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Source: Tropical Conservation Science, 11(1)

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/1940082918794408>


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Tropical Conservation Science
Volume 11: 1–11
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DOI: 10.1177/1940082918794408
journals.sagepub.com/home/trc


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Abstract

Land-use changes are one of the main causes of biodiversity loss. It would be expected that species with restricted habitats and distribution should experience the main negative effects of the modification of natural environments. To exemplify the potential effect of land transformation on restricted species, we focused on the potential habitat loss of six endemic and quasi-endemic species to Mexico (*Ortalis poliocephala*, *Melanerpes chrysogenys*, *Trogon citreolus*, *Pheugopedius felix*, *Uropsila leucogastra*, and *Arremonops rufivirgatus*) whose distributions include the state of Guerrero, in southern Mexico. Species distribution models were generated for each species, and potential habitat loss was evaluated using three temporal vegetation and land-use maps (1997, 2003, and 2013). These analyses were then repeated only for tropical dry forest, one of the most dominant ecosystem in the state of Guerrero and with the most severe transformation rates. The potential habitat of all species decreased considerably, particularly for the last periods; the habitats for *M. chrysogenys* and *T. citreolus* were reduced by 78% in 2013. The potential habitats of *U. leucogastra* and *P. felix* decreased to a lesser extent during the three periods. The reduction tendencies were higher for dry forest than for the remaining habitats, which were ranged from 88% to 93% for *U. leucogastra* and *M. chrysogenys*, respectively. These results suggest major negative potential effects of land transformation on the endemic species' habitat.

Keywords

species distribution models, habitat loss, tropical dry forest, biodiversity loss, conservation

Introduction

Land-use changes and climate change are the main drivers of the loss and degradation of ecosystems, leading to a decline in biodiversity (Jetz, Wilcove, & Dobson, 2007; Sanderson et al., 2002). Changes in land use especially constitute a significant short- and medium-term threat to species persistence (Mas, Pérez, Clarke, & Sanchez-Cordero, 2010; Quesada et al., 2009; Sala et al., 2000) because of transformations that have occurred as a result of the conversion of natural habitats to other land uses (e.g., agricultural, industrial, urban, and extractive; Foley et al., 2005). Despite awareness of the processes and consequences of land-use changes, efforts

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Received 23 March 2018; Revised 18 July 2018; Accepted 19 July 2018

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to the loss or decrease of distributional areas of species in the neotropics have been scarce (e.g., Peterson, Sánchez-Cordero, Martínez-Meyer, & Navarro-Sigüenza, 2006; Ríos-Muñoz & Navarro-Sigüenza, 2009; Sánchez-Cordero, Illoldi-Rangel, Linaje, Sarkar, & Peterson, 2005; Yañez-Arenas, Mandujano, Martínez-Meyer, Pérez-Arteaga, & González-Zamora, 2012), considering that this region possesses the greatest biodiversity in the world, including the highest number of endemisms (Morrone, 2014; Sánchez-González, Morrone, & Navarro-Sigüenza, 2008). The species that inhabit the neotropical region are also the most threatened, due to high deforestation rates that already have caused the loss, degradation, and fragmentation of a wide extension of natural habitats (Lisboa de Carvalho et al., 2017).

In particular, this topic has been little explored in such semiarid environments as tropical dry forest (TDF), an ecosystem that has suffered extensive damage due to its widespread conversion to farmland, accompanied by uncontrolled cattle grazing and fires (Miles et al., 2006). At the global level, approximately 49% of this ecosystem has been converted to other land uses (Banda-R et al., 2016; Hoekstra, Boucher, Ricketts, & Roberts, 2005) while on the American continent close to 66% of this ecosystem has been disturbed (Stoner & Sánchez-Azofeita, 2009). The situation is especially critical in Mexico, where around 300,000 ha are estimated to be deforested annually, and 73% of the original vegetation of TDF has been lost. No other vegetation type is disappearing as rapidly as these forests (Balvanera, Islas, Aguirre, & Quijas, 2000; Trejo & Dirzo, 2000). The natural ecosystems of the state of Guerrero, in southern Mexico, have been especially severely transformed (Instituto Nacional de Estadística y Geografía [INEGI], 2010), reducing the distribution of diverse terrestrial vertebrate species (Botello, Sarkar, & Sánchez-Cordero, 2015). TDF is the most extensive forest cover in the state (representing ca. 25.4% of the forested area); however, it has experienced a high degree of alteration during the past three decades, with up to 20% now being secondary forest (Secretaría de Medio Ambiente y Recursos Naturales, 2013). Individual species, particularly those with specific ecological requirements, have seen their distribution areas drastically reduced as a consequence of land-use changes (e.g., Sánchez-Cordero et al., 2005; Sierra-Morales et al., 2016), which has contributed to disruptions in the ecosystem processes in which they participate (Dirzo, Young, Mooney, & Ceballos, 2011).

Studies evaluating the effects of land-use changes in combination with species distribution models (SDMs), i.e., areas having suitable ecological conditions for species presence; Anderson, Lew, & Peterson, 2003; Soberón & Peterson, 2004) have become increasingly important in the last decade (e.g., Monterrubio-Rico, Renton, Ortega-Rodríguez, Pérez-Arteaga, & Cancino-Murillo, 2010;

Rivera-Ortiz et al., 2013; Sánchez-Cordero et al., 2005; Sierra-Morales et al., 2016). These studies have demonstrated that habitat reduction is a factor that threatens biodiversity, particularly that of endemic species and habitat specialists such as some mammals (Sánchez-Cordero et al., 2005) and birds like jays (Peterson et al., 2006), hummingbirds (Sierra-Morales et al., 2016), and species with low densities naturally, such as parrots (Ríos-Muñoz & Navarro-Sigüenza, 2009). On the other hand, the use of SDMs represents an approach to understand the land-use changes and for reevaluating potential changes in particular species and ecosystems (Thomas, Cameron, Green, Bakkenes, & Beaumont, 2004; Walther et al., 2002). The present study analyzes the effects of land-use changes on the potential habitat of six endemic bird species whose distribution encompasses the state of Guerrero in southern Mexico, one of the most biodiverse in the country and whose modifications in its natural environments are representative of changes happening throughout a large portion of the neotropics. Analysis using this approach can contribute to the refinement of strategies for systematic conservation planning.

Methods

Study Area and Species

The state of Guerrero, in southwestern Mexico (Figure 1), possesses a highly complex topography defined by the convergence of four biotic regions: the Sierra Madre del Sur, the Balsas basin, the Pacific-coast plain, and the Neovolcanic belt. This complex topography comprises a wide range of elevations from sea level to more than 3000 m; and various climates including warm humid, warm subhumid, temperate, and semiarid. These conditions allow diverse vegetation types to thrive, including TDF, oak forest, pine forest, pine-oak forest, cloud forest, tropical-medium forest, riparian forest, mangroves, and extensive areas of secondary vegetation and agricultural (Secretaría de Medio Ambiente y Recursos Naturales, 2013).

To show the potential effect of land transformation on restricted species, we analyzed four birds endemic to Mexico (*Melanerpes chrysogenys*, *Ortalis poliocephala*, *Pheugopedius felix*, and *Trogon citreolus*) and two quasi-endemic species (*Arremonops rufivirgatus* and *Uropsila leucogastra*; González-García & Gómez de Silva, 2003) whose distributions include the state of Guerrero. The quasi-endemic species are those whose distribution exceeds slightly (ca. 25,000 km²) of Mexico's limits to neighboring countries by ecological or orographic continuity (González-García & Gómez de Silva, 2003). One criterion for the selection of these particular species was the fact that their distribution is mostly associated with environments not having substantial

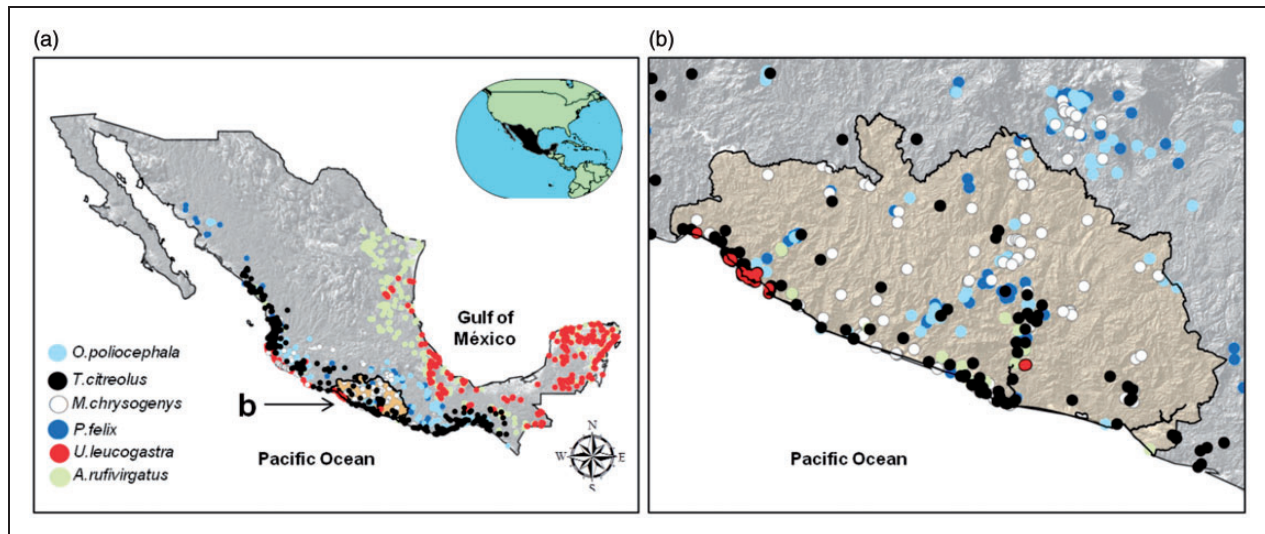


Figure 1. Localities records of the six bird species endemic in (a) whole distributional range in Mexico and (b) distributional range in the state of Guerrero. Colors represent the species records.

modification, particularly TDF (Howell & Webb, 1995; Ortega-Huerta & Vega-Rivera, 2017). A final additional criterion was a sufficiency of locality records, with a minimum number of 200 records along their known distributional range for better SDM performance.

Distributional Data

Information on the distribution of the selected species was obtained primarily using four sources: (a) the Atlas of the Birds of Mexico (Navarro-Sigüenza, Peterson, & Gordillo-Martínez, 2003), which contains data on Mexican birds deposited in scientific collections around the world (Figure 1(a)); (b) the available digital database of eBird (2015), which contains observational records; (c) the global biodiversity information facility, which includes collected birds from diverse regions at both the national and global level; (d) records compiled from fieldwork carried out from 2001 to 2013 in diverse localities throughout the four biotic regions in the state of Guerrero (Figure 1(b)). Fieldwork records were obtained throughout observations and collections as part of diverse regional studies focused on the birds' ecology and biogeography of the state of Guerrero (i.e., Almazán-Núñez, 2009; Almazán-Núñez et al., 2018; Almazán-Núñez & Navarro, 2006; Almazán-Núñez, Puebla-Olivares, & Almazán-Juárez, 2009; Jacinto-Flores, Sánchez-González, & Almazán-Núñez, 2017). All doubtful localities were eliminated, and all of the records were limited to the time interval (1910–2009) covered by the bioclimatic variables used. A total of 4,998 localities records for the six species (Table 1; Figure 1) were gathered, of which *T. citreolus* had the highest number of records and *P. felix* the lowest.

Table 1. Number of Records and Average Values per Species of the AUC Ratios of the SDMs.

Species	Number of records	AUC ratios' values
<i>Ortalis poliocephala</i>	1,189	1.72**
<i>Trogon citreolus</i>	1,244	1.71**
<i>Melanerpes chrysogenys</i>	548	1.79**
<i>Pheugopedius felix</i>	283	1.60**
<i>Uropsila leucogastra</i>	534	1.66**
<i>Arremonops rufivirgatus</i>	700	1.50**

Note. AUC = area under the curve.

** $p < .001$.

Environmental Data

To characterize the environmental niche for SDM performance, we used 19 climate variables from Cuervo-Robayo et al. (2013) derived from interpolated temperature and precipitation data from the 1910 to 2009 period. To avoid overparameterization of the models as a consequence of the high correlation among some of the climate variables, a Pearson correlation analysis was performed (Elith, Kearney, & Phillips, 2010; Elith et al., 2011). Variables with correlation values < 0.85 were selected, resulting in a total of nine climate variables: diurnal temperature range, isothermality, maximum temperature of the warmest month, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the driest trimester, precipitation of the warmest trimester, and precipitation of the coldest trimester. In addition,

five topographic variables were considered (slope, altitude, topographic index, north-south aspect, and east-west aspect), obtained from the Hydro-1K project (<http://edcdaac.usgs.gov/gtopo30/hydro>). All of the environmental variables were resampled at a spatial resolution of 0.0083° per pixel ($\sim 1 \text{ km}^2$) in ArcMap 10.1 (ESRI, Redlands, California, USA). Thus, some estimates are given in km^2 but actually correspond to pixels in geographical coordinates (i.e., degrees).

Species-Distribution Modeling

SDMs were generated using the Genetic Algorithm for Rule Set Production (Stockwell & Noble, 1992; Stockwell & Peters, 1999). This method has been widely used to model bird distributions and has shown a good predictive capacity (Ortega-Huerta & Peterson, 2008; Peterson, 2001). We developed 100 replicate models per species, and the 10 best models were selected in a Genetic Algorithm for Rule Set Production program routine (*best subsets*) according to the balance between low-omission values and median commission values, expressed as percentages for the projected area (Anderson et al., 2003). These models were summed to obtain a final consensus map for each species, confirming that each SDM contained at least 90% of the species records.

Final models were evaluated using a modified area under the curve (AUC) method based on the partial receiver operating characteristic (ROC) curve, as proposed by Peterson, Papes, and Soberón (2008) and performed in the partial ROC software (Barve, 2008). This method gives greater weight to omission errors and measures model performance using AUC ratios with values ranging from zero to two, where values above one indicate that models performed better than a random model ratio (AUC ratios > 1.0). Bootstrap resampling was performed with 1,000 iterations and with replacement of 50% of the original data points. A *Z* test was then performed to determine whether the obtained values of the partial ROC from the SDMs were statistically better than a random model (AUC ratios > 1.0).

Habitat Loss From Land-Use Changes

For the *post hoc* analysis of habitat loss and transformation, we used vegetation and land-use (VLU) maps from INEGI for the years 1997, 2003, and 2013 that correspond with series II, III, and V, respectively (INEGI, 1999, 2005, 2013). We eliminated areas where the original vegetation cover had been modified or replaced, assuming that the modified natural habitats, whether agroecosystems or human settlements (rural and urban), were not suitable for the bird species; while *M. chrysogenys* and *P. felix* can tolerate certain habitat modifications, they require primary habitats for reproduction, refuge, and

feeding (Almazán-Núñez, Arizmendi, Eguiarte, & Corcuera, 2015). The other four species require well-preserved vegetation coverage and density (Howell & Webb, 1995). We estimated the potential loss of natural habitats for each period per species. Finally, since the six species are associated mainly with TDF, the most extended and modified ecosystem in the state (ca. 27% of the total of Guerrero), we also estimated potential natural habitat loss for each period per species in consideration of the primary-vegetation map proposed by INEGI (2003), which describes potential vegetation without considering human-related modifications.

Results

Species-Distribution Modeling

The distribution models of *O. poliocephala* and *M. chrysogenys* encompassed a large part of the state ($\sim 51,600 \text{ km}^2$ and $\sim 49,456 \text{ km}^2$, respectively; Figure 2(a) and (c)), while *T. citreolus*, *A. rufivirgatus*, *P. felix*, and *U. leucogastra* possessed the smaller distributions ($\sim 27,192 \text{ km}^2$, $\sim 26,789 \text{ km}^2$, $\sim 21,976 \text{ km}^2$, and $\sim 11,715 \text{ km}^2$, respectively; Figure 2(b), (d–f)). Each of the final SDMs of the six species showed good predictive capacity and produced significantly accurate results according to the evaluation tests (*Z* test: $p < .001$ in all of the cases), whose AUC ratios were uniformly > 1 for all six species; thus, the generated distributions were better than expected by chance (Table 1).

Potential Habitat Loss Resulting From Land-Use Changes

The distribution analyses for the three periods showed important changes in the potential species distributions (Figures 2 and 3). In general, the potential habitat of the six species showed considerable reduction during all three periods (between 29% and 78%; Table 1; Figure 3). In particular, *O. poliocephala*, *T. citreolus*, and *M. chrysogenys* experienced a potential habitat loss of 64.9%, 66.3%, and 68.3%, respectively, in 1997 and of 75.4%, 77.4%, and 78.3%, respectively, in 2013. *A. rufivirgatus* experienced a potential habitat loss of 58.5% in 1997 and of 70.8% in 2013. Similar values of loss of potential habitat was experienced by *P. felix*. Notably, *U. leucogastra* had experienced a low habitat reduction of 2.6% in 1997, although the loss of its habitat increased considerably in 2003 to 13.7% and in 2013 to 28.9% (Table 2; Figure 3). Thus, the potential habitats of *P. felix* and *U. leucogastra* decreased to a lesser extent during the three analyzed periods (Table 2; Figure 3).

In terms of the loss of potential TDF habitat, the six species experienced a notable reduction of between 88% and 93% (Table 2; Figure 3). *Melanerpes chrysogenys* and

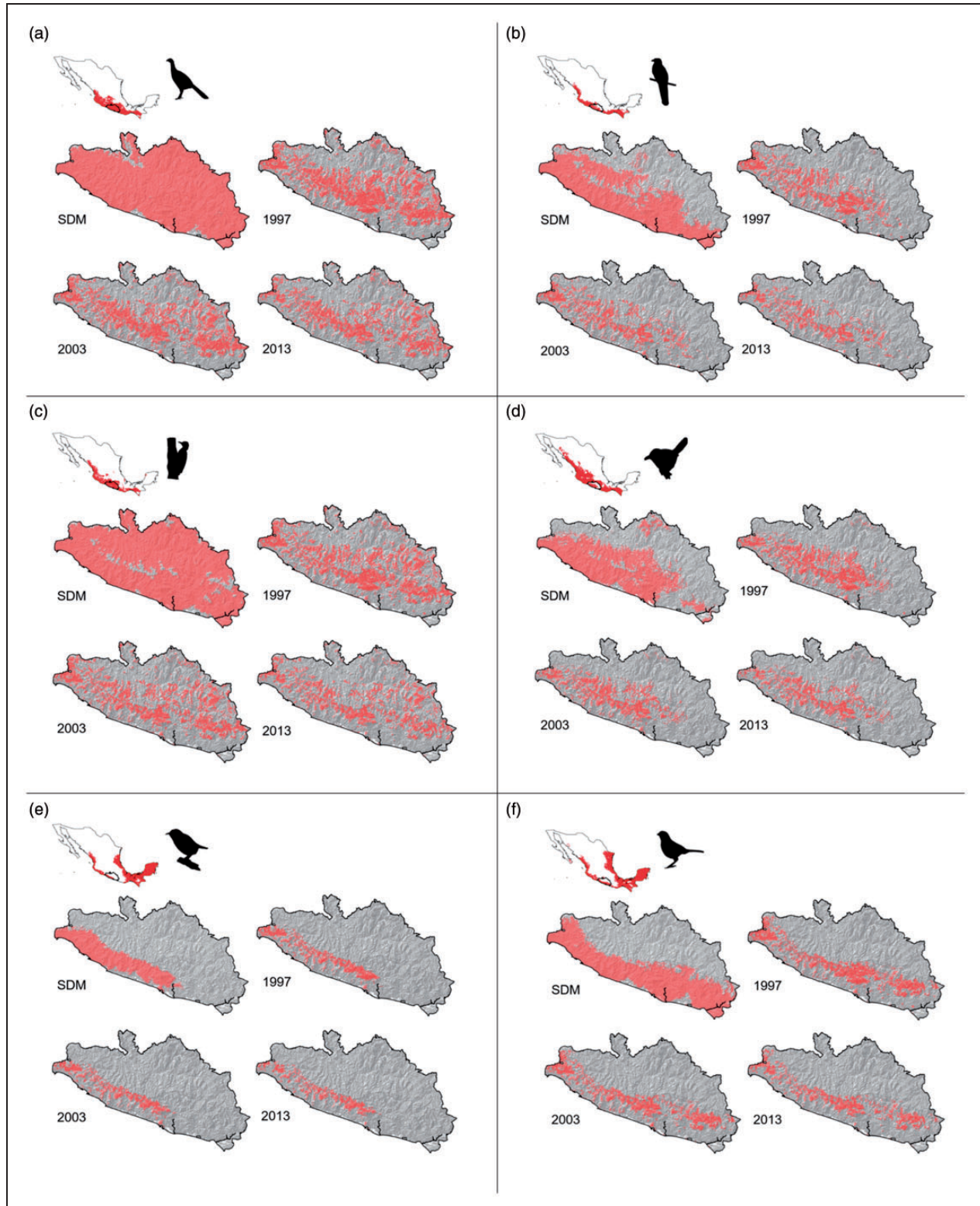


Figure 2. SDMs of the bird species studied in the state of Guerrero and their reduction according to changes in land uses in three periods (1997, 2003, and 2013): (a) *Ortalis poliocephala*, (b) *Trogon citreolus*, (c) *Melanerpes chrysogenys*, (d) *Pheugopedius felix*, (e) *Uropsila leucogastra*, and (f) *Arremonops rufivirgatus*.

SDM = species distribution model.

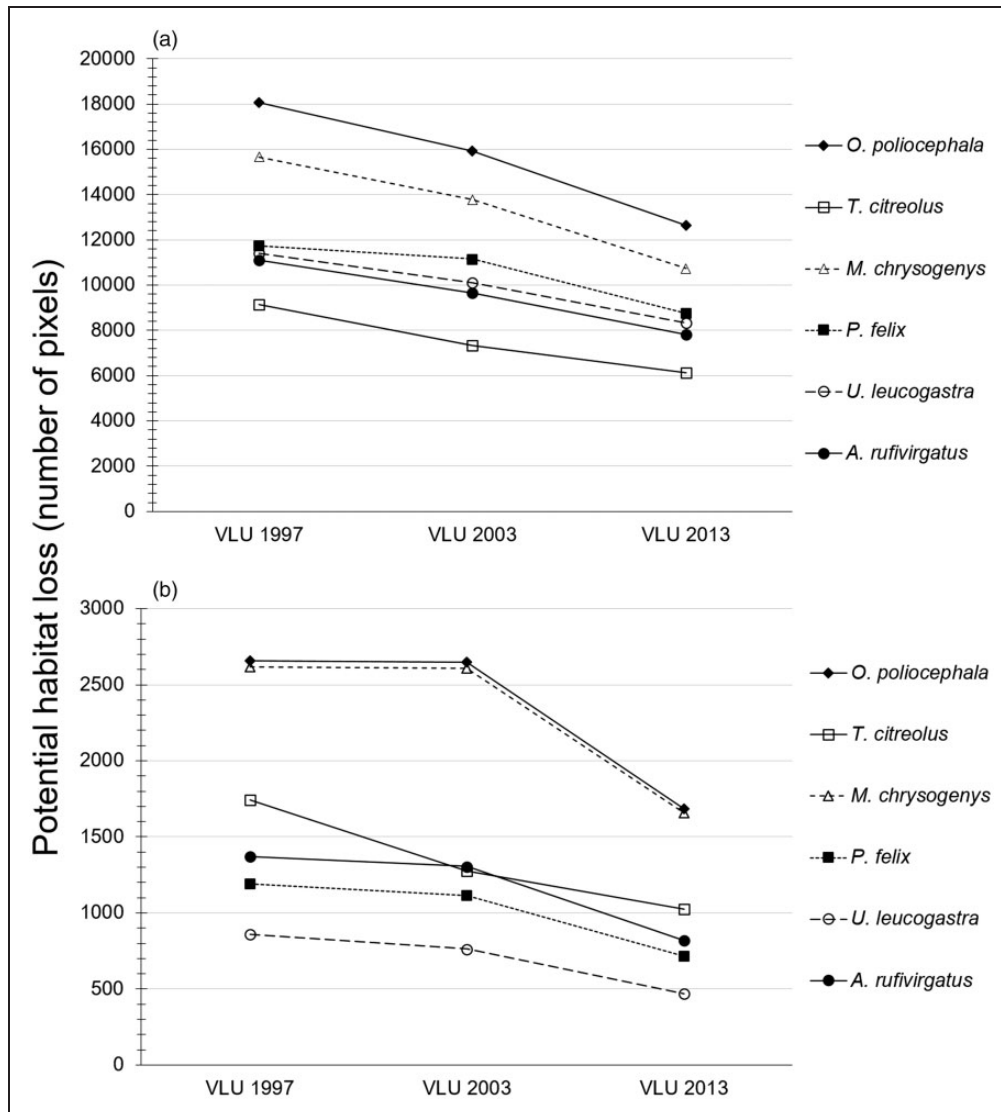


Figure 3. Loss of area of (a) total potential habitat and (b) TDFs potential habitat of bird species endemic in southern Mexico, resulting from land-use changes during three periods.

VLU = vegetation and land-use.

O. poliocephala experienced the greatest losses as a result of land-use modification. In 1997, their potential distribution was reduced to 88.9% and 88.3%, respectively, while in 2013, their habitat was further reduced to 93% for both species. *Uropsila leucogastra* and *P. felix* experienced lower levels of habitat loss over the course of the evaluated periods. In 2003, they experienced potential habitat reductions of 82.3% and 85.2%, respectively, while further reductions were observed in 2013 of 88.4% and 89.4%, respectively (Table 2; Figure 3).

Discussion

The results obtained in this study demonstrate that the geographic distribution of the six species analyzed in the

state of Guerrero have been negatively affected by changes in land use. In addition, the final distribution models of each species assume that the conversion of natural habitats to agroecosystems or human settlements (rural and urban) does not support the persistence of the birds in the long term. For example, although some species may forage in transformed environments (i.e., *M. chrysogenys* and *P. felix*) or in rural towns (*O. poliocephala*), they reproduce and seek refuge in primary habitats or those that have not been altered to a large extent (Gurrola, 2002; Ortega-Huerta & Vega-Rivera, 2017). Other species, such as *T. citreolus*, *A. rufivirgatus*, and *U. leucogastra*, have specific nesting and feeding habits (Howell & Webb, 1995; Wauer, 1998) commonly performed in undisturbed areas, so the conversion

Table 2. Decrease in the Potential Distribution Areas of Endemic Bird Species in the State of Guerrero, Southern Mexico, as a Result of Land-Use Changes During Three Periods (1997, 2003, and 2013).

Species	Total potential distribution (pixels)	VLU 1997	Habitat loss (pixels)	Percentage reduction (%)	VLU 2003	Habitat loss (pixels)	Percentage reduction (%)	VLU 2013	Habitat loss (pixels)	Percentage reduction (%)
Total Guerrero										
<i>O. poliocephala</i>	51,600	18,063	33,537	64.9	15,921	35,679	69.1	12,654	38,946	75.4
<i>T. citreolus</i>	27,192	9,150	18,042	66.3	7,342	19,850	72.9	6,138	21,054	77.4
<i>M. chrysogenys</i>	49,456	15,662	33,794	68.3	13,780	35,676	72.1	10,727	38,729	78.3
<i>P. felix</i>	21,976	11,735	10,241	46.6	11,148	10,828	49.2	8,755	13,221	60.1
<i>U. leucogastra</i>	11,715	11,415	300	2.5	10,101	1,614	13.7	8,327	3,388	28.9
<i>A. rufivirgatus</i>	26,789	11,100	15,689	58.5	9,657	17,132	63.9	7,814	18,975	70.8
Tropical dry forest ^a										
<i>O. poliocephala</i>	22,644	2,656	19,988	88.3	2,647	19,997	88.3	1,682	20,962	92.6
<i>T. citreolus</i>	12,682	1,743	10,939	86.3	1,274	11,408	90.0	1,025	11,657	91.9
<i>M. chrysogenys</i>	23,613	2,619	20,994	88.9	2,609	21,004	89.0	1,655	21,958	93.0
<i>P. felix</i>	7,533	1,191	6,342	84.2	1,116	6,417	85.2	797	6,736	89.4
<i>U. leucogastra</i>	4,296	858	3,438	80.0	762	3,534	82.3	498	3,798	88.4
<i>A. rufivirgatus</i>	9,829	1,369	8,460	86.1	1,305	8,524	86.7	818	9,011	91.7

Note. VLU = vegetation and land-use.

^aThe total potential distribution of birds in TDF (tropical dry forest) was considered according to primary vegetation map proposed by INEGI (2003).

of forests to anthropized environments can significantly affect their population ecology. Other studies analyzing the effects of land-use change in the potential distribution of endemic birds in the neotropical region, coincided with the trends found in our study (Peterson et al., 2006; Ríos-Muñoz & Navarro-Sigüenza, 2009; Sierra-Morales et al., 2016). For example, endemic bird species such as *Amazona auropalliata* and *Lophornis brachylophus* have reduced their distribution in more than 60% as a result of habitat loss (Ríos-Muñoz & Navarro-Sigüenza, 2009; Sierra-Morales et al., 2016), which demonstrates that habitat changes constitute one of the main threats to habitat-restricted species. Furthermore, the analyzed species are not exclusively endemic to the state of Guerrero, but rather to a wider area spanning the lowlands of western Mexico; a region subjected to strong anthropogenic pressures that have affected the distribution of other resident species (e.g., psittacids; Monterrubio-Rico et al., 2016; Ríos-Muñoz & Navarro, 2009) and migratory species (Aid, Carter, & Peterson, 1997; Hutto, 1986). In this context, our results are valuable information for implementing conservation strategies at the local level as well as in neotropical region experiencing constant modifications to natural habitats because of land-use changes.

SDMs are based primarily on environmental suitability or the conditions necessary for species to survive (Peterson, 2001; Sánchez-Cordero et al., 2005). However, it is possible to identify some methodological limitations in the generation of these predictions that could affect the results. For example, the projections of land-use changes during the

three periods, based on data from INEGI, are not completely compatible (Peterson et al., 2006; Ríos-Muñoz & Navarro-Sigüenza, 2009). This is because the VLU maps have inherent differences resulting from the specific methods used in their creation; consequently, the land-use delimitations shown in the VLU maps of each period do not exactly coincide. Even so, the results of the SDMs of this study enabled an approximate visualization of habitat loss and indicated a reduction in the distribution of the studied bird species in the state of Guerrero over the course of the past 15 years (by 2013, habitat loss ranged from 28.9% to 78.3%). However, these hypotheses should be further tested (Illoldi-Rangel, Fuller, Linaje, Sánchez-Cordero, & Sarkar, 2008), although from a biological perspective, the results were consistent with the tendencies exhibited at the national level and in the rest of the neotropics. For instance, the rate of change (76%) of primary vegetation cover at the local level (in the state of Guerrero) is greatest than the rate of change (53%) at the national level (Secretaría de Medio Ambiente y Recursos Naturales, 2013). The analysis of Mas et al. (2010) demonstrated an increase in agricultural and pasture areas in Mexico during two periods (1993–2002 and 2002–2007), corresponding with an increasing rate of deforestation of primary tropical forests. Similar results were observed in Guerrero, particularly for TDF, one of the best-represented ecosystems, which was reduced by more than 54.7% from 1997 to 2013 (INEGI, 2013). This rate of vegetation loss has been maintained since the 1990s for some states in central Mexico (Trejo & Dirzo, 2000).

In TDF, *M. chrysogenys* and *O. poliocephala* experienced the greatest potential habitat loss, while species such as *A. rufivirgatus*, *U. leucogastra*, *P. felix*, and *T. citreolus* were affected to a lesser extent because they can also inhabit other ecosystems, such as tropical medium forest (Howell & Webb, 1995). TDF is one of the more important ecosystems in the neotropics in terms of its extension and biodiversity (Balvanera et al., 2006; Portillo-Quintero & Sánchez Azofoitea, 2010), but it is continually disturbed and transformed into agricultural fields or pastures (Portillo-Quintero & Sanchez-Azofoitea, 2010; Quesada et al., 2009). While TDF was the best-represented ecosystem in the state, comprising 27% of the total area (Secretaría de Medio Ambiente y Recursos Naturales, 2013), the results also indicate that its extent has been largely reduced over the course of the three study periods. Therefore, the population dynamics and dispersion flow of the bird species associated with this ecosystem have been affected. However, the differences in the values of potential habitat loss of TDF among the six species were minimal, ranging from 88.4% to 93%. Indeed, other changes to land use in diverse ecosystems of Guerrero have already led to the local extinction of some bird species, including the military macaw (*Ara militaris*), which was previously found in the coastal areas of Guerrero (Goldman, 1951; Rowley, 1984).

Implications for Conservation

The land-use changes occurring in the state are representative of changes happening throughout a large portion of the neotropics, resulting in a rapid transformation of the primary habitats of many species (Portillo-Quintero & Sanchez-Azofoitea, 2010; Quesada et al., 2009). In addition to land-use changes, the climate change contributes to reduced species populations as a consequence of increasing temperature and decreasing precipitation, resulting in a longer dry season (Golicher, Cayuela, & Newton, 2011). In fact, based on projections of ecological niche models over future scenarios of climate change, Prieto-Torres, Navarro-Sigüenza, Santiago-Alarcón, and Rojas-Soto (2016) have predicted the future disappearance of TDFs in regions such as the Balsas river basin.

The state of Guerrero because of its geographical location has a unique variety of ecosystems that foster high levels of biodiversity. Despite this, Guerrero is one of the Mexican states with the least area destined for conservation, with barely 0.1% of its area enjoying protected status (INEGI, 2010; Koleff & Moreno, 2006). Therefore, it is important to establish strategies for conserving diverse ecosystems, especially those with high biological richness and endemism and those that contain threatened species (Koleff & Moreno, 2006; Koleff & Urquiza-Haas, 2011). Although this study did not include

a social approach, we believe that ecosystem conservation in Guerrero, as in the rest of the tropics, should also include social-participation schemes in order to guarantee that bird-conservation measures are functional and effective and foster the sustainability of natural resources (Almazán-Núñez, Almazán-Juárez, & Ruiz-Gutiérrez, 2011; Durán, 2006). Despite the constant fragmentation of the ecosystems of the neotropics, and particularly those of the state of Guerrero, the region still harbors numerous bird species that engage in reproduction, rest, and feeding activities.

Acknowledgments

The authors thank the biology and ecology students of the Universidad Autónoma de Guerrero for their support during field-work and the collection of biological data. Special thanks are extended to Angel Almazán, Oscar Nova, Elida Moreno, and Marcos Clemente for their logistical project support. The comments of two anonymous reviewers improved substantially the initial version of this manuscript. This project formed part of the collaboration among the members of the academic group “Biodiversity and Sustainable Environmental Management (CA-UAGro 170).” The authors also thank the Facultad de Ciencias Químico-Biológicas for the support provided during the development of this study.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

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