



Predicting co-distribution patterns of parrots and woody plants under global changes: The case of the Lilac-crowned Amazon and Neotropical dry forests

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ABSTRACT

Global climate and land-use changes are the most significant causes of the current habitat loss and biodiversity crisis. Although there is information measuring these global changes, we lack a full understanding of how they impact community assemblies and species interactions across ecosystems. Herein, we assessed the potential distribution of eight key woody plant species associated with the habitat of the endangered Lilac-crowned Amazon (*Amazona finschi*) under global changes scenarios (2050's and 2070's), to answer the following questions: (1) how do predicted climate and land-use changes impact these species' individual distributions and co-distribution patterns?; and (2) how effective is the existing Protected Area network for safeguarding the parrot species, the plant species, and their biological interactions? Our projections were consistent identifying the species that are most vulnerable to climate change. The distribution ranges of most of the species tended to decrease under future climates. These effects were strongly exacerbated when incorporating land-use changes into models. Even within existing protected areas, >50 % of the species' remaining distribution and sites with the highest plant richness were predicted to be lost in the future under these combined scenarios. Currently, both individual species ranges and sites of highest richness of plants, shelter a high proportion (ca. 40 %) of the Lilac-crowned Amazon distribution. However, this spatial congruence could be reduced in the future, potentially disrupting the ecological associations among these taxa. We provide novel evidence for decision-makers to enhance conservation efforts to attain the long-term protection of this endangered Mexican endemic parrot and its habitat.

1. Introduction

Global climate change is recognized as one of the most important drivers of the biodiversity crisis because it alters temperature and precipitation patterns, which modifies species' distribution patterns and forces them to relocate from their current distributional ranges (Lovejoy & Hannah, 2019). During the late 20th and early 21st centuries, the global average temperature has increased by 0.6 °C (IPCC, 2014), and projections for the coming decades are not optimistic (Pandit et al., 2021). Likewise, it is well known that there is strong synergy between climate change and habitat loss due to agricultural activities; this

interaction has led to multiple examples of local and even global extinctions (Ceballos & Ehrlich, 2018). This has a severe impact on biodiversity, but also on ecosystem services, and consequently, on human well-being (Diaz et al., 2018). Therefore, there is growing interest in understanding the combined effects of these global drivers on the spatio-temporal distribution patterns of biodiversity. This information is critical for the implementation of effective mitigation policies and conservation practices (Rebelo et al., 2010; IPBES, 2019).

Ecological niche and species distribution models are methodological frameworks that are used to assess the potential effects of global change on a wide range of species (both aquatic and terrestrial) and at distinct

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geographic scales (Araújo et al., 2019). These approaches use statistical methods to relate geo-referenced occurrence data and environmental variables in order to project species' Grinnellian niches (Rödder & Engler, 2011) and predict habitat suitability for a given species or set of species (see Peterson et al. [2011] for a detailed explanation). These models have been useful for defining core areas of species diversity (Stas et al., 2020), evaluating both evolutionary and ecological hypotheses (Cornejo-Páramo et al., 2020, Esparza-Orozco et al., 2020), and developing conservation strategies (Prieto-Torres et al. 2021a). However, species' co-distribution patterns are often overlooked in the modelling literature (Atauchi et al., 2018, Heinen et al., 2020). This is an important information gap because loss of key species interactions (e.g., between plants and their animal pollinators or seed dispersers) may have detrimental impacts for the species involved and the ecosystem as a whole (Jordano, 2016). Therefore, more research is urgently needed to prevent the loss of yet more species (Hegland et al., 2009).

Neotropical dry forests are some of the most biodiverse ecosystems; at the same time, they have suffered high biodiversity loss due to the impacts of land conversion, global climate change, and their synergistic effects (e.g., Miles et al., 2006, Portillo-Quintero & Sánchez-Azofeifa, 2010, Collevatti et al., 2013, Banda et al., 2016, Prieto-Torres et al., 2016, 2018, 2021, Siyum, 2020). New evidence indicates that the distribution of Neotropical dry forests and the survival of the species that inhabit them could be strongly affected by these anthropogenic threats. A series of recent studies predicted decreases in the distribution ranges of over 50 % of bird species across Neotropical dry forests, with uneven taxonomic and functional reorganization of assemblages, and even the extinction of specialist species (Prieto-Torres, et al. 2016, 2020, 2021a). The outcome of these range reductions could lead to significant changes in beta diversity (i.e., biodiversity turnover) and alter ecosystem functions (e.g., Clavel et al., 2011). Such scenarios could represent further challenges for the long-term conservation of Neotropical dry forests biota. Mexican dry forests are, sadly, particularly vulnerable to these critical scenarios (Prieto-Torres et al., 2016, Allen et al., 2017, Manchego et al., 2017).

Despite increasing knowledge of the ecology, biogeography, and conservation of Mexican dry forest biota over the past 20 years, many biodiversity trends and mechanisms remain poorly understood in the context of future global changes (Prieto-Torres et al., 2020, 2021a). One important drawback in most studies at local and regional scales is that they often consider only abiotic effects. This is critical because areas that are predicted to be climatically suitable but lack (or lose) essential resources (nesting sites, food sources, etc.) may in fact be unsuitable habitat for many animals such as mammals and birds (Brooks et al., 1997, Dirzo & Raven, 2003, Jordano et al., 2009, Renton et al., 2018). From this perspective, the impact and extinction risks generated by climate and land-use change may be even more drastic than the predictions of previous studies. More integrative studies that consider both abiotic and biotic data are needed to evaluate the susceptibility of these interactions and the magnitude of the threat that global changes pose for biodiversity in Neotropical dry forests (Gillespie & Walter, 2001; de la Parra-Martínez, 2011; Renton et al., 2018), particularly for endemic and/or severely threatened species (see Prieto-Torres et al., 2020, 2021b).

The Lilac-crowned Amazon, *Amazona finschi*, is a Mexican endemic bird species that mainly inhabits Neotropical dry forests from southwestern Sonora to northwestern Oaxaca. Population size has been estimated at < 10,000 [4,700–6,700 mature] individuals, confined to a habitat that is currently severely fragmented and is thus decreasing in both size and quality due to anthropogenic activities (Marín-Togo et al., 2012; Monterrubio-Rico, Ortega-Rodríguez, Marín-Togo, Salinas-Melgoza, & Renton, 2009; Renton & Iñigo-Elías, 2003). In fact, previous studies have suggested that this species has undergone rapid population decline (Marín-Togo et al., 2012). It is therefore listed as an Endangered species according to national and international checklists (SEMARNAT, 2010; BirdLife International, 2020). Literature on the

Lilac-crowned Amazon and its important biotic relationships (e.g., tree phenology, cavity resources, feeding, etc.) have determined the presence of current viable populations (e.g., Monterrubio-Rico et al., 2009; Sánchez-Barradas et al., 2017; Renton et al., 2018). However, the potential impacts of landscape conversion and global warming on the co-distribution patterns and interactions between parrots and woody trees are not yet well-evaluated.

In this paper, we intend to: (a) assess how predicted climate change and habitat loss could impact both individual species and the co-distribution patterns of Lilac-crowned Amazon and eight woody tree species with which it is strongly associated; and (b) determine the importance of the existing Protected Area network to safeguard the parrot, the plant species, and their biological interactions. Based on this information, we provide new and more accurate evidence to propose priority actions and guidance for the long-term conservation of this highly vulnerable Mexican endemic parrot species.

2. Material and methods

2.1. Species list and occurrence data

We focused our analyses on the Lilac-crowned Amazon and the following eight woody plant species: *Aralia excelsa*, *Astronium graveolens*, *Brosimum alicastrum*, *Caesalpinia eriostachys*, *Erythrina lanata*, *Jatropha sympetala*, *J. malacophylla*, and *Piranhea mexicana*. Each of these tree species has a distinct geographical distributions pattern (e.g., some are Mexican endemics, while others are found throughout the Neotropics; Table 1), but they are all considered to be key species for feeding (in both dry and rainy seasons) and nesting of Lilac-crowned Amazon populations throughout the parrot's geographical and ecological distribution (Monterrubio-Rico, Ortega-Rodríguez, Marín-Togo, Salinas-Melgoza, & Renton, 2009; Ortega-Rodríguez & Monterrubio-Rico, 2008; Renton, 2001; Renton & Iñigo-Elías, 2003; Renton & Salinas-Melgoza, 1999).

For the parrot and each tree species, occurrence records throughout the species' whole native range (i.e. both within and outside Mexico) were compiled from three sources: (a) the National herbarium of Mexico (MEXU); (b) the specialized literature (e.g., Renton & Iñigo-Elías, 2003; Navarro-Sigüenza & Gordillo-Martínez, 2018), and (c) fieldwork to identify nesting sites across the Mexican states of Michoacán (2001–2005) and Sinaloa (2014–2020). These data were complemented with information from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) and Enciclovida (<https://enciclovida.mx/>). For plants, we also used the collaborative public online databases from the Botanical Information and Ecology Network (BIEN; <https://bien.nceas.ucsb.edu/bien/tools/rbien/>); the Tree flora of the Neotropical Region (NeoTropTree; <https://www.neotropree.info>), and the Latin American Seasonally Dry Tropical Forest Floristic Network (DryFlor; <https://www.dryflor.info>). The Information from GBIF was directly downloaded using the "rgbif" library to R software (Chamberlain et al., 2019). Accession numbers for downloaded GBIF records are detailed in Table 1. All location data were transformed into decimal degrees based on the WGS84 datum.

Occurrence data was then filtered and cleaned to remove imprecise occurrence data that could negatively affect model performance (e.g., records that were duplicated across sources; data lacking collection location and/or year; Roubicek et al., 2010, Boria et al., 2014). Also, each locality was verified and georeferenced when necessary (precision no greater than ± 100 m) using Google Earth Pro and LONGITUDE (<https://www.longitudemaps.com/>). Localities whose coordinates had less than three decimal places were disregarded. We also removed occurrence points located within cities, since these occurrences may not accurately reflect the species' habitat requirements. We used data only from the years of 1970 to 2021 in order to best capture the most recent patterns, especially considering that important climate changes have been recorded over the past four decades (Fick & Hijmans, 2017, Karger

Table 1

List of species considered in this study. For each species, we included the information about taxonomy, digital object identifier (doi) of the species' GBIF entry, the number of independent occurrences used, and the minimum distance among the presence records.

Family	Species	GBIF's doi	Number of presences	Minimum distance among presences (km)
Psittacidae	<i>Amazona finschi</i>	https://doi.org/10.15468/dl.2nytyz	251	6
Anacardiaceae	<i>Astronium graveolens</i>	https://doi.org/10.15468/dl.35tsh3	1,305	15
Araliaceae	<i>Aralia excelsa</i>	https://doi.org/10.15468/dl.skgqrr	213	5
Euphorbiaceae	<i>Jatropha malacophylla</i>	https://doi.org/10.15468/dl.kjkggu	62	5
Euphorbiaceae	<i>Jatropha sympetala</i>	https://doi.org/10.15468/dl.27bz33	74	4
Fabaceae	<i>Caesalpinia eriostachys</i>	https://doi.org/10.15468/dl.cc9nb4	233	9
Fabaceae	<i>Erythrina lanata</i>	https://doi.org/10.15468/dl.wb94zn	218	6
Moraceae	<i>Brosimum alicastrum</i>	https://doi.org/10.15468/dl.6wndyc	1,168	12
Picrodendraceae	<i>Piranhea mexicana</i>	https://doi.org/10.15468/dl.evzrvs	61	3

et al., 2017). Moreover, for records from 2001 to 2021 (i.e., without the same temporality as climatic layers) we performed an outlier exclusion procedure in the environmental space by removing points whose annual mean temperature (Bio 01), annual precipitation (Bio 12), or precipitation seasonality (Bio 15) values fell beyond the upper and lower quartiles of the set of occurrence data within the time range (1970–2000) of bioclimatic variables (Robertson et al., 2016, Prieto-Torres et al., 2020). This step was important to identify problematic or imprecise occurrences with incorrect climate values (Roubicek et al., 2010, Perez-Navarro et al., 2021). Finally, to avoid biases derived from spatial autocorrelation in areas that are heavily represented in the data, we used the “spThin” R library (Aiello-Lammens et al., 2015) to estimate the most appropriate distance between each presence record and its nearest neighbor for each species (see Table 1). After these steps, we retained 3,585 unique occurrence records for all of the species.

2.2. Environmental input data: Current and future scenarios

To characterize the species' environmental niches, we selected predictor variables (with a resolution of 0.00833 grades [ca. 1 km²]) from Worldclim Project 2.1 (Fick & 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 the dimensionality and collinearity of environmental layers, we applied a Principal Component Analysis (see Hanspach et al., 2011) —as

implemented in the “ntbox” R package (Osorio-Olvera et al., 2020)— retaining only the set of five components that explained up to 95 % of the total variance. Also, considering that soil preferences have been suggested as important ecological drivers for plant distribution into dry forests (see Velazco et al., 2017, Silva de Miranda et al., 2018), we included four edaphic variables obtained from SoilGrids v0.5.5 (Hengl et al., 2017): cation exchange capacity, percentage of sand, silt and clay. These variables were used considering four different soil depths (0, 5, 15 and 30 cm), which were then averaged (Silva de Miranda et al., 2018). We decided to use only these edaphic characteristics as predictive variables, since other chemical properties could be affected by climate change (e.g., Chen et al., 2021) and there is no available information about the future projection of those properties.

For models based on future climate projections (2041–2060 [hereafter 2050] and 2061–2080 [hereafter 2070]), we used climate data from the Coupled Model Intercomparison Project 6 (CMIP6; Stoerk et al., 2018) available at the Worldclim web portal. Following Ribeiro et al. (2016), we averaged each of the projected bioclimate climate values for each grid cell among five Models of General Circulation of the Atmosphere and Ocean (CanESM5, ACCESS-ESM1-5, CNRM-CM6-1, IPSL-CM6A-LR, and MIROC6). We selected these global climate models based on the results of GCM compareR's web application (temperature and precipitation close to the average ensemble projection; Fajardo et al., 2020) and because this method has demonstrated improvements in the estimation of zonal-mean atmospheric fields, equatorial ocean subsurface fields, precipitation values and the simulation of El Niño-Southern Oscillation in the Americas (Zelinka et al., 2020, Boucher et al., 2020). All projections were performed using two Shared Socio-economic Pathways scenarios: SSP2-4.5 and SSP5-8.5. Although both SSP scenarios assume an increasing human population, the SSP5-8.5 scenario assumes higher predicted greenhouse emissions and an absence of climate change mitigation policies (Riahi et al., 2017), so the results under this scenario may be interpreted as “pessimistic”.

2.3. Ecological niche and species distribution models

For each species, we modelled the potential distribution using the ensemble modelling approach of the “modler” library in R (see Sánchez-Tapia et al., 2020), which has been very useful in evaluating the impacts of climate change on biodiversity and identifying the most vulnerable species and regions globally (Hao et al., 2019). This approach consists of four main steps: (i) data setup; (ii) model fitting and projection, (iii) partition joining, and (iv) consensus between algorithms (Araújo & New, 2007, Thuiller et al., 2009). Herein, we selected seven algorithms out of those that are available in the “modler” package: Bioclim (Beaumont et al., 2005, Booth et al., 2014), Boosted Regression Trees (Hastie et al., 2001; Elith et al., 2008), Domain (Carpenter et al., 1993), Generalized Linear Models (GLM), Mahalanobis distance (Hijmans et al., 2021), Maxent (Phillips et al., 2017), and Random Forest (Liaw & Wiener, 2002). We selected these algorithms because they had the best predictive performance in terms of Kappa, TSS, and ROC test evaluations (see below).

Because dispersal plays a crucial role in the distributions of organisms and must be considered in the development of such models (Barve et al., 2011), we created an area for model calibration (or “M”; see Soberón & Peterson, 2005) that attempts to reflect the area accessible to each species (e.g., accounting for dispersal barriers). We established “M” (a mask or GIS polygon) based on the intersection of occurrence records with the Terrestrial Ecoregions (Dinerstein et al., 2017) and the Biogeographical Provinces of the Neotropics (Morrone, 2014). These masks were later used to delimit the areas for the environmental variables that were previously selected for the species. For all plant species, models were calibrated using the data available for their entire current range, then cropped to the approximate area of the known distribution of Lilac-crowned Amazon in northwestern Mexico (Fig. 1).

Models were generated by partitioning the localities into training

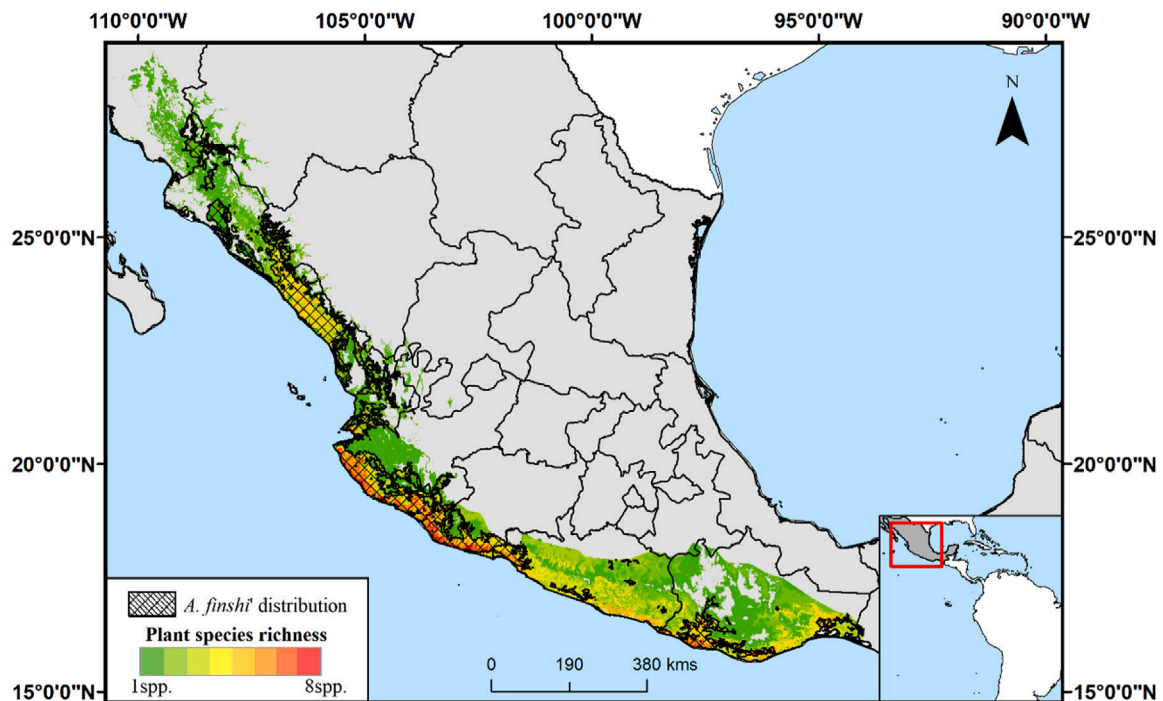


Fig. 1. Map showing the current co-distribution patterns between the Lilac-crowned Amazon (*Amazona finschi*) and eight woody-plant species associated with its habitat use.

and test sets, by the n -fold crossvalidation option, as implemented in the “partition type” function in the “modleR” library (Sánchez-Tapia et al., 2020). Also, because the occurrence dataset consisted only of confirmed presences in the study area, a set of 10,000 pseudo-absences dataset was randomly generated inside the calibration area (M). This last step was repeated 10 times for each algorithm to make sure that the evaluation procedure was independent of the random splitting procedures. Each run was performed with a different selection of the calibration and evaluation datasets, and the proportion of data for calibration was set to 70 %. Prevalence was set to 0.5 to give presences and absences the same importance in the calibration process. All other ModleR parameters were maintained at default settings (see Sánchez-Tapia et al., 2020).

Then, we used the threshold that maximizes true skill statistics (TSS) to convert probabilities of occurrences into presences and absences (Allouche et al., 2006). To generate a consensus map for each species, we added all models’ outputs and calculated the relative number of times that species occurrence was predicted by each model in each cell. Then, we used a congruence threshold equal to or higher than 0.9 (i.e., at least 90 % of maps agreed on their prediction) to obtain a final presence/absence map for each species. Then, we evaluated the performance for each consensus map by calculating the commission and omission error values (Anderson et al., 2003) and the Partial-ROC test (Lobo et al., 2008). Individual performance values for each model are detailed in Appendix S1. For each species, we then obtained the future geographic distribution (for 2050 and 2070 years) using the same methods described above for the current scenario. For each climate scenario, we calculated uncertainty maps across the final models (Campbell et al., 2015; see Appendix S2). For each species, we obtained a single consensus map for each of the scenarios forecasted (current, 2050 SSP2-4.5, 2050 SSP5-8.5, 2070 SSP2-4.5, and 2070 SSP5-8.5), resulting in a total of five maps for each species.

Finally, we used the “ntbox” R package (Osorio-Olvera et al., 2020) to perform a Mobility-Oriented Parity test (MOP; Owens et al., 2013) to identify sites with a high degree of environmental dissimilarity and offer a view of the reliability of our model transfers (i.e., determine areas where strict extrapolation occurs; Owens et al., 2013; Alkische et al., 2017). The MOP consists of measuring the similarity between the closest

30 % of the environmental conditions of the calibration area to each environmental condition in the area of transference, where areas of projection with values of similarity of zero indicate higher uncertainty (Alkische et al., 2017; Osorio-Olvera et al., 2020). Binary maps of MOP results were generated considering only areas with zero similarity as strict extrapolation areas resulting from projections to non-analogous conditions (Owens et al., 2013). Those areas were deleted from our binary results (suitable areas) for the subsequent analyses (Appendix S3). This step is important for proposing conservation areas, since it is most beneficial to protect areas where there is a high degree of certainty that the species of interest will be found (see Velazco et al., 2020).

2.4. Spatial analyses and summary metrics.

Losses and gains of suitable habitat under global climate changes were calculated by subtracting future from current potential distributions. This comparison allowed us to identify areas of climatic stability, i.e., that were suitable under both current and future models. If loss of suitable areas was predicted in future-projected models, we calculated the differences in the bioclimate variables values (Atauchi et al., 2020) and elevation (using a digital elevation model at $\sim 1 \text{ km}^2$ cell size resolution; USGS, 2001) between the distribution area determined by the current model and the area projected under each of the future models. We did this using the three climatic variables (annual temperature [Bio 01], annual precipitation [bio 12], and precipitation seasonality [Bio 15]) that have been defined as the most significant for Neotropical dry forests in previous studies (Werneck et al., 2011; Prieto-Torres & Rojas-Soto, 2016). The increase or decrease in the size of the suitability areas was calculated (in km^2) for all species under two different dispersion scenarios: “contiguous dispersal” (all cells within “M” having suitable conditions in the future could be considered as species range) vs “non-dispersal” (only those cells that are currently occupied could be occupied in the future). Because the non-dispersal scenario allows only decreases in distributional range in response to climate change, it must be considered the most “unfavorable” for the species (Peterson et al., 2002; Prieto-Torres et al., 2021a, 2021b).

To evaluate the impacts of habitat loss (such as areas modified by

humans) in the species models under both current and future scenarios, we used the global land-use and land-cover change simulation scenarios proposed by Chen et al. (2022). These global maps (with a resolution of 1-km from 2015 to 2100) predict which areas will be modified in the future based on the projected demand of the latest IPCC coupling socioeconomic and climate change scenarios, SSP-RCP (for a detailed explanation see Chen et al., 2022). We selected the maps (2020's [current], 2050's and 2070's) containing 20 land types, which were later reclassified into two categories (intact vegetation vs human-modified areas) by discriminating pixels that correspond to deforested areas and extremely disturbed landscapes (e.g., urban areas, barren, cropland and farming areas, etc.). Then, we calculated the percentages of the species' distribution (current, 2050's and 2070's) covered by human modified landscapes.

The assessment of the modification of co-distribution patterns over time was based on two approaches: (a) comparing the geographic patterns between the Lilac-crowned Amazon and each of the woody plant species; and (b) comparing the geographical range of the Lilac-crowned Amazon with the potential species richness of plants (obtained by adding all binary maps of species) in intact natural forest areas. From this perspective, we were able to identify potential breaks among species under future climate scenarios, which could signify possible disruptions of important ecological associations between taxa. All of these analyses were performed using each of the two-dispersal assumptions for the 2050' and 2070's.

2.5. Protected areas network and long-term conservation areas

We evaluated the importance of the existing Mexican protected area network for the species by calculating the proportion of their distributional areas that fall within current Mexican protected areas. To do this, we overlapped the raster of current protected areas with each species' distribution and the sites of high plant richness (i.e., sites whose species richness exceeded half the maximum value observed) for each climate scenario (current and future). Protected areas boundaries were obtained from a shapefile downloaded from the Mexican Comisión Nacional de Áreas Naturales Protegidas (CONANP; available at: https://sig.conanp.gob.mx/website/pagsig/info_shape.htm), selecting both official protected areas and voluntary conservation areas. Then, we determined key regions for *A. finschi*'s long-term conservation based on the consensus of high plant richness maps and the current suitable climate-areas for the Lilac-crowned Amazon. The consensus areas that were outside existing protected areas and where landscapes were not human-modified were considered "priority conservation sites" because they represent areas that are predicted to be suitable in terms of future climate and where essential resources have not yet been lost to human modification and could persist into the future if land use change is prevented (e.g., Prieto-Torres et al., 2021b).

Table 2

Current and projected future distribution of Lilac-crowned Amazon (*Amazona finschi*) and eight woody-plant species associated with its habitat use. Results are shown based on current and two future climate scenarios (SSP2 4.5 and SSP5 8.5) for the years 2050 and 2070 considering the consensus map from the five global climate models used (CanESM5, ACCESS-ESM1-5, CNRM-CM6-1, IPSL-CM6A-LR, and MIROC6). In percent change in area, positive numbers indicate area gain and negative numbers indicate area loss, relative to the current potential distribution area. GCC = Global Climate Change, PAs = Protected Areas.

	Potential distribution area (km ²)	Percent change in area due to GCC	Percent change in area due to GCC + habitat loss	Percent distribution area within PAs	Elevation (Mean ± SD m. a. s.l.)
CURRENT					
<i>A. finschi</i>	81,958	-	-	12.34 %	424.65 ± 355.22
Woody-plants	81,815 ± 61,984	-	-	6.5 ± 2.8 %	511.51 ± 288.19
SSP2 4.5					
2050'S DISPERSAL					
<i>A. finschi</i>	58,153	-29.05 / 13.61	-46.65 %	10.08 %	623.01 ± 418.78
Woody-plants	89,834 ± 68,850	7.43 / 30.37	-21.55 %	6.67 ± 2.9 %	692.14 ± 300.10
2050'S NON-DISPERSAL					
<i>A. finschi</i>	46,996	-42.66 / -	-58.07 %	10.75 %	509.56 ± 358.05
Woody-plants	69,161 ± 63,674	-23.26 / -	-46.45 %	6.89 ± 3.34 %	568.15 ± 322.53
2070'S DISPERSAL					
<i>A. finschi</i>	51,906	-36.67 / 20.47	-50.95 %	9.32 %	775.93 ± 449.90
Woody-plants	88,567 ± 65,563	5.13 / 37.77	-21.65 %	6.69 ± 3.17 %	771.67 ± 277.61
2070'S NON-DISPERSAL					
<i>A. finschi</i>	35,126	-57.14 / -	-68.31 %	12.23 %	572.04 ± 361.35
Woody-plants	62,590 ± 63,094	-34.68 / -	-54.08 %	6.98 ± 3.69 %	597.44 ± 339.51
SSP5 8.5					
2050'S DISPERSAL					
<i>A. finschi</i>	56,296	-31.31 / 14.23	-48.09 %	9.72 %	633.82 ± 422.38
Woody-plants	91,118 ± 68,356	9.82 / 31.31	-19.51 %	6.61 ± 2.78 %	702.32 ± 292.08
2050'S NON-DISPERSAL					
<i>A. finschi</i>	44,636	-45.54 / -	-60.30 %	10.42 %	508.75 ± 356.68
Woody-plants	68,378 ± 63,693	-24.58 / -	-47.27 %	6.86 ± 3.35 %	571.14 ± 324.41
2070'S DISPERSAL					
<i>A. finschi</i>	48,335	-41.03 / 24.66	-52.22 %	7.70 %	886.56 ± 437.91
Woody-plants	85,044 ± 66,314	-2.09 / 43.88	-25.21 %	6.29 ± 3.61 %	817.71 ± 239.73
2070'S NON-DISPERSAL					
<i>A. finschi</i>	28,122	-65.69 / -	-73.44 %	10.33 %	636.42 ± 347.43
Woody-plants	56,749 ± 62,872	-44.68 / -	-60.52 %	6.63 ± 3.88 %	625.41 ± 354.92

3. Results

3.1. Species models and current parrot-woody plant co-distribution patterns

The current predicted distribution area for the Lilac-crowned Amazon was ca. 82,000 km², showing a mean elevational range of 424.65 ± 355.22 m a.s.l., located mainly along the Pacific coast from southern Sinaloa to southeastern Oaxaca (Fig. 1). The model showed an important degree of overlap (24.1 %) with highly human-modified areas, while established Mexican protected areas cover only 12.3 % of its current distribution area (Table 2). For plant species, the distribution areas ranged from 20,016 km² (*P. mexicana*) to 198,337 km² (*A. graveolens*), with an average elevation of 511.5 ± 288.2 m a.s.l (see Appendix S4). The plant species' predicted distribution overlapped highly human-modified areas by 31.9 ± 9.5 % (mean ± standard deviation). Furthermore, 38.0 % of high plant richness areas under the current distribution overlapped with highly human-modified areas. The degree of overlap between plant species and current protected areas averaged 6.5 ± 2.8 % among individual species range and 6.1 % for high plant richness sites (Table 2).

Finally, the average overlap between each plant species' distributional range and the Lilac-crowned Amazon's distribution was 37.0 % (Table 3). The area of co-occurrence between Lilac-crowned Amazon

Table 3
Summary of area of overlapping distribution between the Lilac-crowned Amazon (*Amazona finschi*) and each of the associated woody plants under global change climate and land-use change scenarios. Overlap values are shown in extent (km²) and proportion (%) with respect to *A. finschi*'s total distribution under each dispersal scenario.

Species	Climate scenarios				
	Current	2050/ SSP245	2070/ SSP245	2050/ SSP585	2070/ SSP585
DISPERSAL					
<i>Aralia excelsa</i>	12,678 (15.5 %)	12,456 (21.5 %)	13,417 (25.8 %)	13,714 (24.4 %)	7,589 (15.7 %)
<i>Astronium graveolens</i>	44,604 (54.4 %)	40,544 (69.7 %)	42,177 (81.3 %)	40,963 (72.8 %)	41,438 (85.7 %)
<i>Brosimum alicastrum</i>	25,326 (30.9 %)	21,063 (36.2 %)	21,780 (42.0 %)	20,662 (36.7 %)	21,018 (43.5 %)
<i>Caesalpinia eriostachys</i>	31,193 (38.1 %)	24,304 (41.8 %)	22,643 (43.6 %)	24,320 (43.2 %)	22,390 (46.3 %)
<i>Erythrina lanata</i>	62,478 (76.2 %)	50,405 (86.7 %)	45,600 (87.9 %)	48,625 (86.4 %)	42,543 (88.0 %)
<i>Jatropha malacophylla</i>	34,025 (41.5 %)	31,629 (54.4 %)	27,848 (53.7 %)	30,466 (54.1 %)	25,570 (52.9 %)
<i>Jatropha sympetala</i>	12,363 (15.1 %)	10,349 (17.8 %)	7,943 (15.3 %)	10,376 (18.4 %)	6,511 (13.5 %)
<i>Piranhea mexicana</i>	19,644 (24.0 %)	17,913 (30.8 %)	15,381 (29.6 %)	17,959 (31.9 %)	13,496 (27.9 %)
Mean values	37.0 %	44.9 %	47.4 %	46.0 %	46.7 %
NON-DISPERSAL					
<i>Aralia excelsa</i>	–	6,422 (13.7 %)	4,594 (13.1 %)	6,456 (14.5 %)	3,049 (10.8 %)
<i>Astronium graveolens</i>	–	31,412 (66.8 %)	27,144 (77.3 %)	31,109 (69.7 %)	23,074 (82.0 %)
<i>Brosimum alicastrum</i>	–	12,014 (25.6 %)	7,941 (22.6 %)	10,858 (24.3 %)	5,832 (20.7 %)
<i>Caesalpinia eriostachys</i>	–	16,640 (35.4 %)	10,669 (30.4 %)	15,899 (35.6 %)	6,659 (23.7 %)
<i>Erythrina lanata</i>	–	39,988 (85.1 %)	29,457 (83.9 %)	37,462 (83.9 %)	23,165 (82.4 %)
<i>Jatropha malacophylla</i>	–	18,488 (39.3 %)	11,644 (33.1 %)	17,262 (38.7 %)	7,305 (26.0 %)
<i>Jatropha sympetala</i>	–	5,486 (11.7 %)	2,966 (8.4 %)	5,066 (11.3 %)	1,637 (5.8 %)
<i>Piranhea mexicana</i>	–	12,108 (25.8 %)	8,076 (23.0 %)	11,566 (25.9 %)	5,101 (18.1 %)
Mean values	–	37.9 %	36.5 %	38.0 %	33.7 %

and each plant species had on average 33.1 % of surface overlapped with highly human-modified areas. The average richness (among the eight plant species considered) within Lilac-crowned Amazon's distribution was of 3.9 ± 1.9 spp. The regions with the highest plant species richness within the Lilac-crowned Amazon's distribution were in the states of Colima, Jalisco, Michoacán, and Oaxaca (Fig. 1).

3.2. Impacts of future climate change and habitat loss

The future scenarios were qualitatively similar in their predicted patterns, though (as expected) the pessimistic scenarios (SSP5.85 and non-dispersal models), predicted more severe decreases in species' potential areas (Fig. 2; Table 2; Appendix S4). According to the resulting model predictions: (i) the distribution ranges of most of the species tended to decrease under future climates (2050 and 2070), regardless of SSP/dispersal scenario, due mainly to increased mean annual temperature (by more than 1.9 °C) and precipitation seasonality (by ~ 0.6); (ii) under the future scenarios, the area (i.e. km²) of overlap between plants species' and Lilac-crowned Amazon ranges will decrease significantly (on average -17.8 % [dispersal scenarios] and -56.3 % [non-dispersal]) compared to the present (Table 3); (iii) there was an average 10.10 % increase in the number of high plant richness sites (red grids in Figs. 1 and 2) if we assume that species can disperse to novel habitat areas, but a reduction of 18.36 % if we assume that they cannot; and (iv) both individual species and sites with high species richness will occupy higher elevation zones (regardless of dispersal scenario) than the current distribution (Appendix S4). The MOP analysis (Appendix S3) indicated that strict extrapolative areas occur mostly beyond the potential distributional areas predicted by models in the future climates across Mexico (on average < 2 % of predicted suitable areas were with strict extrapolation areas).

When considering the combined effects of future climate and land-use changes, species distributions decreased by an average of 19.51–47.27 % by 2050 and 21.65–60.52 % by 2070 (Table 2). In both dispersal scenarios, the Lilac-crowned Amazon showed important reductions (greater than 45 %) of potential distribution in non-human-modified areas in the future. Also, most plant species' future ranges overlapped with currently highly human-modified areas, which are most likely unsuitable for the species. This fact is particularly important for two species (*J. sympetala* and *P. mexicana*), for which more than 50 % of their future distribution fell within these human-modified areas. Furthermore, an average of ~ 26 % [dispersal scenario] – 34 % [non-dispersal scenario] of remnant sites of high plant richness in the future will overlap with highly human-modified areas. In fact, the 19.0 % [dispersal scenario] – 23.9 % [non-dispersal scenario] of estimated overlapping areas between the Lilac-crowned Amazon and woody plants in the corresponded with highly human-modified areas.

3.3. Protected area network and long-term conservation areas

Our models predicted a reduction (on average 1.50 ± 28.04 % [dispersal scenario] – 32.90 ± 23.88 % [non-dispersal scenario]) in suitable areas for both the parrot and plant species within the limits of several protected areas in the future (Table 2; Appendix S4). Existing Mexican protected areas had an average of only 4.57 % overlap with the sites of high plant richness identified for the future. The consensus of the suitable climate areas for high plant richness maps and the current suitable area for the Lilac-crowned Amazon showed low (i.e., 12,284 km²) overlap values. Approximately 39.1 % (i.e., 4,798 km²) of the surface of these long-term climate-resilient areas overlapped within current highly human-modified areas, while only 5.46 % (i.e., 671 km²) were found within existing protected areas. These priority conservation areas and highly climate resilient sites (i.e., ~6,800 km²) are mostly located in Michoacán (41.73 %), Jalisco (29.08 %), Oaxaca (16.5 %), and Colima (8.88 %). The environmental conditions will continue to be adequate for the tree species within the Chamela-Cuixmala protected

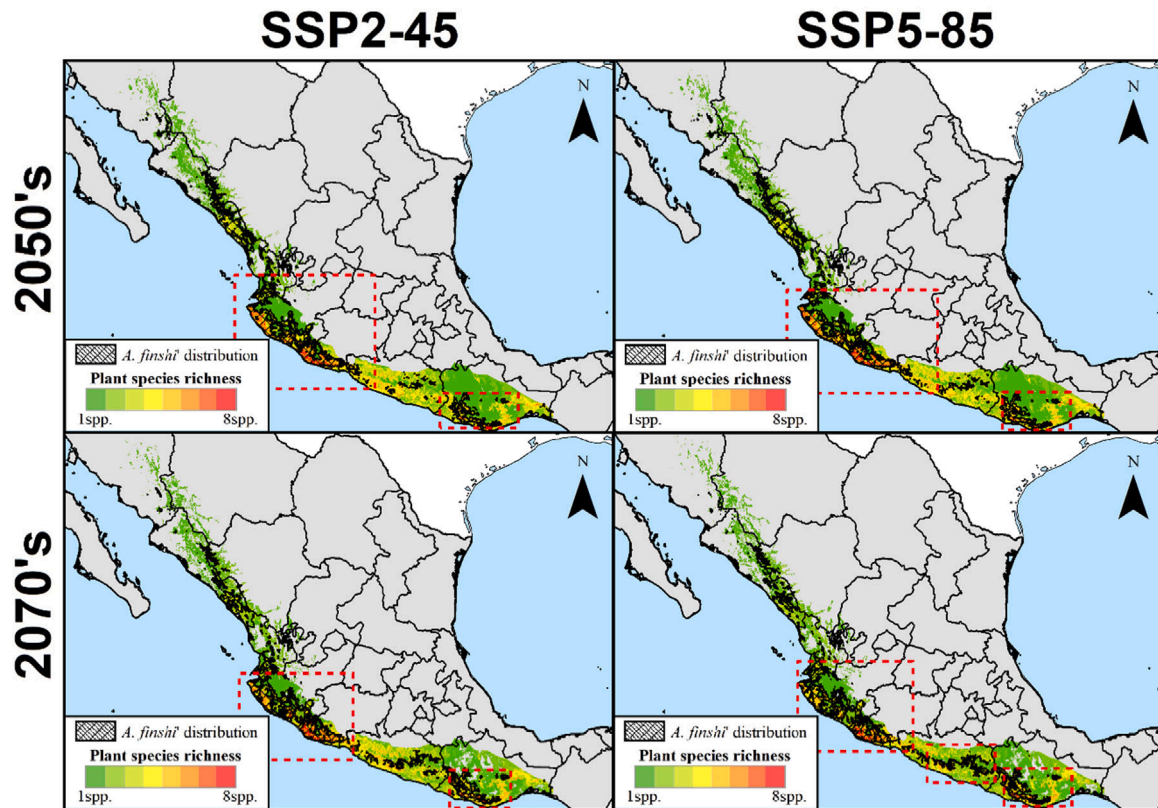


Fig. 2. Species co-distribution patterns for the Lilac-crowned Amazon (*Amazona finschi*) and the eight woody-plant species associated with its habitat use projected under two Shared Socio-economic Pathways scenarios (SSP2-4.5 and SSP5-8.5) for the years 2050 and 2070 and considering the contiguous dispersal ability of species. Dotted red lines in maps show areas where high plant richness sites overlap with *A. finschi*'s distribution. [Supplementary Figure S1](#) shows the maps of species richness patterns projected to future climate conditions assuming non-dispersal ability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area (Fig. 3).

4. Discussion

Our results indicated that Lilac-crowned Amazon and its associated plants are likely to undergo non-uniform spatio-temporal changes across Mexico in the future. The displacement and decreased size and continuity of the distribution areas of most of the species we examined suggest a bleak scenario, which could increase their vulnerability to extinction. Furthermore, these results predicted potential changes in the availability of mutualist partners that, as suggested by [Correa-Lima et al. \(2019\)](#), could lead to a decoupling of the interactions and have detrimental effects for ecosystem function (see [Renton et al., 2018](#)). In this respect, current and future conservation policy and decision-making must focus not only on providing new sites where the species are protected individually, but also where they co-occur, in order to protect important species interactions.

Although distribution models indicate that the central Pacific region (mainly across coastal areas from Jalisco to Oaxaca states) constitutes the regions with the most suitable conditions for the Lilac-crowned Amazon, the current distribution of this species across the southern part of that region (Guerrero and Oaxaca) is limited by other important biotic (competition) and anthropogenic factors ([Ríos-Muñoz & Navarro-Sigüenza, 2009](#)). This species has been practically extirpated from areas where human activities including cattle ranching and the expansion of urban settlements have removed the natural vegetation and reduced available habitat and resources for this species ([Renton & Iñigo-Elías, 2003](#); [Ríos Muñoz & Navarro-Sigüenza, 2009](#)). This reduction of available habitat is compounded by the presence of *A. autumnalis*, a competing species with the same food guild, nesting, and reproductive

requirements ([Gómez de Silva, Oliveras de Ita, & Medellín, 2005](#); [Navarro-Sigüenza et al., 2014](#)).

From this perspective, areas predicted to be climatically suitable in the future but where essential *A. finschi*'s resources (e.g., nesting sites) are lost to land use change are likely to be unsuitable for this specialized parrot ([Ortega-Rodríguez & Monterrubio-Rico, 2008](#)). Although many parrot species are being increasingly forced to live and breed in fragmented or modified landscapes, several studies highlight the importance of large and old trees with suitable nest cavities as a key habitat requirement for their reproduction and, therefore, survival ([de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015](#); [De Labra-Hernández & Renton, 2016](#); [Flores-López et al., 2020](#)). Further research to assess the susceptibility of species and interspecific interactions to environmental changes must be considered a top priority. Monitoring programs will be essential, especially for the species and areas predicted to suffer the most. Modeling may help to anticipate where these areas are in order to implement programs before the situation becomes critical.

Models have indicated that precipitation seasonality (Bio 15) is a limiting factor for the distribution and breeding of the Lilac-crowned Amazon ([Monterrubio-Rico et al., 2015](#)). The amount of precipitation can affect the reproductive success of this parrot due to its influence on plant phenology and food availability ([Renton, 2001, 2009](#); [Renton & Salinas-Melgoza, 2004](#); [de la Parra-Martínez, 2011](#); [Renton et al., 2015, 2018](#)). This is a critical point, since recent studies have demonstrated a spatially heterogeneous decrease in annual precipitation across Mexico over the past one hundred years ([Cuervo-Robayo et al., 2020](#)). Adding this to future climate models, the species will most likely be pushed to higher elevations where humidity will be a key limiting factor for the biota ([Buermann et al., 2011](#)). Lilac-crowned Amazon nests have been

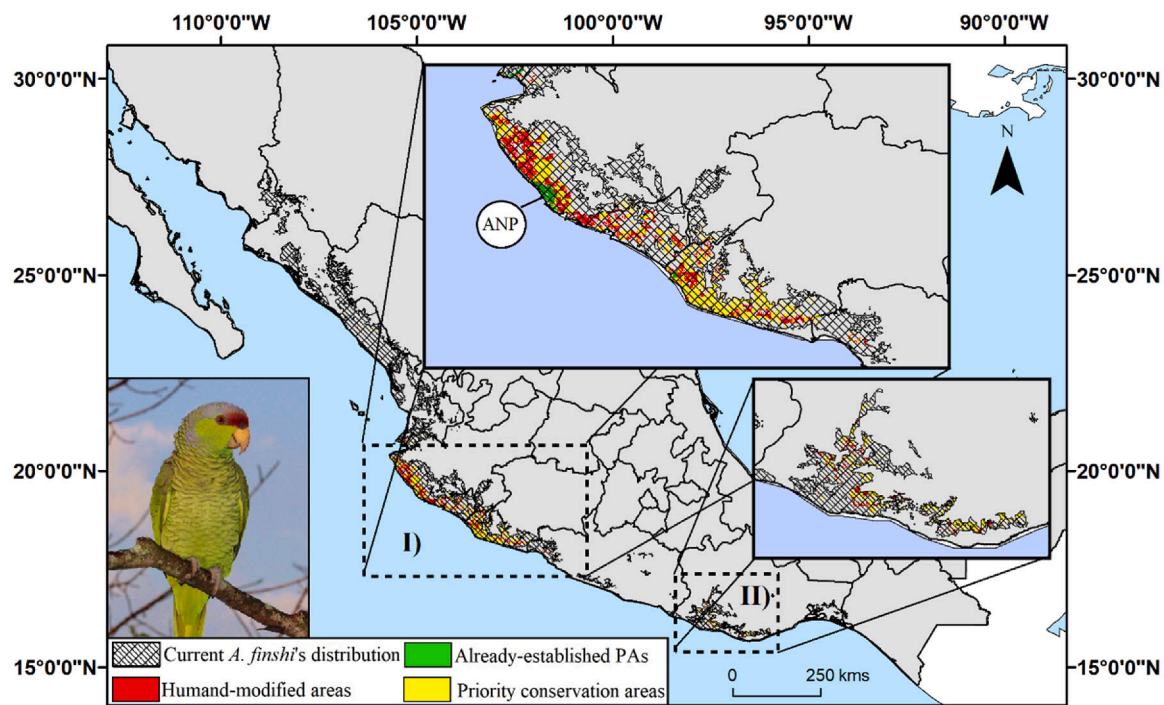


Fig. 3. Priority conservation areas identified for the long-term protection of the Lilac-crowned Amazon (*Amazona finschi*) and the eight-woody plant species associated with its habitat use. The long-term climate-resilient areas identified herein are represented by both colors: yellow (intact vegetation) and red (highly human-modified areas in future scenarios). The circle in the map indicates the location of the Chamela-Cuixmala Protected Area in the northwestern Mexico. The photograph of *A. finschi* is from the website iNaturalist (CC BY-NC 4.0; Available in: <https://www.naturalista.mx/observations/35520971>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observed above 600 m a.s.l. (Ortega-Rodríguez & Monterrubio-Rico, 2008), above the mean elevational range previously known for the species. Unfortunately, if low-elevation species like Lilac-crowned Amazon and their associated plants are unable to quickly adapt to new environments at higher elevations, their population size will decrease, further threatening their survival. To date the adaptability of these species is unclear, and much more research is needed on this topic (Ortega et al., 2019).

Finally, it is important to note that because the Lilac-crowned Amazon is a canopy seed predator, decreases in its population size could also affect Neotropical dry forest dynamics such as tree diversity (Renton, 2001, Dirzo & Raven, 2003). Thus, the potential extinction of Lilac-crowned Amazon could have a cascading effect, harming interspecific relationships (Renton et al., 2018) and consequently, the ecological integrity and regeneration of Neotropical dry forests at the northernmost limit of its range (Manson et al., 2009). Although our results are alarming, they should be taken with caution given the risk of predicting the adaptive potential of species to future conditions, since adaptive potential is in fact influenced by many additional factors that we do not evaluate here, such as reproductive rate, physiological capacity, and habitat requirements (Peterson et al., 2002, Ortega-Rodríguez & Monterrubio-Rico, 2008, Ortega et al., 2019). For instance, parrots tend to show high dietary plasticity in response to anthropogenic pressures (Renton, 2001, Renton et al., 2015) by obtaining their food resources from a wide variety of plants. Also, although they are apparently less flexible in their nesting requirements, this species has been seen to exploit different tree species for nesting across their range (Renton & Salinas-Melgoza, 2004, Monterrubio-Rico et al., 2009).

4.1. Conservation implications

Despite the increasing conservation efforts for Psittacines in Mexico, here we document important knowledge gaps that potentially affect the long-term protection of Lilac-crowned Amazon. Important efforts for

conservation of other parrot species have been aimed at reducing habitat destruction, making artificial nests, surveilling nests, relocating individuals and captive breeding (Enkerlin, 2000), as well as establishing refuges or conservation areas (Íñigo-Elías, 2000). However, these immediate actions to preserve land or individuals, although important, will not be sufficient to ensure the long-term conservation of Lilac-crowned Amazon. Future management actions must also focus on maintaining suitable habitats in suitable but unprotected areas and mitigating the impacts of global climate change and land use change. As our results indicate, the proportion of the species' range contained within protected areas will substantially decrease in the future, and most of the priority areas that are highly resilient to climate and land use changes are, in fact, located outside the current protected areas. This reinforces the idea that current protected areas are ineffective and insufficient for safeguarding biodiversity into the future. This is unsurprising considering that the Neotropical dry forests accounts for only a small proportion of protected areas (<10 %) and its biota is woefully underrepresented within them (Banda et al., 2016, Prieto-Torres et al., 2018). Future efforts to maximize the performance of the protected network and species protection must be reviewed.

From this perspective, the priority conservation areas we identify in this study provide insights into where to focus future efforts for protection of the Lilac-crowned Amazon. Areas in the states of Colima, Jalisco, Michoacán, and Oaxaca are identified by our models as “safe places” for conservation of the Lilac-crowned Amazon—in other words, sites with adequate resources for the species where human-induced changes are not expected in the near future. Thus, it can be inferred that the conservation of these areas is of vital importance. Resources and efforts should be directed toward the long-term maintenance and preservation of these invaluable spaces. One option for achieving that protection is the establishment of natural biological corridors and ecotourism programs that involve local populations and therefore contribute to reduced extraction of both plant and parrot species. Similar approaches could be applied to study the conservation status of

other parrot species in Mexico, especially considering that at a national scale, more than 86 % of these taxa have shown alarming reductions relative to their original ranges (>80–86 %) (Ríos-Muñoz & Navarro-Sigüenza, 2009). We hope that these findings will trigger the interest of conservationists and policymakers and motivate them to delve more deeply into the conservation of this and other Mexican endemic parrots.

5. Conclusions

Our study represents an important step toward understanding about combined effects of global climate and land use changes on the distribution, habitat quality, and main interspecific interactions of the endangered Mexican endemic Lilac-crowned Amazon. In the near future, the combined impacts of drastic climate and land-use changes are expected to strongly diminish conservation opportunities for this species. We argue that analyzing individual drivers of global changes is unrealistic and could promote poor long-term biodiversity conservation policies, especially for endemic and endangered species like the Lilac-crowned Amazon. Furthermore, species' responses to these changes are not expected to be uniform. These results indicate that to efficiently plan for these species, increasing the total land area protected is not a sufficient solution; better comprehension of species' extinction risk and breakdown of its ecological associations are critical steps for facilitating and empowering future management strategies and conservation plans. Here, we identified important opportunities to improve the level of long-term protection by placing protected areas strategically in "safe places" where a lack of current intensive human land use could increase the political will for its protection.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2022.126323>.

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