Received: 2 April 2020 | Revised: 4 July 2020 | Accepted: 2 August 2020

DOI: 10.1111/ddi.13153

BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Insights for protection of high species richness areas for the conservation of Mesoamerican endemic birds

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Funding information
The Rufford Foundation, Grant/Award Number: 16017-1 and 20284-2; Idea Wild, CONACyT, Grant/Award Number: 152060; CONABIO, Grant/Award Number: JM071

Editor: Alice Hughes

Abstract

Aim: To assess the representativeness values of Mesoamerican endemic birds within the current network of protected areas (PAs) to determine high-priority and complementary conservation areas to maximize the long-term protection of species.

Location: From central Mexico to southern Panama.

Methods: We selected 180 bird species that are geographically restricted to Mesoamerica and estimated their potential ranges using species distribution models. Then, using two different removal rules in ZONATION software, we assessed the species' representativeness levels within the current PA network. We also defined forest remnants that could be used to strategically expand PAs (to reach Aichi biodiversity targets) and maximize the species protection, explicitly considering anthropic pressures.

Results: Current PAs cover ~13% of the land area of Mesoamerica, representing an average of ~19% of the total potential distribution for the endemic bird species considered. We also observed that there is <30% overlap between current PAs and the priority areas we define. Our prioritization analyses showed that strategically increasing protection coverage to 17%, as stipulated in the Aichi targets, would substantially increase the representativeness values of PAs (regardless of the removal rule used) and would increase the range by >35% for all species and >29% for threatened species. The consensus priority conservation areas identified were mainly distributed in Costa Rica (~48%), Mexico (~28%), and Panama (~10%).

Main conclusions: Consistent with the global picture, Mesoamerican PAs showed low representativeness of their vulnerable endemic avifauna; therefore, well-informed decisions to guide conservation strategies are imperative. We provide insights about where future conservation efforts should focus to accomplish a representative and well-connected regional PA network.

KEYWORDS

conservation policy, high-priority areas, protected areas, species distribution models, systematic conservation planning

1 | INTRODUCTION

Biodiversity conservation is critical, in part because the interaction of biotic communities with the physical habitat results in several ecosystem services that support human well-being (Cardinale et al., 2012). Paradoxically, species extinction rates due to human activities are currently 1,000 times higher than extinctions due to natural causes, and during this century, they are predicted to increase tenfold because of the accumulation of human impacts on natural ecosystems (De Vos, Joppa, Gittleman, Stephens, & Pimm, 2015). Developing methodologies that quickly provide accurate information for decision makers about what geographical areas must be prioritized is an urgent step towards reducing this extensive biodiversity loss and ensuring the provision of ecosystem services. This is particularly important in heavily threatened ecosystems that host high levels of species richness and endemism as well as agriculture and human settlement (e.g., Nori et al., 2016; Peters et al., 2019; Prieto-Torres, Nori, & Rojas-Soto, 2018; Strassburg et al., 2017).

Currently, twenty-five terrestrial biodiversity “hotspots” have been identified worldwide based on exceptional concentrations of species/habitat diversity. These sites encompass ~44% of the Earth's plant species and 35% of its vertebrates in just 1.4% of the land surface (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Thus, they are the focus of many conservation programmes aiming to reduce the current rate of biodiversity loss (Cincotta, Wisnewski, & Engelman, 2000). For instance, ~38% of these hotspots are currently legally protected as parks and reserves that range from highly restrictive areas where all human activities are excluded to more inclusive management strategies involving local communities (see Schwartzman, Moreira, & Nepstad, 2000). Among these hotspots, Mesoamerica is considered among the most important high species richness sites for conservation across the Americas (Myers et al., 2000).

This biologically complex region extends from central Mexico to southern Panama and northern Colombia. It is mainly composed of highly fragmented tropical forest patches that vary in size and extent. Mesoamerica has wide topographic and climatic variability and a complex biogeographical history, all of which have promoted important biotic interchange events and extensive diversification in situ due to climatic changes and geological processes (Llorente, 1996; Prieto-Torres, Rojas-Soto, Santiago-Alarcón, Bonaccorso, & Navarro-Sigüenza, 2019; Ramamoorthy, Bye, Lot, & Fa, 1998; Ríos-Muñoz & Navarro-Sigüenza, 2012; Stehli & Webb, 1985). However, much this biodiversity remains unprotected. About ~72% of the Mesoamerican tropical forest ecosystems have already been converted to urban or agricultural uses (Bryant, Nielsen, & Tangley, 1997; Miller, Chang, & Johnson, 2001; Portillo-Quintero & Sánchez-Azofeifa, 2010; Weinzettel, Vačkář, & Medková, 2018). For most of the countries in this region, current protected areas (PAs) cover only a small proportion of the total surface area (less than 15%), which is far from the goal of 17% proposed in the Aichi targets (UNEP, 2010). Thus, generating a PA network that adequately represents the biodiversity in the long-term protection of these areas is an urgent task (Rodrigues et al., 2004; Venter et al., 2016).

From this perspective, different conservation planning schemes have been developed over the last decade (Ball, Possingham, & Watts, 2009; Ciarleglio, Wesley Barnes, & Sarkar, 2009; Moilanen et al., 2014; Sarkar & Illoldi-Rangel, 2010) promoting well-informed decisions to expand the PA network and contribute to the viability of long-term protection of biodiversity and ecosystem function (Watson, Grantham, Wilson, & Possingham, 2011). Generally, these approaches are based on the distribution of key biodiversity features (typically species distribution) and anthropic variables to identify the most important sites for conservation that are also compatible with sustained human development (Brum et al., 2017; Kukkala et al., 2016). However, in practice, it is difficult to compile this information comprehensively, assuring both spatial and taxonomic representation (Carvalho, Brito, Pressey, Crespo, & Possingham, 2010). Unfortunately, information on the distribution for most species is incomplete, and when it exists, data are generally biased by site accessibility (Gaston & Rodrigues, 2003; Peterson, 2001). Thus, considering the immense efforts required to define maps of species' distributional ranges, the use of computational algorithms to generate species distribution models (SDMs) is an effective and widely accepted method to obtain accurate species distribution maps (Araújo et al., 2019; Peterson, 2001; Soberón & Peterson, 2005). This approach has been applied on a global scale in biogeography, macroecology and particularly in conservation planning (Araújo et al., 2019; Costa, Nogueira, Machado, & Colli, 2010; Hidasi-Neto et al., 2019; Nori, Villalobos, & Loyola, 2018; Prieto-Torres & Pinilla-Buitrago, 2017). In fact, combining SDMs and site-selection algorithms could provide more accurate data for reserve design in regions where protection of high-diversity areas at the lowest cost is urgent (e.g., Elith & Leathwick, 2009; Lessmann, Fajardo, Muñoz, & Bonaccorso, 2016; Pawar et al., 2007; Prieto-Torres et al., 2018).

Given that spatial and taxonomic representation of biodiversity is often poor at the regional level, species-level surrogates are often necessary in a conservation context to ensure that critical habitats and ecosystems within the region are not missed (Lessmann et al., 2016; Peralvo, Sierra, Young, & Ulloa, 2006). Birds, as a charismatic and well-known group of vertebrates, are good surrogates and defining areas that are important for bird conservation is an excellent first step to delineating areas that are important for conservation efforts more generally (Barnagaud et al., 2017; Kati et al., 2004). Besides, birds are important indicators of landscape conditions due to their strong vulnerability to environmental alterations (Chambers, 2008; Fahrig, 2003; Foley et al., 2005; Imbeau, Monkkonen, & Desrochers, 2001; Lawton et al., 1998; O'Connell, Jackson, & Brooks, 2000; Sekercioglu, 2006). In this sense, protecting birds is expected to provide benefits to other taxa (Gregory et al., 2005; Larsen, Bladt, Balmford, & Rahbek, 2012; Roberge & Angelstam, 2004). Therefore, birds have long attracted the attention of scientists, decision makers and non-governmental organizations

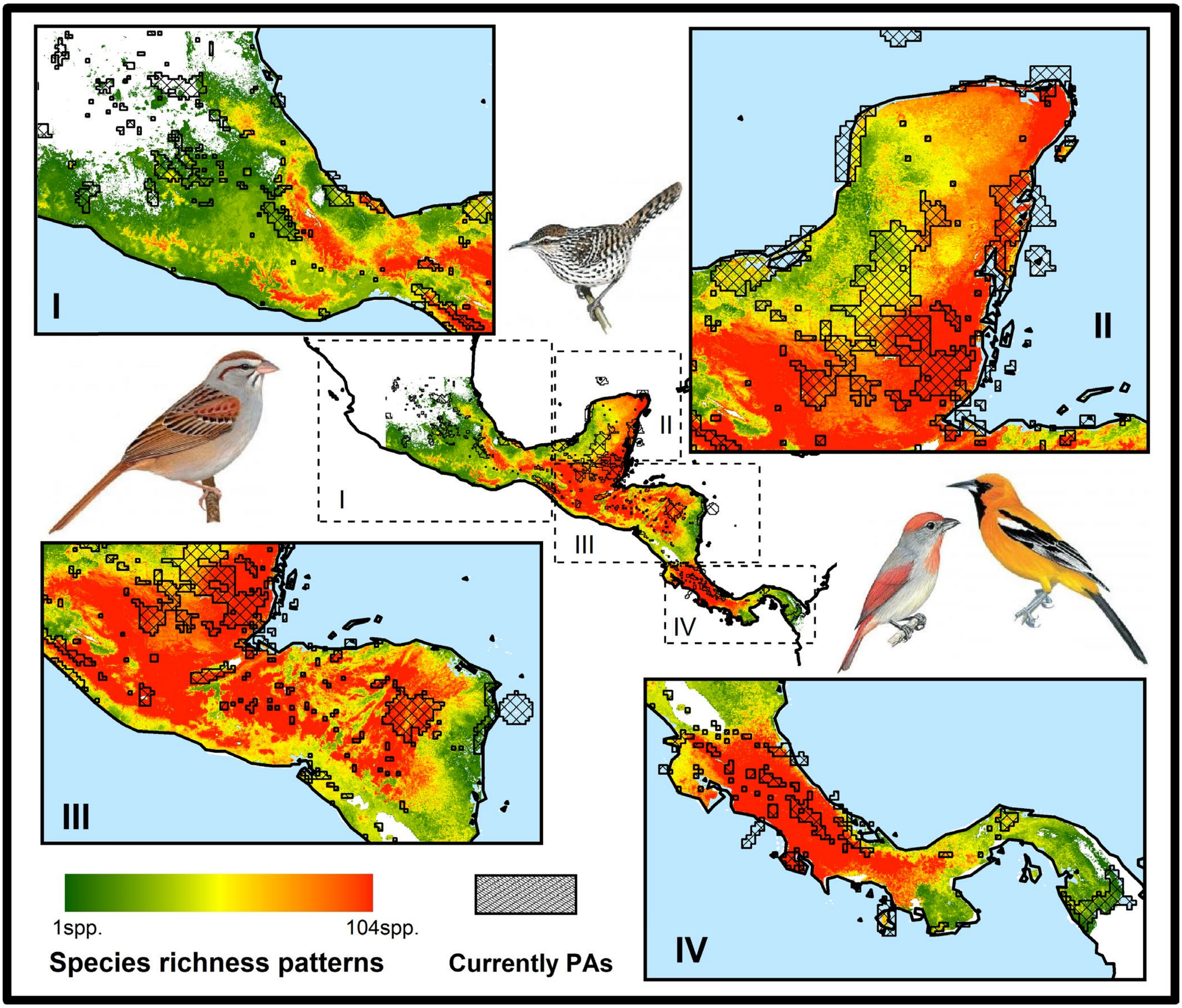

FIGURE 1 Species richness distribution patterns of Mesoamerican endemic bird species ($n = 182$), showing the location of current protected areas according to the World Database of Protected Areas (UNEP & WCMC, 2019). A total of ~199,300 km^2 (i.e., 12.9%) of Mesoamerican terrestrial surface was covered by designed PAs (see Table 1). Birds (from left to right) in maps are *Peucaea sumichrasti* (NT); *Campylorhynchus yucatanicus* (NT); *Piranga roseogularis* (LC); and *Icterus auratus* (DD). The bird pictures were taken from Birds of the World's website (The Cornell Lab of Ornithology; Available in: https://birdsoftheworld.org/bow/home)

to highlight and promote conservation policies and needs (e.g., Kujala, Burgman, & Moilanen, 2013; Prieto-Torres et al., 2018; Triviño, Kujala, Araújo, & Cabeza, 2018).

In this study, we focus on endemic bird species as indicators of overall diversity patterns across the region because Mesoamerica has high levels of endemism for birds (Eissermann & Avendaño, 2018; García-Moreno, Cortés, García-Deras, & Hernández-Baños, 2006; Navarro-Sigüenza & Sánchez-González, 2003; Peterson, Escalona-Segura, & Griffith, 1998; Peterson et al., 2003; Prieto-Torres et al., 2019; Sánchez-González, Morrone, & Navarro-Sigüenza, 2008; Sánchez-Ramos et al., 2018). Therefore, considering that endemic species reflect a unique history of the Earth and its biota, failure to protect them would result in major losses of unique species diversity for this highly threatened region and its ecosystems. In this context, using SDMs and conservation planning protocols (based on ZONATION software), we aim to (a) assess the current representativeness levels of Mesoamerican endemic bird species within existing PAs and (b) determine high-priority areas for conservation that complement the current PA network to maximize species representation and protection, in a way that considers the anthropic context. This information allows us to provide new and more accurate data on which areas require attention and therefore represents an important step to guide future establishment of new and efficient conservation areas across Mesoamerica.

TABLE 1 Current area of designated protected areas (PAs) and the additional area identified as priority conservation areas to increase coverage to match Aichi targets (17%) in Mesoamerica by country

			Priority conservation areas analyses					
			CAZ		ABF		Consensus area	
Countries	Current PA area (km^2)	% Of total PA area	km^2	%	km^2	%	km^2	%
Belize	7,609	4.61	2,152	4.05	332	0.63	266	1.42
Costa Rica	10,026	6.08	9,035	17.03	30,030	56.61	8,917	47.64
El Salvador	52	0.03	–	–	–	–	–	–
Guatemala	23,329	14.14	1,787	3.37	4,790	9.03	1,385	7.40
Honduras	9,263	5.61	8,573	16.16	361	0.68	11	0.06
Mexico	90,743	55.01	26,014	49.04	6,659	12.55	5,153	27.53
Nicaragua	13,896	2.42	3,064	5.78	1,882	2.55	1,162	6.21
Panama	10,051	6.09	2,425	4.57	8,996	16.96	1,823	9.74
Total	164,969		53,050		53,050		18,716	

Note: The number and total area per PA was obtained from maps produced by the World Database of Protected Areas (UNEP & WCMC, 2019). Data for Mexico include only the part of the country that is within Mesoamerica (south of the Transmexican Volcanic Belt).

2 | METHODS

2.1 | Study area

The geographical range for this study was the Mesoamerican region (Figure 1), with an area of ca. 1,130,019 km^2 extending from central Mexico to the Darien in eastern Panama (De Albuquerque, Blas, Beier, Assunção-Albuquerque, & Cayuela, 2015; DeClerck et al., 2010). This biogeographical designation of Mesoamerica is delimited by the Transmexican Volcanic Belt, which marks the southern range limits of several nearctic taxa and northern range limits of several neotropical taxa (Escalante, Sánchez-Cordero, Morrone, & Linaje, 2007). This region encompasses all sub-tropical and tropical ecosystems (grouped into five biomes, over 60 vegetation type and 41 ecoregions) and is considered both a centre of origin and a corridor for terrestrial species (Olson et al., 2001; Jiménez & López, 2007). Thus, during the last 30 years, great efforts have been made to conserve representative samples of these ecosystems, resulting in more than 3,800 PAs (including National Parks and wilderness areas) throughout the region (Jiménez & López, 2007; IUCN & UNEP-WCMC, 2019).

2.2 | Species selection and occurrence records

We created a complete list of the permanent resident and endemic bird species inhabiting Mesoamerica, defined as species whose distributional range is limited only to the study area. This list was compiled from sources that offer information on the habitat characteristics for each species (e.g., Howell & Webb, 1995; Prieto-Torres et al., 2019; Stotz, Fitzpatrick, Parker, & Moskovits, 1996), online scientific collection databases (i.e., Cornell Lab of Ornithology-Birds of North America [https://birdsna.org/Species-account/bna/species/], BirdLife International [http://datazone.birdlife.org/] and the Handbook of the birds of the world [HBW; https://hbw.com/species]), and from a database of presence records (described below). For this first avifauna list, we compiled the data for historical occurrence records by species (using only data from 1950 to 2018 to match the temporal extent of climatic data) from diverse sources: (a) Atlas of Birds of Mexico (Navarro-Sigüenza, Peterson, & Gordillo-Martínez, 2002, 2003); (b) online databases (Global Biodiversity Information Facility [GBIF; https://www.gbif.org/] and eBird [https://ebird.org/home]); and (c) the scientific literature (e.g., *Biologia Centrali-Americana*; Salvin & Godman, 1879–1904). Access number for downloaded GBIF records for each species is detailed in the Appendix S1.

Next, to identify problematic or imprecise species occurrences, we compared the spatial distribution of records obtained with the species ranges defined by the Neotropical Birds website (see details at https://neotropical.birds.cornell.edu) and removed all mismatched records. For cases where the geographical information of localities was dubious (e.g., likely data transcription errors), the lat–long coordinates were verified using ArcMap v.10 (ESRI, 2011) and Google Earth, and records located outside Mesoamerica and those with geographical information that could not be verified were eliminated. We also removed points located within cities because these occurrences may not reflect the habitat requirements of species. These steps were important to identify problematic or imprecise species occurrence data with incorrect climate values because the choice of climate baseline and reduction of sampling bias affects model performance for each species (Boria, Olson, Goodman, & Anderson, 2014; Roubicek et al., 2010). Likewise, for this study we decided to exclude species with less than 15 independent occurrence records available because low sample size may affect model performance (Owens et al., 2013; Pearson, Raxworthy, Nakamura, & Peterson, 2007). After discarding individual species models that were not statistically significant (see below), our full dataset contained 48,477 individual records of 180 endemic species––belonging to 12 orders, 34 families and 125 genera (see Appendix S1)––which we then used to build our models.

2.3 | Environmental data

Because building species distribution models relies on the environmental variables associated with occurrence points of the bird species, we gathered 19 bioclimatic variables summarizing aspects of precipitation and temperature for the Earth's surface from the layers of WorldClim 2.0 (Fick & Hijmans, 2017) as well as three topographic variables (Digital Elevation Model, Aspect, and Slope) from the Hydro1k project (USGS, 2001). Although topographic variables are not commonly used in SDM studies, they were included here because numerous examples (e.g., Cauwer, Muys, Revermann, & Trabucco, 2014; Kübler et al., 2016; Mota-Vargas, Rojas-Soto, Lara, & Castillo-Guevara, 2013; Prieto-Torres & Pinilla-Buitrago, 2017; Rheingantz, Saraiva de Menezes, & Thoisy, 2014) show that these variables can be used as proxies for other type variables that are correlated with species' physiological requirements (e.g., microclimate, edaphic conditions). In addition, because habitat preferences have been suggested to be important driver for distribution and ecology of tropical biota (Burney & Brumfield, 2009; Harvey et al., 2008; Harvey, Aleixo, Ribas, & Brumfield, 2017; Pimm, Raven, Peterson, Şekercioğlu, & Ehrlich, 2006), we also included the dissimilarity of the enhanced vegetation index (EVI) variable from the Global Habitat Heterogeneity project (Tuanmu & Jetz, 2015; available at http://www.earthenv.org). In this sense, we used the difference in EVI between adjacent pixels (i.e., dissimilarity values) as a proxy for vegetation type and land cover. All these layers had a spatial resolution of 30 arc seconds (~1 km^2 per pixel). For each species, collinearity among environmental variables (see Beaumont, Hughes, & Poulsen, 2005) was reduced by only retaining variables with Pearson correlations <0.70 and variance inflation factor (VIF) <10, as implemented in the "corrplot" (Wei & Simko, 2017) and "usdm" (Naimi, 2017) libraries in R software (R-Core-Team, 2019). Detailed information about the set of environmental variables used for each species is shown in Appendix S1.

2.4 | Species distribution models

To construct the potential distributional area models for each bird species, we used MaxEnt 3.4.1 (Phillips, Anderson, & Schapire, 2006), which uses the maximum entropy principle to calculate the most likely distribution of focal species as a function of occurrence localities and environmental variables (Elith et al., 2011). Although other computer programs are also available for modelling species' distribution ranges, we decided to use MaxEnt because it has been proven to perform better when only presence data are available (Elith et al., 2011), as is our case. This software produces robust models with ≥15 occurrence points are available for each species (Elith et al., 2011; Wisz et al., 2008).

On the other hand, given that SDMs must consider historical factors affecting species' distributions, we used specific areas for model calibration for each species, known as the accessible area or *M* (Barve et al., 2011; Soberón & Peterson, 2005). For each species, a mask or GIS polygon delimiting this calibration area was established based on the intersection of occurrence records with the WWF Terrestrial Ecoregions (Olson et al., 2001) and the Biogeographical Provinces of the Neotropical region (Morrone, 2014). In effect, we assumed that this defined region has been explored by each species (i.e., reached by dispersal from existing populations) and thus represents both the species' tolerance limits as well as historical and ecological barriers to dispersal (such as rivers or valleys) across the Mesoamerican region.

All models were run with no extrapolation to avoid artificial projections from extreme values of ecological variables (Elith et al., 2011; Owens et al., 2013). Other MaxEnt parameters were set to default. We used the bootstrap resampling option from MaxEnt to calibrate the habitat suitability models of each species, which randomly resampled 75% of the occurrence data (training points) 100 times to generate the models (i.e., replicates), while using the remaining 25% of the dataset (testing points) to assess the model's accuracy by computing the area under receiver operating characteristic curves (AUC; Elith et al., 2006; Fielding & Bell, 1997). Then, we retained for subsequent analyses only the model that represented the mean environmental suitability value for each species. We converted continuous cloglog habitat suitability probability outputs for each species (Phillips et al., 2006) into binary presence–absence maps by setting the decision threshold to "10th percentile training presence." We used this threshold criterion to minimize over-predictions in our final binary maps, allowing better recovery of species' distributional areas (Liu, White, & Newell, 2013). Finally, model performance was evaluated by calculating the commission and omission error values (Anderson, Lew, & Peterson, 2003) and the partial ROC curve test (Peterson, Papes, & Soberón, 2008) using the same remaining 25% of the dataset (i.e., testing points). To generate only the "best hypothesis map" for each species, we compared our final maps against available distributional information of each species (i.e., Cornell Lab of Ornithology-Birds of North America, the BirdLife International and the Handbook of the birds of the world [HBW]). Models with high commission errors and/or models that were not statistically significant were excluded from subsequent analyses. Finally, we classified the current species ranges based on the number of sites (pixels) they occupied as small (in the lower quartile, <16,270 pixels), intermediate or large (in the upper quartile, >121,740 pixels).

2.5 | Conservation prioritization

ZONATION 4.0.0b (Moilanen et al., 2005, 2014) was used to determine high-priority areas for the conservation of endemic bird species across Mesoamerica. This software establishes a hierarchical prioritization of areas of the study region, allowing the identification of key sites for the conservation of species and areas for an optimally balanced expansion of an existing reserve network. This is based on biodiversity features (here, bird species distribution) and different "penalization" variables (here, anthropic pressures) for each pixel (Di Minin, Veach, Lehtomäki, Montesino Pouzols, & Moilanen, 2014; Moilanen, 2007; Moilanen et al., 2005, 2014). The way the "loss of conservation" value is aggregated across features within a pixel depends on so-called "cell-removal rules" (Di Minin et al., 2014). Here, we decided to run our analysis implementing two different removal rules: core area zonation (CAZ) and additive benefit function (ABF). The most important difference between these rules is that ABF assigns higher importance to cells with many features and retains a higher average proportion of features (i.e., prioritizes high species richness), while the CAZ prioritizes areas containing rare and/or highly weighted species. A detailed explanation of the use of ZONATION is available in Di Minin et al. (2014).

For our prioritization analyses, we assigned weighting values from 1 to 12 to species based on their IUCN conservation status (IUCN, 2019) and distributional ranges. We generated this index by multiplying a value indicating the species' conservation status (Least Concern [LC] = 1, Near Threatened [NT] = 2, Vulnerable [VU] and Data Deficient [DD] = 3, Endangered [EN] = 4 and Critically Endangered [CR] = 5) by a value indicating the category of distributional ranges of the species in Mesoamerica (small = 3, intermediate = 2 and large = 1; e.g., Nori et al., 2016; Prieto-Torres et al., 2018). To select optimal areas for PA expansion, we included the existing PAs in Mesoamerica as a hierarchical mask in our analyses. From this last perspective, ZONATION tends to identify the best part of the landscape for an optimal and balanced expansion (i.e., complementarity) by first considering existing PAs, then including additional areas that compensate specific ecological losses and satisfy the targets while minimizing cost (Di Minin et al., 2014). Shape files of PAs were downloaded from the World Database of Protected Areas (IUCN & UNEP-WCMC, 2019) considering all the IUCN categories of PAs available within the surface. We used a Kolmogorov–Smirnov (KS) test in R software (R-Core-Team, 2019) to test whether there was higher species concentration(i.e., richness) of endemic avifauna in PA sites compared to non-PA sites (Prieto-Torres & Pinilla-Buitrago, 2017).

Given that most bird species cannot be adequately protected in highly modified areas (Pimm et al., 2014) because human influence tends to diminish habitat quality, and therefore, the potential for conservation, it was important to prevent the software from assigning high conservation values to highly modified areas. To do this, we assigned negative weight values to pixels with >50% cover loss and extremely disturbed landscapes in a reclassified land cover map (Defourny et al., 2016) and to pixels with high human influence in the Global Terrestrial Human Footprint map (Venter et al., 2016; WCS & CIESIN, 2005). By assigning negative weights to these pixels, the sum of the positive (i.e., the summary of biodiversity features) and negative weighted was zero, allowing a balanced solution for prioritization (Faleiro, Machado, & Loyola, 2013; Moilanen et al., 2011). Both ABF and CAZ prioritizations were run with the "edge removal" function activated and BLP (Boundary Length Penalty distribution smoothing) set to 0.5. This function forces the program to remove cells from the defined edges-to-area ratio of remaining landscape, increasing the connectivity of priority and protected areas in the landscape (Moilanen et al., 2014). ZONATION's warp factor was set at the default (warp factor = 10). All variables had a spatial resolution of 0.008333° (~1 km^2) and were cropped to the study area (from 7° to 22°N and from −102° to −97°W; see Figure 1).

After running the prioritization analyses, we plotted performance curves for both analyses to quantify the proportion of the original occurrences retained for each biodiversity feature, at each top fraction of the landscape chosen for conservation (Di Minin et al., 2014; Moilanen et al., 2014). We generated two performance curves, one for all species and one for only threatened species (CR, EN, VU). This allowed us to determine the representativeness of the current PA network and the priority areas reaching 17% of the available territory, as proposed in the Aichi targets (UNEP, 2010). Finally, to determine the relative importance of current PAs within Mesoamerica, we repeated these prioritization analyses but did not include the shape file of PA features as a hierarchical mask (see above). Graphical results of this last step are provided as Appendix S1.

3 | RESULTS

Our species distribution models showed highly significant AUC ratios from the partial ROC test (ranging from 1.15 to 1.99, $p < .05$) and low omission errors (mean of 16.4 ± 9.9 [i.e., 7.3 ± 9.9 occurrence points]), indicating that the models were statistically better than random. Thus, the species distribution models were considered accurate under these performance diagnostics. Overall, our species models showed spatial distributional ranges from 1,584 to 555,300 km^2 (mean of 99,448 ± 120,109 km^2). We observed that 25.0% of species had small distributional ranges within the region, 50.0% had intermediate range sizes, and 25.0% had large distributional ranges (Figure 1). According to the IUCN (see Appendix S1) only 20 of these species are classified as threatened (EN and VU), 10 as NT, one as DD and 149 species as LC. In addition, species richness patterns for endemic birds across Mesoamerica tended to be highest in areas that are considered boundaries between highly biodiverse ecosystems, such as tropical dry forests and cloud forests throughout Mexico, Guatemala, Costa Rica and Panama (Figure 1). In contrast, low species richness values were found along the coast and the Caribbean slope. Overall, we observed no significant differences ($p > .05$) for species richness values between areas within (16.6 ± 14.9 spp.) and outside (16.5 ± 12.5 spp.) the existing PA network.

Currently, a total of ~165,000 km^2 (i.e., 13.1%) of the surface of the region is covered by PAs (Table 1, Figure 1). This level of protection across regions represents, on average, 19.3% of the distribution area of the endemic bird species analysed here (Figure 2a), and only 16.7% of the distribution of threatened species. A total of eight countries had PAs, three of them (Mexico [55.01%], Guatemala [14.14%] and Nicaragua [8.42%]) account for ~78% of current PA extent within the region (Table 1). Overall, we observed that 16.1% of

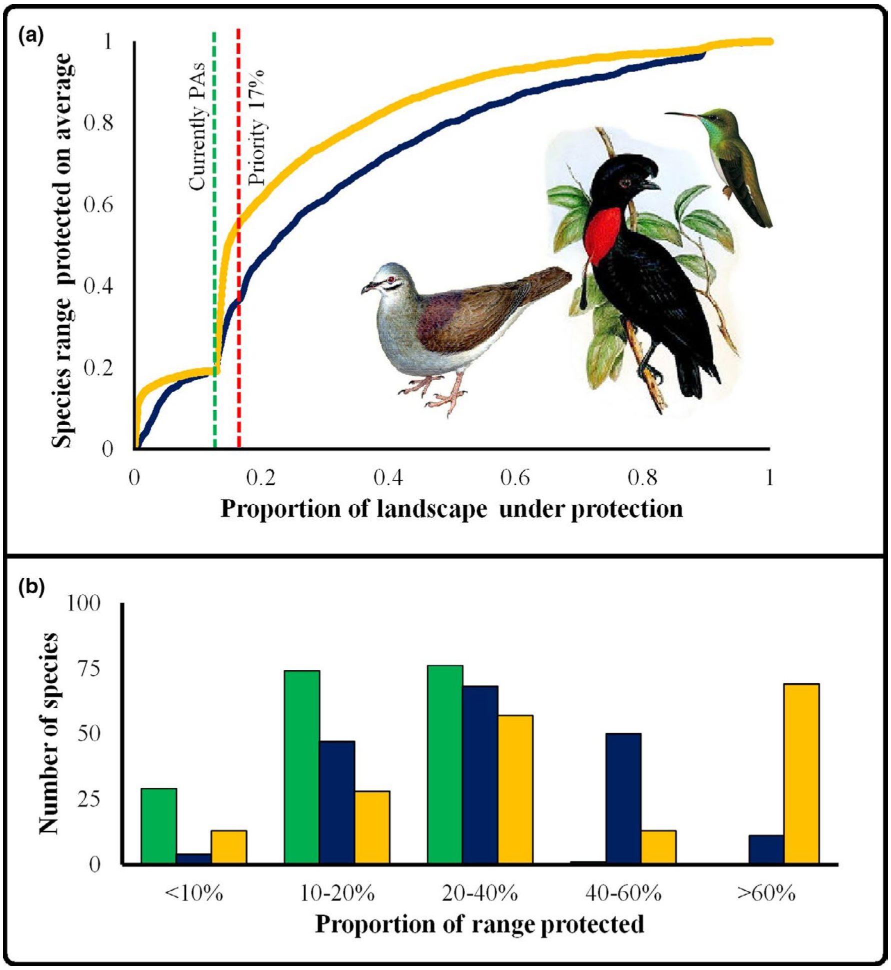

FIGURE 2 Levels of protection for Mesoamerican endemic bird species considering the current protected areas (PA) network and the expanded 17% of surface with high priority. (a) Performance curves of the prioritization models considering all endemic species and only threatened endemic species in the Mesoamerican region, showing the proportion of available grid cells that are protected (*x*-axis) and the corresponding average species range protected (*y*-axis); (b) histogram showing the average percentage of geographical distribution and bird species number found inside the current PAs network (green colour) and the priority 17% in Mesoamerica region (CAZ [blue colour] and ABF [yellow colour]). Birds (from left to right) in the maps are *Zentrygon lawrencii* (LC); *Cephalopterus glabricollis* (EN); and *Amazilia boucardi* (EN). The bird pictures were taken from iNaturalista (https://www.naturalista.mx/), the Wikipedia (https://es.wikipedia.org/wiki/Cephalopterus_glabricollis), and the Birds of the World (The Cornell Lab of Ornithology; https://birdsoftheworld.org/bow/home) websites

birds (n = 29 spp.) have <10% of their distribution represented in PAs, for 41.1% (n = 74) of species between 10% and 20% of their ranges are protected, and for 42.2% (n = 76), between 20% and 40% is protected (Figure 2b). The best represented bird groups within the current PAs were, on average, the Trogoniformes (n = 4 spp.; 27.8% of their distribution within PAs), Galliformes (n = 10 spp.; 25.7%) and Columbiformes (n = 5 spp.; 22.9%). The bird taxa with lowest representativeness values within PAs were Gruiformes (n = 1 spp.; 9.3%) and Tinamiformes (n = 1 spp.; 10.4%).

According to our prioritization analyses, by protecting an additional 3.9% (i.e., 53,050 km^2) of the total area (reaching a summed coverage of 17% of study area; Figure 3), the representativeness of the PAs network would substantially increase, covering between 38.4% (using CAZ rules) and 56.6% (using ABF rules) of all endemic species (Figure 2a). Protecting the identified priority areas would increase the proportions of species' ranges covered by PAs; regardless of which remove rule was used. The number of species for which only <10% of their distribution range is protected would drop to 4.7%, 20.8% of species would have between the 10 and 20% protected, 34.7% between 20% and 40%, and for 39.8% of species, >40% of their distributions area would be under protection (Figure 2b). These potential conservation areas included between 32.5% (CAZ rules) and 43.8% (ABF rules) of the distributions of threatened endemic species.

Considering a total protected area covering 17% of the total surface of Mesoamerica, the two algorithms shared 35.3% (~18,700 km^2) of the area designated as priority selected surface (Figure 3; see Appendix S2). Combining these consensus priority conservation areas with current PAs cover, on average, 35.00% of the distribution area for all the endemic bird species analysed here and 29.13% of the distribution area of threatened species. Considering these combined current PA and consensus surfaces, we observed that best represented bird

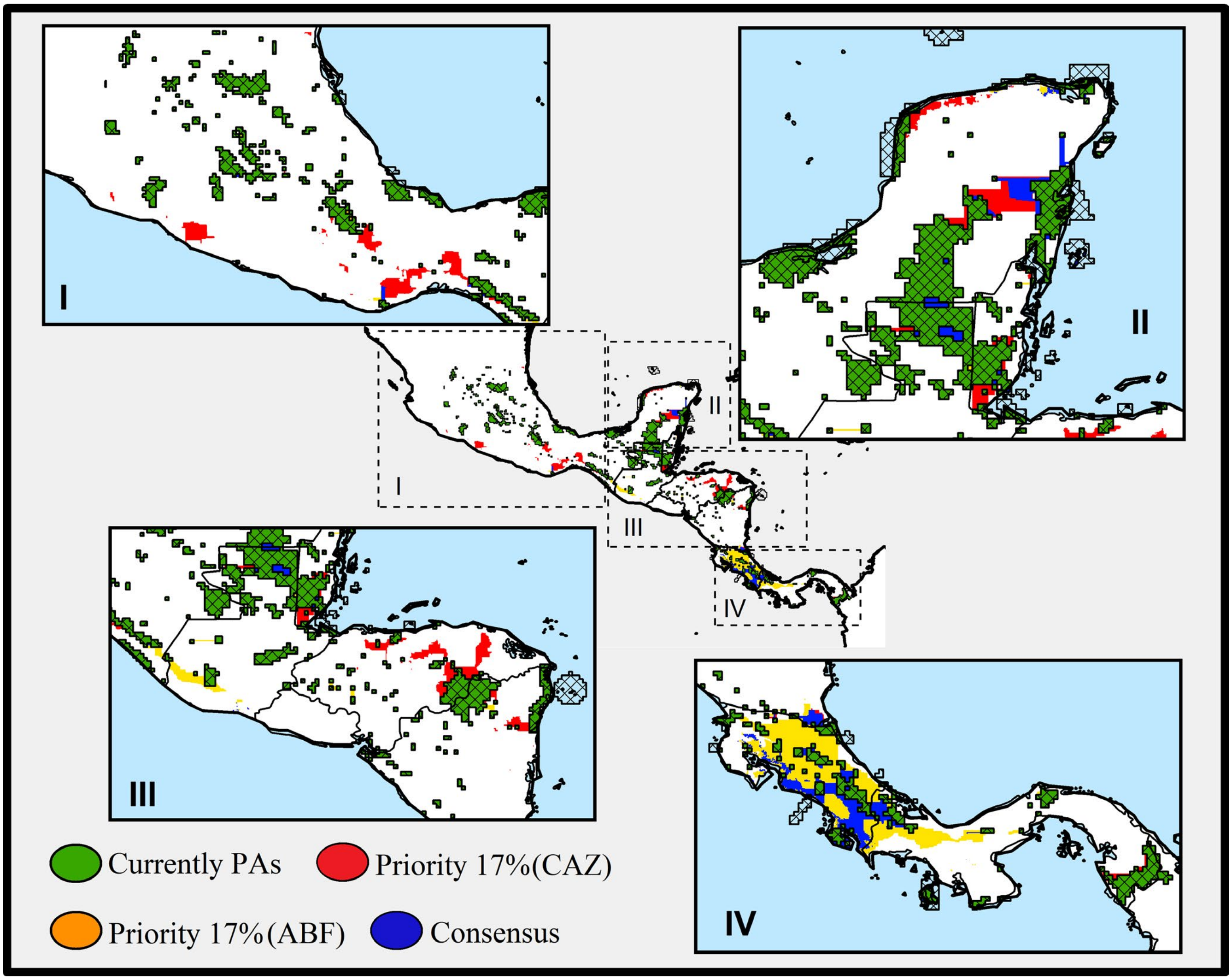

FIGURE 3 Maps showing existing protected areas of the region (green), potential expansion areas identified in our spatial prioritization analysis for each analysis (CAZ [red] and ABF [yellow] removal rules) and the areas where they overlap (consensus [blue])

groups within this prioritization scenarios were Columbiformes (35.8% of their distribution within PAs), Passeriformes ($n = 99$ spp.; 33.9%) and Trogoniformes (31.6%). Also, it is important to note that these combined areas have significantly ($p < .001$) higher species richness per site than the areas outside them: 21.57 ± 16.04 spp. inside PAs versus 11.47 ± 12.36 spp. PAs outside.

The consensus of priority conservation areas covered broad areas adjacent to current PAs, mostly across Costa Rica (47.64% of the identified priority areas are in this country), Mexico (27.53%) and Panama (9.74%; Table 1). On the other hand, consistent with Olson et al.'s proposal (2001), we observed that most consensus areas identified herein were distributed in five ecosystems (Table 2): Isthmian-Atlantic moist forests (27.13%), Talamancan montane forests (22.60%), Yucatán moist forests (18.94%), Petén-Veracruz moist forests (10.61%) and Isthmian-Pacific moist forests (9.04%). Finally, the prioritization without including the PA mask showed little overlap with the current PA network (14.4% using ABF and 29.5% using CAZ); Appendix S3).

4 | DISCUSSION

Our spatial conservation prioritization analyses showed that the current PA network is poorly representative of the distributional ranges of endemic bird species in Mesoamerica and does not efficiently cover the conservation needs. Using this macroecological approach, we identified sites that are important for species conservation through several practical methods, such as aggregation methods, uncertainty analysis, species prioritization and replacement cost analysis for current or proposed reserves (Di Minin et al., 2014). This is important because current and future conservation decision- and policy-making should focus not only on the need to increase the area of the current PA network in this region where there is strong land use pressure (~72% of original vegetation already lost; Miller et al., 2001; Portillo-Quintero & Sánchez-Azofeifa, 2010; Weinzettel et al., 2018), but also on ecological processes such as increased connectivity between ecosystems. Increased connectivity would increase dispersion rates, speciation

TABLE 2 Current area (in km^2 and percentage) of the current Protected Areas (PAs) and the complementary conservation areas estimated to increase coverage to match the 17% Aichi target throughout Mesoamerica by terrestrial ecosystem

Ecosystem	Current PAs (km^2)	%	Consensus area (km^2)	%
Isthmian-Pacific moist forests	2,050	1.24	5,078	27.13
Talamancan montane forests	5,991	3.63	4,230	22.60
Yucatán moist forests	18,109	10.98	3,544	18.94
Petén-Veracruz moist forests	33,670	20.41	1,985	10.61
Isthmian-Atlantic moist forests	5,724	3.47	1,692	9.04
Costa Rican seasonal moist forests	955	0.58	743	3.97
Central American dry forests	2,900	1.76	575	3.07
Sierra Madre del Sur pine-oak forests	1,075	0.65	433	2.31
Yucatán dry forests	1,324	0.80	162	0.87
Southern Mesoamerican Pacific mangroves	1,887	1.14	50	0.27
Others	88,884	55.34	224	1.20
	164,969	100.00	18,716	100.00

Note: The number and total area per protected area was obtained from maps produced by World Database of Protected Areas (UNEP & WCMC, 2019). Results were estimated based on the 10 most important ecosystems found.

and the richness of surrogate taxa, in addition to increasing the area of critical habitats for species with some degree of vulnerability (Torres-Morales, Guillen, & Ruiz-Sánchez, 2019). In addition to integrating socioeconomic, legal and political actions and strategies to conserve biodiversity and sustain rural livelihoods in agricultural landscapes in the Mesoamerican region may help to further strengthen the conservation of several taxa (e.g., Harvey et al., 2008; Nori et al., 2013).

Our results showed that less than a quarter of the current PAs coincide with areas designated by ZONATION as important for conservation. In other words, if PAs could be optimally placed from scratch, they would not be in the places they are currently located. This indicates that despite the increase in the extent of terrestrial PAs over the last decade (Jones et al., 2018; Watson, Dudley, Segan, & Hockings, 2014; Watson et al., 2011), PAs are generally not located in the most suitable or important sites to protect the endemic biota across region, leaving the overall conservation picture for birds in this region quite weak. This last scenario could be even more critical if we consider recent evidence that invasive species are present in PAs (Liu et al., 2020; Rico-Sánchez et al., 2020), which can directly and/or indirectly threaten the biota and ecosystem integrity. The Mesoamerican biota meet the main conditions of high vulnerability and extreme irreplaceability to be considered a global conservation priority (sensu Margules & Pressey, 2000), making well-informed decisions are crucial for policymakers at both national and international scales to promote the long-term conservation of biodiversity in this region.

From this perspective, our results have key implications for the conservation of bird diversity and endemism in Mesoamerica, providing new and more accurate evidence of which areas require attention (Tables 1 and 2). Firstly, according to the prioritization analyses (whether due to rarity or species richness), PA area needs to be increased to include the identified priority areas to accurately include their biodiversity. This is consistent with previous studies that have highlighted the need for additional PAs to avoid in major losses of species diversity throughout the region in the long term (e.g., De Albuquerque et al., 2015; Prieto-Torres, Lira-Noriega, & Navarro-Sigüenza, 2020; Prieto-Torres, Navarro-Sigüenza, Santiago-Alarcón, & Rojas-Soto, 2016; Prieto-Torres et al., 2018; Sánchez-Azofeifa, Powers, Fernandes, & Quesada, 2013). Secondly, the moist forests are the least protected biome across the region and had the highest deforestation rate in recent decades (Defourny et al., 2016; Hansen et al., 2013). Thus, urgent actions to protect this biome are required, especially in Costa Rica, Mexico and Panama where results showed important conservation gaps in areas with particularly high levels of both bird diversity and endemism (e.g., Howell & Webb, 1995; Prieto-Torres et al., 2019; Stotz et al., 1996) and for which conservation priorities have been previously identified (e.g., Devenish, Díaz-Fernández, Clay, Davidson, & Yépez-Zavala, 2009; Stattersfield, 1998). 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 fact, we showed that it is possible to greatly improve the efficiency of Mesoamerican PAs (e.g., increasing the species representativeness levels by more than 65%) by strategically expanding the current network by only 3.9%. This efficiency is important given ongoing deforestation and limited funding for conservation (e.g., Pouzols et al., 2014; Pringle, 2017; Wallace, Barborak, & MacFarland, 2003). The picture is particularly alarming in Costa Rica, where our results suggest that an extension of more than 50% of the current PAs surface is needed, as well as in Panama, with at least an additional 18% of PA surfaces required (Table 1).

Mesoamerican biodiversity cannot be protected in reserves alone, since they are too isolated, too expensive to manage and too controversial in a region where poverty alleviation remains a more immediate priority than conservation. For instance, most of the birds occurring in Mesoamerica are widely distributed across the region, and most endemic species' ranges include at least two countries (e.g., Howell & Webb, 1995; Prieto-Torres et al., 2019; Sánchez-Ramos et al., 2018; Stotz et al., 1996). Thus, we argue for the implementation of trans-boundary policy collaborations for future conservation initiatives (Pouzols et al., 2014). This is particularly important considering that while most countries are behind the Aichi target connectivity element (Saura et al., 2018; Torres-Morales et al., 2019), in particular cases such as El Salvador and Honduras (Figures 1 and 2), only about half of the area currently under protection is effectively connected (Komar, 2002). Maintaining connectivity is particularly important and challenging in Mesoamerica because of the region's altitudinal and latitudinal gradients, which act as natural barriers to species movement and can increase the vulnerability of biodiversity to climate change and agricultural expansion (Harvey et al., 2008). The priority conservation areas identified here could play a key role in halting biodiversity loss while acting as corridors to allow gene flow and migration between PAs (Dulloo et al., 2008). Likewise, future studies should address the contribution of the priority conservation areas defined here to the connectivity requirements and spatial movements for taxa we did not analyse, such as migratory species.

Fortunately, although each country maintains its own ministries of the environment, they all participate in the Central American System of Protected Areas (SICAP) formed in 1992, which has allowed the development of programmes such as the Mesoamerican Biological Corridor (DeClerck et al., 2010; Hilty, Chester, & Cross, 2012; Miller et al., 2001). This conservation programme seeks to apply the Convention on Biological Diversity's ecosystem approach to support conservation initiatives that are strongly linked to sustainable rural livelihoods, while simultaneously integrating regional scale PA connectivity. This is particularly important because it is an ongoing coordinated effort among countries to reach the Aichi targets, which has allowed some Mesoamerican PAs to progress through a variety of regional, national and internationally recognized reserves. In fact, most of the prioritized areas identified in this study have been identified by other previous conservation proposals and recognized at a global scale, such as the Maya Biosphere Reserve, the Sierra de las Minas Biosphere Reserve, Costa Rica's Área de Conservación Guanacaste and Darién National Park (DeClerck et al., 2010; Hilty et al., 2012; UNEP & WCMC, 2019). Thus, future executable actions based on our results could be possible. Our consensus for priority conservation areas is a 44.1% match with those defined by Nori, Loyola, and Villalobos (2020) as priority areas for conservation and research of terrestrial vertebrates (mammals, birds and amphibians) in Mesoamerica. This suggests that our results also may represent important sites for entire biotas across the region. However, future studies including additional avian and non-avian taxa are needed to generate a comprehensive proposal for PA's expansion.

Nevertheless, considering that conservation prioritization often takes place at smaller scales (Wallace et al., 2003), we also argue that additional land is not the only requirement to meet a given conservation goal. While studies like this one provide essential scientifically based information on a coarse scale, conservation actions can only be executed through the joint action of academia, NGOs, local communities and policymakers (Nori et al., 2016; Prieto-Torres et al., 2018). Undoubtedly, biodiversity conservation in human-modified landscapes of Mesoamerica cannot be effectively advanced if it cannot be defined and measured. Thus, the implementation of interdisciplinary and complementary programmes (including vegetation restoration) are crucial to ensure conservation in the region (Whitbeck, 2004; DeClerck et al., 2010; Galloway et al., 2005; Hansen et al., 2008; Janzen, 2000; Portillo-Quintero & Sánchez-Azofeifa, 2010). In fact, there are some recent positive and effective experiences of joint action between public and private entities in pursuit of conservation goals in Mesoamerica, such as Costa Rica's Área de Conservación Guanacaste (see Janzen, 2000; Whitbeck, 2004) and the "*Ejidos* Conservation Areas" project (Mexico; see Castillo, Magaña, Pujadas, Martínez, & Godínez, 2005). In this sense, we believe that conservation policymakers could use our results as clues to define where to implement future conservation plans, including the expansion of the PA network or other forms of protection. However, the PAs will benefit only by strengthening the capacity of local government to integrate voluntary conservation and development projects, best practices for land use planning and land use regulations that buffer PAs (e.g., Chazdon et al., 2009; Harvey et al., 2008), as well as preventing the introduction of non-native species, strengthening environmental legislation and increasing the presence of authorities (Liu et al., 2020; Rico-Sánchez et al., 2020).

On the other hand, it is worth noting that only 20 endemic bird species are currently categorized as threatened and 10 as near threatened (IUCN, 2019). This is a surprisingly low number considering the dramatic conversion processes occurring in the region and the susceptibility of bird species to these phenomena (DeClerck et al., 2010; Galloway et al., 2005; Hansen et al., 2008; Portillo-Quintero & Sánchez-Azofeifa, 2010), as well as the low degree of protection provided by the current PAs. Given this situation, it is important to permanently monitor and constantly update the conservation status of all endemic vertebrates in the region (Prieto-Torres et al., 2018; Sarkar, Sánchez-Cordero, Londoño, & Fuller, 2008). This information is indispensable to determine spatial priorities in the region and guide effective conservation policies. Given the large information gaps regarding the biodiversity of the region, future studies should update spatial priorities of the Mesoamerican region as new information is generated, including studies contemplating climate change scenarios (see Prieto-Torres et al., 2016, 2020), which is an important limitation in our study.

Under future climates scenarios, species will be pushed towards higher elevations in order to track their climatic niches, which could produce local extinctions or drastic modifications in the distribution of habitat specialists and, consequently, a reassortment of biotic assemblages within the current PA network (e.g., Golicher, Cayuela,

& Newton, 2012; Prieto-Torres et al., 2016,2020). In fact, previous studies suggest that climate-induced range contractions for species could have similar effects on taxa considered Threatened, Data Deficient and Least Concern (e.g., Hidasi-Neto et al., 2019; Prieto-Torres et al., 2020). Thus, adding new areas to preserve both current and future potential species ranges could represent a less costly and more effective strategy for guiding conservation decision-making to maximizing the long-term protection of biota (Hannah et al., 2007; Prieto-Torres et al., 2016; Triviño et al., 2018).

Of concern is the conservation of forest-dependent species that are unable to persist in an agricultural matrix, even when there is significant on-farm tree cover (e.g., Nori et al., 2013). Approaches evaluating conservation status for species in human-modified landscapes, in both spatial and temporal terms, are essential for shedding light on the ecological mechanisms underlying the persistence of wild biodiversity in those areas (Donovan & Strong, 2003; Nori et al., 2013) and the critical roles that species play in local ecosystems (Gardner et al., 2009). The identification of conservation areas for birds that are endemic, threatened or both, as well as areas with a high concentration of species in general (i.e., high species richness), coupled with the possible effects of future climate change, would maximize the performance of the current PA network (De Albuquerque et al., 2015; Hannah et al., 2007; Prieto-Torres et al., 2018, 2020; Triviño et al., 2018).

Clearly, the fate of Mesoamerican biodiversity is fundamentally dependent on successful establishment and management of PAs and corridors, as well as informing conservationists and policymakers about where to focus future conservation expansion efforts. Although the existing PA network provides protection and conservation of Mesoamerican ecosystems, our analysis shows that representativeness within the current PAs is still far from complete for many endemic and threatened birds in the region. In fact, all but the largest PAs exist in a wider landscape dominated by human-altered ecosystems where most of the native biota is unprotected. Therefore, large-scale studies would be an important step to guide the establishment of new conservation areas that are efficient for the entire Mesoamerican region.

ACKNOWLEDGEMENTS

Thanks to the curators of the multiple institutions worldwide who have supplied data, access to collections and invaluable logistic support. We also thank Javier Nori to provide the shapefile layer of priority areas for conservation of and research focused on terrestrial vertebrates to compare the results from this study. JER-A thanks CONACyT and the Universidad Nacional Autónoma de México (Posgrado en Ciencias Biológicas) for support of his postdoctoral scholarship. DAP-T also extends his gratitude to the Universidad Nacional Autónoma de México (Dirección General de Asuntos del Personal Académico, DGAPA-UNAM, México) for support of a postdoctoral scholarship. The financial and logistical support for this project was provided by The Rufford Foundation (DAP-T: projects 16017-1 and 20284-2), Idea Wild, CONACyT (AGNS: project 152060) and CONABIO (AGNS: project JM071). We thank Lynna Kiere, Luis A. Sánchez-González, and two anonymous reviewers for helpful comments on previous versions of the manuscripts.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13153.

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. Readers interested in other materials may request them from the corresponding author [JERA].

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BIOSKETCH

Jorge E. Ramírez-Albores is a researcher focused to characterizing the spatio-temporal distributional patterns of biodiversity across the Neotropics, with the aim of informing environmental policies and ecosystems management for their long-term conservation.

Author contributions: J.E.R.-A., A.G.-M. and A.G.N.-S. conceived and designed the study. J.E.R.-A., L.E.S.-A. and D.A.P.-T. did the data compilation and environmental variable selection. J.E.R.-A. and D.A.P.-T. performed the species distribution models and conservation priority analyses. J.E.R.-A. and D.A.P.-T. led the writing of the manuscript, with substantial contributions from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Ramírez-Albores JE, Prieto-Torres DA, Gordillo-Martínez A, Sánchez-Ramos LE, Navarro-Sigüenza AG. Insights for protection of high species richness areas for the conservation of Mesoamerican endemic birds. *Divers Distrib*. 2020;00:1–16. https://doi.org/10.1111/ddi.13153