportion of these “safe places” does not match the places targeted for agriculture expansion in future scenarios (Fig. 4); thus, executable actions could be possible if there is also political will.

Our study also highlights the need to review the threat status for several species and to expand conservation practices to ecosystems that are underrepresented within the PAs. This could help national and local governments, as well as NGOs, civil society, and business to assess and prioritize strategies and monitoring studies for species and sites for forest or landscape restoration. Of particular concern are both seasonally dry forests and cloud forests, which despite having high levels of species richness are the least protected, have the highest deforestation rates over the last decade, and are at high risk from GCC (Ponce-Reyes et al., 2012; Prieto-Torres et al., 2016, 2021a; Mayani-Parás et al., 2020). However, it is not just more land that is needed to guarantee the medium- and long-term conservation of hummingbirds; management actions should also focus on maintaining suitable habitats in unprotected areas, on mitigation of GCC impacts (Esperon-Rodríguez et al., 2019), and on assessing the effectiveness of conservation efforts under different anthropogenic practices (e.g., Naime et al., 2020; Sánchez-Romero et al., 2021). This is very important considering that endemic and threatened species —such as *B. xantusii*, *C. forficatus*, and *D. eliza*— are in fact distributed outside from the highly resilient priority areas identified herein.

Additional efforts involving complementary programs for vegetation restoration are also crucial to avoid not only the loss of biodiversity, but also the loss of ecosystem services. In fact, optimal biodiversity maintenance requires habitat conservation in concert with restoration activities at the landscape scale—the latter will likely be increasingly important in a world of changing climate (see von Holle et al., 2020). Therefore, it will be important to pro-

mote and financially support forest protection and/or restoration. In this sense, the “payment for ecosystem services” to landowners that preserve forest remnants represents a positive and effective strategy to reach this important goal (Naime et al., 2020; Sánchez-Romero et al., 2021). From this perspective, we argue that most Mexican municipalities have to be challenged to promote the protection of their biodiversity with significant actions to decrease the species extinction risk. Therefore, we hope that these new findings and proposals will trigger the interest of biologists, conservationists and policy-makers and motivate them to delve more deeply into long-term conservation of biodiversity in Mexico.

### Author contributions

DAP-T and MCA conceived and designed the study. DAP-T, LENR and MCA compiled the database of available records. DAP-T and DRF performed the ecological niche models, spatio-temporal analyses, and MOP tests. All authors contributed to the statistical analysis and interpretation of results, as well as the writing of the manuscript.

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### Competing interests statement

The authors declare no conflicts of interest.

### Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials. Interested readers to other material could to request them from the both first [DAP-T: davidprietorres@gmail.com] and corresponding author [MCA: coro@unam.mx].

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pecon.2021.07.001>.

## References

- Alkhishe, A.A., Peterson, A.T., Samy, A.M., 2017. Climate change influences on the potential geographic distribution of the disease vector tick *Ixodes ricinus*. *PLoS One* 12, e0189092. <http://dx.doi.org/10.1371/journal.pone.0189092>.
- Altshuler, D.L., Dudley, R., McGuire, J.A., 2004. Resolution of a paradox: hummingbird flight at high elevation does not come without a cost. *Proc. Natl. Acad. Sci. U.S.A.* 101, 17731–17736. <http://dx.doi.org/10.1073/pnas.0405260101>.
- Anderson, R., Lew, D., Peterson, A., 2003. Evaluating predictive models of species' distributions: Criteria for selecting optimal models. *Ecol. Model.* 162, 211–232. [http://dx.doi.org/10.1016/S0304-3800\(02\)00349-6](http://dx.doi.org/10.1016/S0304-3800(02)00349-6).
- Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., 2019. Standards for distribution models in biodiversity assessments. *Sci. Adv.* 5, eaat4858. <http://dx.doi.org/10.1126/sciadv.aat4858>.
- Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* 16 (6), 743–753. <http://dx.doi.org/10.1111/j.1466-8238.2007.00359.x>.
- Araújo, M.B., Rozenfeld, A., 2014. The geographic scaling of biotic interactions. *Ecography* 37 (5), 406–415. <http://dx.doi.org/10.1111/j.1600-0587.2013.00643.x>.
- Arbeláez-Cortés, E., Navarro-Sigüenza, A.G., 2013. Molecular evidence of the taxonomic status of western Mexican populations of *Phaethornis longirostris* (Aves: Trochilidae). *Zootaxa* 3716, 81–97. <http://dx.doi.org/10.11646/zootaxa.3716.1.7>.
- Arenas-Navarro, M., García-Oliva, F., Torres-Miranda, A., Téllez-Valdés, O., Oyama, K., 2020. Environmental filters determine the distribution of tree species in a threatened biodiversity hotspot in western Mexico. *Bot. Sci.* 98, 219–237. <http://dx.doi.org/10.17129/botsci.2398>.
- Arizmendi, M.C., Berlanga, H., Rodríguez-Flores, C., Vargas-Canales, V., Montes-Leyva, L., Lira, R., 2016. Hummingbird conservation in Mexico: the natural protected areas system. *Nat. Areas J.* 36, 366–376.
- Arizmendi, M.C., Berlanga-García, H., 2014. *Colibríes de México y Norteamérica*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.
- Atauchí, P.J., Auca-Chutas, C., Ferro, G., Prieto-Torres, D.A., 2020. Present and future potential distribution of the endangered *Anairetes alpinus* (Passeriformes: Tyrannidae) under global climate change scenarios. *J. Ornithol.* 161, 723–738. <http://dx.doi.org/10.1007/s10336-020-01762-z>.
- Atauchí, P.J., Peterson, A.T., Flanagan, J., 2018. Species distribution models for Peruvian plantcutter improve with consideration of biotic interactions. *J. Avian Biol.* 49, jav-01617. <http://dx.doi.org/10.1111/jav.01617>.
- Barve, N., Barve, V., Available from: <https://github.com/narayanibarve/ENMGadgets>. (Accessed November 15, 2020) 2016. ENMGadgets: tools for pre and post processing in ENM workflow. R package version 0.0.14.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222, 1810–1819. <http://dx.doi.org/10.1016/j.ecolmodel.2011.02.011>.
- Battey, C.J., 2019. Ecological release of the Anna's Hummingbird during a northern range expansion. *Am. Nat.* 194, 306–315. <https://orcid.org/0000-0002-9958-4282>.
- Beck, J., Böller, M., Erhardt, A., Schwanghart, W., 2014. Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecol. Inform.* 19, 10–15. <http://dx.doi.org/10.1016/j.ecoinf.2013.11.002>.
- Berlanga, H., Rodríguez-Contreras, V., Oliveras de Ita, A., Escobar, M., Rodríguez, L., Vieyra, J., Vargas, V., 2008. *Red de Conocimientos sobre las Aves de México (AVESMX)*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.
- Bolochio, B.E., Lescano, J.N., Cordier, J.M., Loyola, R., Nori, J., 2020. A functional perspective for global amphibian conservation. *Biol. Conserv.* 245, 108572. <http://dx.doi.org/10.1016/j.biocon.2020.108572>.
- Bregman, T.P., Sekercioglu, C.H., Tobias, J.A., 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biol. Conserv.* 169, 372–383. <http://dx.doi.org/10.1016/j.biocon.2013.11.024>.
- Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.R., Guisan, A., 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Glob. Change Biol.* 12, 1079–1093. <http://dx.doi.org/10.1111/j.1365-2486.2006.01157.x>.
- Buermann, W., Chaves, J.A., Dudley, R., McGuire, J.A., Smith, T.B., Altshuler, D.L., 2011. Projected changes in elevational distribution and flight performance of montane Neotropical hummingbirds in response to climate change. *Glob. Change Biol.* 17, 1671–1680. <http://dx.doi.org/10.1111/j.1365-2486.2010.02330.x>.
- Buzato, S., Sazima, M., Sazima, I., 2000. Hummingbird-pollinated floras at three Atlantic Forest sites. *Biotropica* 32, 824–841. <http://dx.doi.org/10.1111/j.1744-7429.2000.tb00621.x>.
- Campbell, L.P., Luther, C., Moo-Llanes, D., Ramsey, J.M., Danis-Lozano, R., Peterson, A.T., 2015. Climate change influences on global distributions of dengue and chikungunya virus vectors. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 370, 20140135. <http://dx.doi.org/10.1098/rstb.2014.0135>.
- Carroll, C., Dunk, J.R., Moilanen, A., 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest. *USA. Glob. Change Biol.* 16, 891–904. <http://dx.doi.org/10.1111/j.1365-2486.2009.01965.x>.
- Chávez-González, E., Vizenin-Bugoni, J., Vázquez, D.P., MacGregor-Fors, I., Dáttilo, W., Ortiz-Pulido, R., 2020. Drivers of the structure of plant–hummingbird interaction networks at multiple temporal scales. *Oecologia* 193, 913–924. <http://dx.doi.org/10.1007/s00442-020-04727-4>.
- Chesser, R.T., Billerman, S.M., Burns, K.J., Cicero, C., Dunn, J.L., Kratter, A.W., Lovette, I.J., Mason, N.A., Rasmussen, P.C., Remsen Jr., J.V., Stotz, D.F., Winker, K., 2020. Sixty-first supplement to the American Ornithological Society's check-list of North American birds. *The Auk* 137. <http://dx.doi.org/10.1093/auk/ukaa030>, ukaa030.
- Cobos, M.E., Peterson, A.T., Barve, N., Osorio-Olvera, L., 2019. kuenm: an R package for detailed development of ecological niche models using Maxent. *PeerJ* 7, e6281. <http://dx.doi.org/10.7717/peerj.6281>.
- Comisión Nacional para el Conocimiento y Uso de la Biodiversidad [CONABIO], 2016. Sitios de atención prioritaria para la conservación de la biodiversidad. Escala 1 (1), 000 000. <http://www.conabio.gob.mx/informacion/gis/>. (Accessed May 28, 2021).
- Cook, B.I., Mankin, J.S., Marvel, K., Williams, A.P., Smerdon, J.E., Anchukaitis, K.J., 2020. Twenty-first century drought projections in the CMIP6 forcing scenarios. *Earth's Future* 8. <http://dx.doi.org/10.1029/2019EF001461>, e2019EF001461.
- Coordinación de Análisis Territorial, 2015. Límites y regionalización de los Corredores Biológicos del sureste de México, 2015. Second Edition. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Escala 1:250000. <http://www.conabio.gob.mx/informacion/gis/>. (Accessed May 28, 2021).
- Cornejo-Páramo, P., Lira-Noriega, A., Ramírez-Suástegui, C., Méndez-de-la-Cruz, F.R., Székely, T., Urrutia, A.O., Cortez, D., 2020. Sex determination systems in reptiles are related to ambient temperature but not to the level of climatic fluctuation. *BMC Evol. Biol.* 20, 103. <http://dx.doi.org/10.1186/s12862-020-01671-y>.
- Correa-Lima, A.P.A., Varassin, I.G., Barve, N., Zwiener, V.P., 2019. Spatio-temporal effects of climate change on the geographical distribution and flowering phenology of hummingbird-pollinated plants. *Ann. Bot.* 124, 389–398. <http://dx.doi.org/10.1093/aob/mcz079>.
- Cuervo-Robayo, A.P., Ureta, C., Gómez-Albore, M.A., Meneses-Mosquera, A.K., Téllez-Valdés, O., Martínez-Meyer, E., 2020. One hundred years of climate change in Mexico. *PLoS One* 15, e0209808. <http://dx.doi.org/10.1371/journal.pone.0209808>.
- de Matos Sousa, N.O., Lopes, L.E., Costa, L.M., Motta-Junior, J.C., de Freitas, G.H.S., Dornas, T., de Vasconcelos, M.F., Nogueira, W., Tolentino, V.C.D.M., De-Carvalho, C.B., Barbosa, M.O., Ubaid, F.K., Nunes, A.P., Malacco, G.B., Marini, M.A., 2021. Adopting habitat-use to infer movement potential and sensitivity to human disturbance of birds in a Neotropical Savannah. *Biol. Conserv.* 254, 108921. <http://dx.doi.org/10.1016/j.biocon.2020.108921>.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pinte, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghanzhanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpo, Y., Kindt, R., Barnekow-Lillesø, J.-P., van Breugel, P., Graudal, L., Vogt, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67, 534–545. <http://dx.doi.org/10.1093/biosci/bix014>.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17, 43–57. <http://dx.doi.org/10.1111/j.1472-4642.2010.00725.x>.
- Escobar, L.E., Lira-Noriega, A., Medina-Vogel, G., Peterson, A.T., 2014. Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: use of Maxent and NicheA to assure strict model transference. *Geospat. Health* 9, 221–229. <http://dx.doi.org/10.4081/gh.2014.19>.
- Esparza-Orozco, A., Lira-Noriega, A., Martínez-Montoya, J.F., Pineda-Martínez, L.F., Méndez-Gallegos, S., de, J., 2020. Influences of environmental heterogeneity on amphibian composition at breeding sites in a semi-arid region of Mexico. *J. Arid Environ.* 182, 104259. <http://dx.doi.org/10.1016/j.jaridenv.2020.104259>.
- Esperon-Rodríguez, M., Beaumont, L.J., Lenoir, J., Baumgartner, J.B., McGowan, J., Correa-Metrio, A., Camac, J.S., 2019. Climate change threatens the most biodiverse regions of Mexico. *Biol. Conserv.* 240, 108215. <http://dx.doi.org/10.1016/j.biocon.2019.108215>.
- ESRI, 2010. *ArcMap 10.0*. Environmental System Research Institute, Inc., New York.

- Fajardo, J., Corcoran, D., Roehrdanz, P.R., Hannah, L., Marquet, P.A., 2020. GCM compareR: A web application to assess differences and assist in the selection of general circulation models for climate change research. *Methods Ecol. Evol.* 11, 656–663, <http://dx.doi.org/10.1111/2041-210X.13360>.
- FAO—Organization for Food and Agriculture for the United States [FAO], Electronically published in the internet. Available from: <http://www.fao.org/forestry/fro/fra/index.jsp>, 2001.
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37, 4302–4315, <http://dx.doi.org/10.1002/joc.5086>.
- Goettsch, B., Durán, A.P., Gaston, K.J., 2019. Global gap analysis of cactus species and priority sites for their conservation. *Conserv. Biol.* 33, 369–376, <http://dx.doi.org/10.1111/cobi.13196>.
- Graham, L.J., Weinstein, B.G., Supp, S.R., Graham, C.H., 2017. Future geographic patterns of novel and disappearing assemblages across three dimensions of diversity: A case study with Ecuadorian hummingbirds. *Divers Distrib* 23, 944–954, <http://dx.doi.org/10.1111/ddi.12587>.
- Greig, E.I., Wood, E.M., Bonter, D.N., 2017. Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. *Proc. Royal Soc. B: Biol. Sci* 284 (1852), 20170256, <http://dx.doi.org/10.1098/rspb.2017.0256>.
- Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B., McCullough, I.M., 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends Ecol. Evol.* 29, 390–397, <http://dx.doi.org/10.1016/j.tree.2014.04.006>.
- Hannah, L., Midgley, G., Anđelman, S., Araújo, M., Hughes, G., Martínez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. *Front Ecol Environ* 5, 131–138, [http://dx.doi.org/10.1890/1540-9295\(2007\)5\[131:PANIAC\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2).
- Hanspach, J., Kühn, I., Schweiger, O., Pompe, S., Klotz, S., 2011. Geographical patterns in prediction errors of species distribution models. *Glob. Ecol. Biogeogr* 20, 779–788, <http://dx.doi.org/10.1111/j.1466-8238.2011.00649.x>.
- Harsch, M.A., HilleRisLambers, J., 2016. Climate warming and seasonal precipitation change interact to limit species distribution shifts across Western North America. *PLoS One* 11, e0159184, <http://dx.doi.org/10.1371/journal.pone.0159184>.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? *Ecol Lett* 12, 184–195, <http://dx.doi.org/10.1111/j.1461-0248.2008.01269.x>.
- Hidalgo, H.G., 2021. Climate variability and change in Central America: What does it mean for water managers? *Front. Water* 2, 632739, <http://dx.doi.org/10.3389/frwa>.
- Humphries, C.J., van Wright, R.L., Williams, P.H., 1991. *Biodiversity reserves: Setting new priorities for the conservation of wildlife*. *Parks* 2, 34–38.
- Infante, S.D., Lara, C., Arizmendi, M.C., 2020. Temporal dynamics of the hummingbird-plant interaction network of a dry forest in Chamela, Mexico: a 30-year follow-up after two hurricanes. *PeerJ* 8, e8338, <http://dx.doi.org/10.7717/peerj.8338>.
- Instituto Nacional de Estadística Geografía e Informática [INEGI] - Comisión Nacional para el Conocimiento y Uso de la Biodiversidad [CONABIO] - Instituto Nacional de Ecología [INE], 2008. *Ecorregiones Terrestres de México*. Escala, 1:1000000. <http://www.conabio.gob.mx/>. (Accessed March 05, 2021).
- International Union for Conservation of Nature categories [IUCN], <https://www.iucnredlist.org/>, 2015. (Accessed 22 January 2021).
- Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., Watson, J.E., 2018. One-third of global protected land is under intense human pressure. *Science* 360, 788–791, <http://dx.doi.org/10.1126/science.aap9565>.
- Kindt, R., Available at: <http://cran.r-project.org/web/packages/BiodiversityR/>. (Accessed May 25, 2020) 2016. BiodiversityR: Package for community ecology and suitability analysis. R package version 2.7-1.
- Lara, C., Feria-Arroyo, T.P., Dale, J., Muñoz, J., Arizmendi, M.C., Ornelas, J.F., Raúl Ortiz-Pulido, R., Rodríguez-Flores, C.I., Díaz-Valenzuela, R., Martínez-García, V., Díaz-Palacios, A., Partida, R., Enríquez, P.L., Rangel-Salazar, J.L., Schondube, J., 2012. Potential effects of the climate change in the distribution of hummingbirds: a study case with hummingbirds from the genus *Amazilia* and *Cyananthus*. *Ornitol. Neotrop.* 23, 57–70.
- Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789, <http://dx.doi.org/10.1111/jbi.12058>.
- Lovejoy, T.E., Hannah, L., 2019. *Biodiversity and climate change: transforming the biosphere*. Yale University Press, London, UK.
- Margules, C., Sarkar, S., 2009. *Planeación Sistemática de la Conservación*. Universidad Nacional Autónoma de México (UNAM), Comisión Nacional de Áreas Naturales Protegidas (CONANP) y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico City, Mexico.
- Mason-Romo, E.D., Ceballos, G., Lima, M., Martínez-Yrizar, A., Jaramillo, V.J., Maass, M., 2018. Long-term population dynamics of small mammals in tropical dry forests, effects of unusual climate events, and implications for management and conservation. *Forest Ecol Manag* 426, 123–133, <http://dx.doi.org/10.1016/j.foreco.2018.05.058>.
- Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S., Stolton, S., Viconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O., Watson, J.E.M., 2020. Area-based conservation in the twenty-first century. *Nature* 586, 217–227, <http://dx.doi.org/10.1038/s41586-020-2773-z>.
- Mayani-Parás, F., Botello, F., Castañeda, S., Munguía-Carrara, M., Sánchez-Cordero, V., 2020. Cumulative habitat loss increases conservation threats on endemic species of terrestrial vertebrates in Mexico. *Biol. Conserv.* 253, 108864, <http://dx.doi.org/10.1016/j.biocon.2020.108864>.
- Mazariegos, O.Ch., 2010. *Of birds and insects; The hummingbird myth in ancient Mesoamerica*. *Ancient Mesoamerica* 21, 45–61.
- Mendoza-Ponce, A.V., Corona-Núñez, R.O., Kraxner, F., Estrada, F., 2020. Spatial prioritization for biodiversity conservation in a megadiverse country. *Anthropocene* 32, 100267, <http://dx.doi.org/10.1016/j.ancene.2020.100267>.
- Merow, C., Smith, M.J., Edwards Jr, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, E., Wüest, R.O., Zimmermann, N.E., Elith, J., 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography* 37, 1267–1281, <http://dx.doi.org/10.1111/ecog.00845>.
- Morrone, J.J., 2014. Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782, 1–110, <http://dx.doi.org/10.11646/zootaxa.3782.1.1>.
- Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol. Evol.* 5, 1198–1205, <http://dx.doi.org/10.1111/2041-210X.12261>.
- Naime, J., Mora, F., Sánchez-Martínez, M., Arreola, F., Balvanera, P., 2020. Economic valuation of ecosystem services from secondary tropical forests: trade-offs and implications for policy making. *For. Ecol. Manag.* 473, 118294, <http://dx.doi.org/10.1016/j.foreco.2020.118294>.
- Naimi, B., Available at: <https://cran.r-project.org/web/packages/usdm/>. (Accessed November 15, 2020) 2015. usdm: Uncertainty analysis for species distribution models. R package version 1.
- Navarro-Sigüenza, A.G., Peterson, A.T., Gordillo-Martínez, A., 2003. *Museums working together: The atlas of the birds of Mexico*. *Bull. Br. Orn. Club* 123A, 207–225.
- Nori, J., Loyola, R., Villalobos, F., 2020. Priority areas for conservation of and research focused on terrestrial vertebrates. *Conserv. Biol.* 34, 1281–1291, <http://dx.doi.org/10.1111/cobi.13476>.
- Ochoa-Ochoa, L.M., Rodríguez, P., Mora, F., Flores-Villela, O., Whittaker, R.J., 2012. Climate change and amphibian diversity patterns in Mexico. *Biol. Conserv.* 150, 94–102, <http://dx.doi.org/10.1016/j.biocon.2012.03.010>.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326, <http://dx.doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Ortega, J.C., Machado, N., Diniz-Filho, J.A.F., Rangel, T.F., Araújo, M.B., Loyola, R., Bini, L.M., 2019. Meta-analyzing the likely cross-species responses to climate change. *Ecol. Evol.* 9, 11136–11144, <http://dx.doi.org/10.1002/ece3.5617>.
- Osoorio-Olvera, L., Lira-Noriega, A., Soberón, J., Peterson, A.T., Falconi, M., Contreras-Díaz, R.G., Martínez-Meyer, E., Barve, V., Barve, N., 2020. ntbox: An r package with graphical user interface for modelling and evaluating multidimensional ecological niches. *Methods Ecol. Evol.* 11, 1199–1206, <http://dx.doi.org/10.1111/2041-210X.13452>.
- Owens, H.L., Campbell, L.P., Dornak, L.L., Saupé, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E., 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol. Model.* 263, 10–18, <http://dx.doi.org/10.1016/j.ecolmodel.2013.04.011>.
- Pauw, A., 2019. A Bird's-Eye View of Pollination: Biotic Interactions as Drivers of Adaptation and Community Change. *Annu. Rev. Ecol. Syst.* 50, <http://dx.doi.org/10.1146/annurev-ecolsys-110218-024845>.
- Pearson, R., Martínez-Meyer, E., Andrade Velázquez, M., Caron, M., Corona-Núñez, R., Davis, K., Paz Durán, A., García Morales, R., Hackett, T., Ingram, D., Loyola Díaz, R., Lescano, J., Lira-Noriega, A., López-Maldonado, Y., Manuschevich, D., Mendoza, A., Milligan, B., Mills, S., Moreira-Arce, D., Nava, L., Oostra, V., Owen, N., Prieto-Torres, D.A., Rodríguez Soto, C., Smith, T., Suggitt, A., Tejo Haristoy, C., Velázquez-Tibatá, J., Díaz, S., Marquet, P., 2019. Research priorities for maintaining biodiversity's contributions to people in Latin America. *UCL Open: Environment* 1, 02, <http://dx.doi.org/10.14324/111.444/ucloe.000002>.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34, 102–117, <http://dx.doi.org/10.1111/j.1365-2699.2006.01594.x>.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.G., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.i., Martin, V.Y., McCormack, F.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N.P., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnelli, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355 (6332), <http://dx.doi.org/10.1126/science.aai9214>.
- Pérez-Navarro, M.A., Bloennimann, O., Esteve, M.A., Moya-Perez, J.M., Carreño, M.F., Guisan, A., Lloret, F., 2021. Temporal variability is key to modelling the climatic niche. *Divers. Distrib.* 27, 473–484, <http://dx.doi.org/10.1111/ddi.13207>.
- Peterson, A.T., Cobos, M.E., Jiménez-García, D., 2018. Major challenges for correlational ecological niche model projections to future climate conditions. *Ann. New York Acad. Sci.* 1429, 66–77, <http://dx.doi.org/10.1111/nyas.13873>.
- Peterson, A.T., Navarro-Sigüenza, A.G., Martínez-Meyer, E., Cuervo-Robayo, A.P., Berlanga, H., Soberón, J., 2015. Twentieth century turnover of Mexican

- endemic avifaunas: Landscape change versus climate drivers. *Sci. Adv.* 1, e1400071, <http://dx.doi.org/10.1126/sciadv.1400071>.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H., Stockwell, D.R., 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* 416, 626, <http://dx.doi.org/10.1038/416626a>.
- Peterson, A.T., Papeš, M., Soberón, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* 213, 63–72, <http://dx.doi.org/10.1016/j.ecolmodel.2007.11.008>.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. *Ecological niches and geographic distributions*. Princeton University Press, New Jersey.
- Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: An open-source release of Maxent. *Ecography* 40, 887–893, <http://dx.doi.org/10.1111/ecog.03049>.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197, <http://dx.doi.org/10.1890/07-2153.1>.
- Ponce-Reyes, R., Reynoso-Rosales, V.H., Watson, J.E., VanDerWal, J., Fuller, R.A., Pressey, R.L., Possingham, H.P., 2012. Vulnerability of cloud forest reserves in Mexico to climate change. *Nat. Clim. Change* 2, 448–452, <http://dx.doi.org/10.1038/nclimate1453>.
- Prieto-Torres, D.A., Lira-Noriega, A., Navarro-Sigüenza, A.G., 2020. Climate change promotes species loss and uneven modification of richness patterns in the avifauna associated to Neotropical seasonally dry forests. *Perspect. Ecol. Conserv.* 18, 19–30, <http://dx.doi.org/10.1016/j.pecon.2020.01.002>.
- Prieto-Torres, D.A., Navarro-Sigüenza, A.G., Santiago-Alarcon, D., Rojas-Soto, O.R., 2016. Response of the endangered tropical dry forests to climate change and the role of Mexican Protected Areas for their conservation. *Glob. Change Biol.* 22, 364–379, <http://dx.doi.org/10.1111/gcb.13090>.
- Prieto-Torres, D.A., Nori, J., Rojas-Soto, O.R., Navarro-Sigüenza, A.G., 2021a. Challenges and opportunities in planning for the conservation of Neotropical seasonally dry forests into the future. *Biol. Conserv.* 257, 109083, <http://dx.doi.org/10.1016/j.biocon.2021.109083>.
- Prieto-Torres, D.A., Sánchez-González, L.A., Ortiz-Ramírez, M.F., Ramírez-Albores, J.E., García-Trejo, E.A., Navarro-Sigüenza, A.G., 2021b. Climate warming affects spatio-temporal biodiversity patterns of a highly vulnerable Neotropical avifauna. *Clim. Change* 165, 57, <http://dx.doi.org/10.1007/s10584-021-03091-3>.
- Qiao, H., Soberón, J., Peterson, A.T., 2015. No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. *Methods Ecol. Evol.* 6, 1126–1136, <http://dx.doi.org/10.1111/2041-210X.12397>.
- Ramírez-Albores, J.E., Prieto-Torres, D.A., Gordillo-Martínez, A., Sánchez-Ramos, L.E., Navarro-Sigüenza, A.G., 2021. Insights for protection of high species richness areas for the conservation of Mesoamerican endemic birds. *Divers. Distrib.* 27, 18–33, <http://dx.doi.org/10.1111/ddi.1315>.
- Riahi, K., Van Vuuren, D.P., Kriegler, E., Edmonds, J., O'Neill, B.C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuarea, J.C., KC, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., Ebi, K., Hasegawa, T., Havlik, P., Humpenöder, F., Da Silva, L.A., Smith, S., Stehfest, E., Bosetti, V., Eom, J., Gernaat, D., Masui, T., Rogelj, J., Streffer, J., Drouet, L., Krey, V., Luderer, G., Harmsen, M., Takahashi, K., Baumstark, L., Doelman, J.C., Kainuma, M., Klimont, Z., Marangoni, G., Lotze-Campen, H., Obersteiner, M., Tabeau, A., Tavoni, M., 2017. The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: an overview. *Glob. Environ. Change* 42, 153–168, <http://dx.doi.org/10.1016/j.gloenvcha.2016.05.009>.
- Robertson, M.P., Visser, V., Hui, C., 2016. Biogeography: an R package for assessing and improving data quality of occurrence record datasets. *Ecography* 39, 394–401, <http://dx.doi.org/10.1111/ecog.02118>.
- Rödger, D., Engler, J.O., 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecol. Biogeogr.* 20, 915–927, <http://dx.doi.org/10.1111/j.1466-8238.2011.00659.x>.
- Rodrigues, A.S., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428, 640–643, <http://dx.doi.org/10.1038/nature02422>.
- Rodríguez-Flores, C.I., Ornelas, J.F., Wethington, S., Arizmendi, M.C., 2019. Are hummingbirds generalists or specialists? Using network analysis to explore the mechanisms influencing their interaction with nectar resources. *PLoS One* 14, e0211855, <http://dx.doi.org/10.1371/journal.pone.0211855>.
- Sánchez-Ramos, L.E., Gordillo-Martínez, A., Gutiérrez-Arellano, C.R., Kobelkowsky-Vidrio, T., Ríos-Muñoz, C.A., Navarro-Sigüenza, A.G., 2018. Bird diversity patterns in the nuclear Central American highlands: a conservation priority in the northern Neotropics. *Trop. Conserv. Sci.* 11, 1940082918819073, <http://dx.doi.org/10.1177/1940082918819073>.
- Sánchez-Romero, R., Balvanera, P., Castillo, A., Mora, F., García-Barrios, L.E., González-Esquível, C.E., 2021. Management strategies, silvopastoral practices and socioecological drivers in traditional livestock systems in tropical dry forests: An integrated analysis. *For. Ecol. Manag.* 479, 118506, <http://dx.doi.org/10.1016/j.foreco.2020.118506>.
- Schuchmann, K.L., 1999. *Family Trochilidae (Hummingbirds)*. In: *Del Hoyo, J., Elliot, A., Sargatal, J. (Eds.), Handbook of the Birds of the World. Volume 5: Barn-owls to Hummingbirds*. Lynx Edicions, Barcelona, Spain, pp. 468–680.
- Schulenberg, T.E., <https://birdsoftheworld.org/bow/home/>, 2019. (Accessed 22 January 2021).
- Sinervo, B., Lara Reséndiz, R.A., Miles, D.B., Lovich, J.E., Ennen, J.R., Müller, J., Ennen, J.R., Müller, J., Cooper, R.D., Rosen, P.C., Stewart, J.A.E., Santos, J.C., Sites Jr., J.W., Gibbons, P.M., Goode, E.V., Hillard, L.S., Welton, L., Agha, M., Caetano, G., Vaughn, M., Meléndez Torres, C., Gadsden, H., Casteñada Gaytán, G., Galina Tessaro, P., Valle Jiménez, F.I., Valdez Villavicencio, J., Martínez-Méndez, N., Woolrich Piña, G., Luja Molina, V. de la Vega Pérez, A.D., Arenas Moreno, D.M., Domínguez Guerrero, S., Fierro, N., Butterfield, S., Westphal, M., Huey, R.B., Mautz, W., Sánchez-Cordero, V., Méndez de la Cruz, F.R., White Paper for the Environmental Working Group of the UC-Mexico Initiative. <https://escholarship.org/uc/item/4xk077hp>. (Accessed 13 March 2021) 2017. Climate change and collapsing thermal niches of Mexican endemic reptiles.
- Smith, D.M., Finch, D.M., Stoleson, S.H., 2014. Nest-location and nest-survival of black-chinned hummingbirds in New Mexico: a comparison between rivers with differing levels of regulation and invasion of nonnative plants. *Southwest. Nat.* 59, 193–198, <http://dx.doi.org/10.1894/F06-TEL-02.1>.
- Soberón, J., Peterson, A.T., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2, 1–10, <http://dx.doi.org/10.17161/bi.v2i0.4>.
- Sonne, J., Martín González, A.M., Maruyama, P.K., Sandel, B., Vizentin-Bugoni, J., Schleuning, M., Abrahamczyk, S., Alarcón, R., Araujo, A.C., Araújo, F.P., Mendes de Azevedo, S., Baquero, A.C., Cotton, P.A., Toftemark Ingversen, T., Kohler, G., Lara, C., Guedes Las-Casas, F.M., Machado, A.O., Graco Machado, C., Maglianesi, M.A., Cerqueira Moura, A., Nogueira-Bravo, D., Oliveira, G.M., Oliveira, P.E., Ornelas, J.F., da Cruz Rodrigues, L., Rosero-Lasprilla, L., Rui, A.M., Sazima, M., Timmermann, A., Galarda Varassin, I., Wang, Z., Watts, S., Fjeldsá, J., Svenning, J.-C., Rahbek, C., Dalsgaard, B., 2016. High proportion of smaller ranged hummingbird species coincides with ecological specialization across the Americas. *Proc. R. Soc. B* 283, 20152512, <http://dx.doi.org/10.1098/rspb.2015.2512>.
- Stoerk, T., Wagner, G., Ward, R.E., 2018. Policy brief—Recommendations for improving the treatment of risk and uncertainty in economic estimates of climate impacts in the sixth Intergovernmental Panel on Climate Change assessment report. *Rev. Environ. Econ. Policy* 12, 371–376, <http://dx.doi.org/10.1093/reep/rey005>.
- Stotz, D.F., Fitzpatrick, J.W., Parker III, T.A., Moskovits, D.K., Snow, D., 1996. *Neotropical birds: ecology and conservation*. University of Chicago Press, USA.
- Thuiller, W., Lavorel, S., Araújo, M.B., 2005. Niche properties and geographic extent as predictors of species sensitivity to climate change. *Glob. Ecol. Biogeogr.* 14, 347–357, <http://dx.doi.org/10.1111/j.1466-822X.2005.00162.x>.
- Urban, M.C., Richardson, J.L., Freidenfelds, N.A., 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. *Evol. Appl.* 7, 88–103, <http://dx.doi.org/10.1111/eva.12114>.
- Ureta, C., Cuervo-Robayo, A.P., Calixto-Pérez, E., González-Salazar, C., Fuentes-Conde, E., 2018. A first approach to evaluate the vulnerability of islands' vertebrates to climate change in Mexico. *Atmósfera* 31, 221–254, <http://dx.doi.org/10.20937/atm.2018.31.03.03>.
- Van Asselen, S., Verburg, P.H., 2013. Land cover change or land-use intensification: simulating land system change with a global-scale land change model. *Glob. Chang. Biol.* 9, 3648–3667, <http://dx.doi.org/10.1111/gcb.1233>.
- Velazco, S.J.E., Ribeiro, B.R., Laureto, L.M.O., Júnior, P.D.M., 2020. Overprediction of species distribution models in conservation planning: A still neglected issue with strong effects. *Biol. Conserv.* 252, 108822, <http://dx.doi.org/10.1016/j.biocon.2020.108822>.
- von Holle, B., Yelenik, S., Gornish, E.S., 2020. Restoration at the landscape scale as a means of mitigation and adaptation to climate change. *Curr. Landsc. Ecol. Rep.* 5, 85–97, <http://dx.doi.org/10.1007/s40823-020-00056-7>.
- Weiss, K.C., Ray, C.A., 2019. Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. *Ecography* 42, 2012–2020, <http://dx.doi.org/10.1111/ecog.04387>.
- Yesson, C., Brewer, P.W., Sutton, T., Caihness, N., Pahwa, J.S., Burgess, M., Gray, W.A., White, R.J., Jones, A.C., Bisby, F.A., Culham, A., 2007. How global is the global biodiversity information facility? *PLoS One* 2, e1124, <http://dx.doi.org/10.1371/journal.pone.0001124>.
- Zamora-Gutierrez, V., Pearson, R.G., Green, R.E., Jones, K.E., 2018. Forecasting the combined effects of climate and land use change on Mexican bats. *Divers. Distrib.* 24, 363–374, <http://dx.doi.org/10.1111/ddi.12686>.
- Zappa, G., Shepherd, T.G., 2017. Storylines of atmospheric circulation change for European regional climate impact assessment. *J. Clim.* 30, 6561–6577, <http://dx.doi.org/10.1175/JCLI-D-16-0807.1>.
- Zelinka, M.D., Myers, T.A., McCoy, D.T., Po-Chedley, S., Caldwell, P.M., Ceppi, P., Klein, S.A., Taylor, K.E., 2020. Causes of higher climate sensitivity in CMIP6 models. *Geophys. Res. Lett.* 47, <http://dx.doi.org/10.1029/2019GL085782>, e2019GL085782.