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Cumulative habitat loss increases conservation threats on endemic species of terrestrial vertebrates in Mexico

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ABSTRACT

Habitat loss is the main threat to biodiversity conservation worldwide, deteriorating areas with remnant suitable habitat and thus reducing species distribution ranges, and increasing the risk of local and regional population extirpations. We used ecological niche models projected as species potential distributions of endemic terrestrial vertebrates and quantified spatiotemporal cumulative habitat loss trajectories projected in species extant distributions, using land use and land cover vegetation maps (LULC) time series (1985, 1993, 2002, 2007, 2011, and 2014). Of a total of 996 species, only 311 species produced robust species potential distribution models. Significant differences in habitat loss in species extant distributions were observed from 1985 to 2002, which coincided with high national habitat loss rates. No significant differences were observed in the following LULC time series. According to the IUCN Red List, only 78 of our species are at risk. However, IUCN's criterion A only considers habitat loss in species extant distributions over the last 10 years, but if we consider the cumulative habitat loss from 1985 to 2014, 227 species lost >30% of their distribution. Thus, we suggest that the impact of cumulative habitat loss in species distributions should be considered when determining conservation threats. Furthermore, we analyzed the impact at each of Mexico's ecoregions, and found that habitat loss in species extant distributions appeared to be related to geographic locations of species distribution ranges rather than to the distribution area *per se*. Thus, we consider that assessing extinction risks at a local level is critical for future biodiversity conservation.

1. Introduction

Habitat loss is the main cause of threat to biodiversity conservation worldwide where, approximately, 46% of forests have disappeared (Crowther et al., 2015; Johnson et al., 2017). It has been estimated that between 1990 and 2016, 1.3 million km^2 of forest were lost, and rampant habitat loss still continues today (World Bank: World Development Indicators, 2016). High rates of habitat loss observed in pantropical ecosystems pose a particularly high risk to these habitats holding exceptional high biodiversity (Hansen et al., 2013; Alroy, 2017; Giam, 2017). For example, it is estimated that approximately 17% of the Amazonian rainforest has been transformed in the last 50 years, and habitat loss rates are disproportionately high with, approximately, 75,000 km^2/year loss for forests with >50% tree cover (Hansen et al., 2013; Giam, 2017). These studies examined the effects of increasing habitat loss on biodiversity loss due to area reductions of ecosystems and vegetation types or in species richness in groups of species, but impacts on individual species have been poorly studied (Alroy, 2017; Giam, 2017). At the species level, this impact of cumulative habitat loss has profound consequences in reducing their distribution ranges, increasing risks of local and regional population extirpations in species of terrestrial vertebrates, and posing higher threats to species conservation (Dirzo et al., 2014; Ceballos et al., 2017). Thus, it is expected that cumulative habitat loss is related to increasing conservation threats on species.

Mexico is a megadiverse country, holding approximately 10% of the biota worldwide, with a high species richness and endemicity (Conservation International, 2000; United Nations CBD, 1992; Sarukhán et al.,

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2009; Martínez-Meyer et al., 2014). An estimated 5700 species of terrestrial vertebrates occur in Mexico, representing 9% of its biodiversity worldwide, and the number of species of amphibians, reptiles, and mammals are ranked within the first four countries globally (Llorente-Bousquets and Ocegueda, 2008; Conabio, 2014). It is estimated that 66% of species of amphibians, 56% species of reptiles, 29% species of mammals, and 17% species of birds are endemic to Mexico (Koleff et al., 2008; Conabio, 2014). However, Mexico shows high annual deforestation rates over 1% nationwide (FAO, 2001), where more than 13.5 million ha of ecosystems have been lost in the last 50 years, resulting in a cumulative natural vegetation loss of 30%; only 48% of the country retains primary vegetation with most of its native biota (INEGI, 2014; SEMARNAT, 2016). This significant habitat loss threatens biodiversity conservation by decreasing species richness, species distribution ranges, population abundance, and genetic diversity both at the national and regional scales (Best et al., 2001; Challenger and Dirzo, 2009; Fahrig, 2003; Steffan-Dewenter et al., 2002; Venier and Fahrig, 1996).

Habitat loss has been associated with loss of biodiversity in Mexico (Toledo et al., 1989; Myers, 1998; Kinnaird et al., 2003; Challenger and Dirzo, 2009), but some studies have estimated the impact on individual species (Sánchez-Cordero et al., 2005, 2009; Fuller et al., 2007; Botello et al., 2015a, 2015b; Mayani-Parás et al., 2019). The impact of regional habitat loss on species distribution ranges is poorly known with potential consequences of severe habitat fragmentation and local population extirpations (Botello et al., 2015a, 2015b; Monroy-Gamboa et al., 2019). Habitat loss deteriorates critical areas holding suitable remnant habitat in species distribution ranges posing threats to their conservation. Further, several studies have related reductions in species distribution ranges for assigning conservation status using the IUCN criteria (Rodrigues et al., 2006) and Mexican ecological regulations (Norma Oficial Mexicana 059). For example, a species conservation status is partly assigned according to the percentage of reduction in its distribution range due to habitat loss (Peterson et al., 2000; Ortega-Huerta and Peterson, 2004; Sánchez-Cordero et al., 2005, 2009; Botello et al., 2015a, 2015b). There is a need to revise species conservation threats given the cumulative habitat loss at both national and regional levels (SEMARNAT, 2016).

Ecological niche modeling projected as species potential distributions provide a conceptual and methodological approach for addressing these challenges (Guisan and Thuiller, 2005; Merow et al., 2013). Ecological niche models and species distribution models are empirical models that relate field observations to predictive environmental variables, based on statistical or expected response surfaces (Guisan and Zimmermann, 2000). This approach has become a very powerful method to test ecological hypotheses about the potential distribution of species, and to evaluate the possible impacts of environmental changes on such distributions (Guisan and Hofer, 2003). Using point occurrences of species, environmental variables, and vegetation layers in a GIS platform, we can quantitatively project spatiotemporal cumulative habitat loss trajectories into species extant distributions. Such an information platform can determine current conservation threats on a species by species case and identify critical areas for prioritizing biodiversity conservation. This study aimed to quantify spatiotemporal cumulative habitat loss trajectories associated with the extant distributions of endemic species of terrestrial vertebrates. We also analyzed the impact of cumulative habitat loss into species extant distribution to determine conservation threats on the endemic species of terrestrial vertebrates both nationwide and in ecoregions.

2. Material and methods

2.1. Study site and point occurrence data

The study included continental endemic species of terrestrial vertebrates distributed in Mexico. Point occurrence distributional data for 996 species were obtained from the website Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; accessed on 25 January 2018). All occurrence data points prior to 1970 (since the data used from WorldClim corresponded to the period between 1970 and 2000, and the records before 1970 are less accurate), points that had a resolution lower than 2 decimals of a degree or no geographic coordinates (decimal lat = 0, empty, 99, −99), fossil records, alive specimens from zoos, data obtained from iNaturalist (www.iNaturalist.com.mx; since those records do not have collected and verifiable specimens), and records that were found within the same pixel of the bioclimatic variables from WorldClim (1km^2; see below), were excluded. An outlier removal procedure in the environmental space was conducted using the reverse jackknife algorithm and by its position in the interquartile range, according to the values of the environmental layers (Robertson et al., 2016). The remaining occurrence data were projected in ArcMap, and all occurrence points that still did not coincide with the currently recognized distribution of the species were eliminated. Only those species with 10 or more occurrence points after data cleaning were used, leaving a total of 37,366 records corresponding to 311 species (62 species of amphibians, 117 species of reptiles, 80 species of birds, 52 species of mammals). The minimum number of 10 records per species was defined based on published information for an adequate species distribution modeling approach in Maxent (Wisz et al., 2008).

2.2. Species potential distributions

To obtain the modeling area for each species (M region; Soberon and Peterson, 2005), the polygons of the terrestrial ecoregions of Mexico (INEGI, CONABIO, INE, 2008) that contained the corresponding occurrence data were selected (Barve et al., 2011; Di Febbraro et al., 2016; Mateo et al., 2015); a buffer zone of 50 km was included around the polygons used as a cutting template. Nineteen climatic variables (~1 km^2) from the WorldClim database (https://www.worldclim.org/; accessed on 31 January 2018) were used as environmental variables to construct species potential distributions (Hijmans et al., 2005). A correlation analysis of variables was performed using the variance inflation factor (VIF); those with a correlation threshold >0.7 were considered redundant and only one was included to avoid possible multicollinearity (Venette, 2017).

Ecological niche models were generated in R software (R Core Team, 2014) with the ENMeval library (Muscarella et al., 2014). To parameterize the model, 10,000 background points were selected within the modeling area. Presence data were divided into training and testing groups using the block method (Hijmans, 2012), and five regularization multipliers and 13 feature classes were established to adjust the models, giving a total of 65 models per species. The best model was selected based on the omission rate and area under the curve (AUC), which measures the likelihood that a randomly selected presence point is located in a raster cell, with a higher probability value for species occurrence than a randomly selected absence point. This was then projected into a discrete presence/absence map through a maximum sensitivity plus specificity threshold (Liu et al., 2005), representing the points classified as inside or outside a species potential distribution (Liu et al., 2011). All maps were entered into the ConsNet software package (Ciarleglio et al., 2009, 2010) with a rack in which each cell measured 0.78 km^2. To obtain the area of species potential distributions, this value was multiplied by the numbers of cells occupied by each species nationwide and for each ecoregion (INEGI, CONABIO, INE, 2008).

2.3. Species extant distributions

The official Mexican land use and land cover vegetation maps (LULC) produced by the Mexican National Institute of Statistics, Geography, and Informatics (INEGI; Capa Digital de Uso de Suelo y Vegetación) were used in the following time series: LULC 1985, LULC 1993, LULC 2002, LULC 2007, LULC 2011, and LULC 2014 (INEGI, 2003; 2004; 2005; 2011; 2013; 2017). The LULC 1985 time series was built based on a multitemporal LANDSAT satellite image composition from 1973 to 1985. The LULC 1985 time series was included to expand the range to almost 30 years (1985 to 2014) for our analyses. Habitat loss included transformed areas into single-crop agriculture, rural or urban settlements, and bare soil, which are presumed unsuitable habitats for endemic species of terrestrial vertebrates (see Sánchez-Cordero et al., 2005, 2009; Botello et al., 2015a, 2015b). These maps were entered into the ConsNet software package (Ciarleglio et al., 2009, 2010) as permanently excluded areas. Species extant distributions were obtained by excluding areas of habitat loss (*e.g.*, retaining only areas holding remnant natural habitat) for each LULC time series, totaling six extant distribution models for each endemic species of terrestrial vertebrate. For each species, the area of its potential distribution was compared with the area of its extant distribution and the percentage of habitat loss for each LULC time series was obtained. Species were divided into four groups according to the percentage of habitat loss for each LULC time series, following recommendations by the IUCN (Rodrigues et al., 2006): (1) Species that lost <30%; (2) Species that lost 30–50%; (3) Species that lost 50–80%, and (4) Species that lost >80% of their distribution, respectively. Furthermore, the average distribution reduction of the endemic species of terrestrial vertebrates occurring on each ecoregion was obtained to determine the impact of cumulative habitat loss at the regional level.

2.4. Statistical analysis

Normality on our data was tested using a Kolmogorov-Smirnov test. A one-way repeated-measures analysis of variance (ANOVA) and a multiple comparison test (Tukey's HSD) were used to determine differences between the percentages of distribution reduction for the LULC time series. Also, a one-way ANOVA was performed to determine differences of species distribution reductions due to habitat loss in ecoregions between groups of endemic terrestrial vertebrates, considering only the 2014 LULC time series. All statistical analyses were used with the statistical package StatSoft (2007) STATISTICA.

3. Results

Information from a total of 996 species of endemic species of terrestrial vertebrates was obtained. Only 311 species showed enough point occurrences and robust species potential distribution models: 62 of 275 species of amphibians (23%), 117 of 474 species of reptiles (25%), 80 of 98 species of birds (82%), and 52 of 159 species of mammals (33%). Most species occurred in the Transvolcanic Belt, followed by the Pacific coast and in southern Mexico. Few species with enough point occurrences and robust potential distribution models occurred in northern Mexico, the Baja California Peninsula, and the Yucatan Peninsula.

Overall, the distribution range reductions due to habitat loss for the endemic species of terrestrial vertebrates were significantly different between the six LULC time series (Greenhouse-Geisser adjusted $F = 259.29$, $df = 2.34$, $p < 0.001$; Fig. 1). In the LULC 1985 time series, of the 311 species included, 149 species lost <30%, 122 species lost 30–50%, 39 species lost 50–80%, and one species lost >80% of their distributions, respectively (Supplementary Material 1). The cumulative habitat loss increased significantly in the species extant distributions modeled in the LULC 1993 time series (HSD: $p < 0.001$): 110 species lost <30%, 24 species increased losses from <30% to 30–50%, 15 species increased losses from 30 to 50% to 50–80%, and one species increased loss from 50–80% to >80% of their distributions. There was a significant difference between species extant distribution reductions between the LULC 1993 and LULC 2002 time series (HSD: $p < 0.001$): an additional 16 species lost >30%, and seven species increased losses from 30–50% to 50–80% of their distributions, respectively. There were no significant differences in species extant distribution modeled between the LULC 2002 and LULC 2007 time series, LULC 2007 and LULC 2011 time series, and LULC 2011 and LULC 2014 time series (HSD: $p = 0.214$; $p = 0.53$; and $p = 0.945$, respectively). In the LULC 2014 time series, only 84 species lost <30%, while 227 species (73% of the total, including 43 species of amphibians, 87 species of reptiles, 60 species of birds, and 37 species of mammals) lost >30% of their distributions: 160 species lost ≥30%, 65 species lost ≥50% and 2 species lost ≥80% of their distributions (Figs. 2 and 3). Overall, all endemic species of terrestrial vertebrates showed a reduction between the LULC 1985 and LULC 2014 in their species extant distributions. In particular, 92 species (including 15 species of amphibians, 32 species of reptiles, 31 species of birds, and 14 species of mammals), increased to a higher category of the percentage of distribution reduction due to habitat loss (Fig. 2).

When each terrestrial vertebrate group was analyzed separately (Fig. 1), a similar pattern of reduction in species extant distributions was observed. The highest habitat loss observed in the extant distributions was between the LULC 1985 and LULC 1993 time series, and between the LULC 1993 and LULC 2002 time series. No further significant reductions in species extant distributions were observed in the following LULC time series (Fig. 2). There were no significant differences in the reduction of species extant distributions in the LULC 2014 time series between the different groups of terrestrial vertebrates (species of amphibians: % of distribution reduction [Mean ± SD] = 40.56 ± 1.99, N = 62; species of reptiles: 40.49 ± 1.50, N = 117; species of birds: 35.14 ± 1.52, N = 80; species of mammals: 37.37 ± 2.25, N = 52; $F = 1.753$, $df = 3$, $p = 0.156$). Further, we observed no correlation between the habitat loss in species extant distributions and the area of species potential distribution in all LULC time series for all groups, and for each group of endemic species of terrestrial vertebrates ($p > 0.1$ in all cases).

Species distribution reductions due to habitat loss were significantly different between the ecoregions ($F = 124.088$, $df = 94$, $p < 0.001$). Species occurring in 49 ecoregions, most of them located in northern Mexico, including the ecoregions of the Great Plains, the North American Deserts and the Western Sierra Madre, and some ecoregions in the Southern Sierra Madre, showed an average of <30% of habitat loss in their distributions. Species occurring in the remaining 46 ecoregions showed an average of ≥30% habitat loss of their distributions (Figs. 3 and 4). The ecoregions where species showed a higher percentage of habitat loss in their distributions were the Transvolcanic Belt System, the Mexican High Plateau and the Gulf of Mexico Humid Coastal Plains and Hills, corresponding mainly to the Temperate Sierras, Southern Semi-Arid Highlands, and Tropical Humid Forests (INEGI, CONABIO, INE, 2008). In particular, species occurring in seven ecoregions lost on average ≥80% of their distributions (Figs. 3 and 4).

4. Discussion

We were able to analyze approximately one-third of all endemic species of terrestrial vertebrates. The endemic species of amphibians, reptiles, and mammals represented less than 35% of the total species of each group, while the endemic species of birds represented over 80% of this group. Given that most of the endemic species of terrestrial vertebrates have restricted distributions with a low number of point localities, we were not able to produce robust ecological niche models projected as species potential distributions (Pearson et al., 2007). Nonetheless, we feel that our study is adequate as the endemic species of terrestrial vertebrates included in it showed both national and ecoregional representations (Mayani-Parás et al., 2019).

Habitat loss is the main threat to biodiversity conservation worldwide (Crowther et al., 2015; Johnson et al., 2017) and this is the case for Mexico (SEMARNAT, 2016). For example, the cumulative habitat loss reached 13.7 million ha of natural habitats reductions over the last 50 years and has significantly reduced the area of most ecosystems and vegetation types, as well as reducing species distribution ranges (Sánchez-Cordero et al., 2005, 2009; Fuller et al., 2007; Botello et al., 2015a, 2015b). Temperate ecosystems, including montane cloud forest,

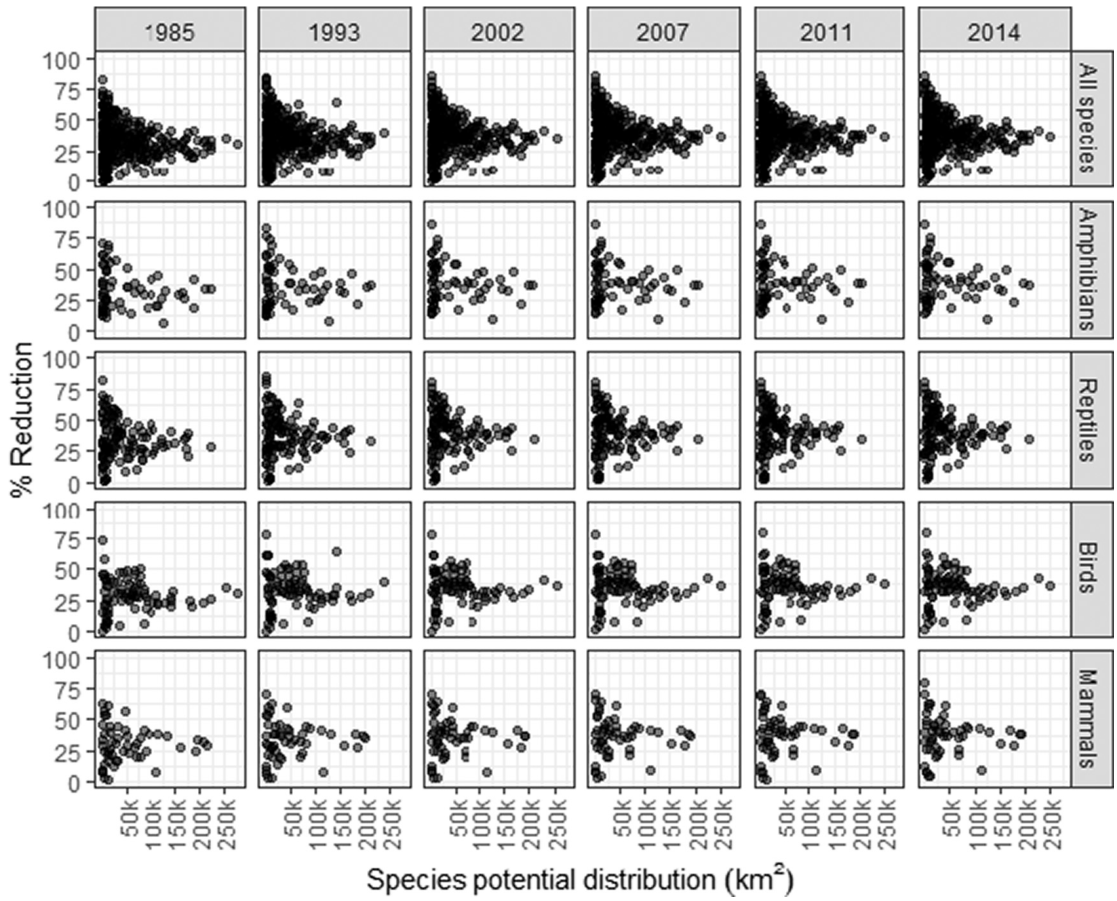

Fig. 1. Relationship between percentage of reduction in species distribution range due to cumulative habitat loss (Y-axis), and species potential distributions (X-axis) of all selected endemic terrestrial vertebrates, and in amphibians, reptiles, birds and mammals, respectively, in the LULC time series (1985, 1993, 2002, 2007, 2011, and 2014) of the INEGI.

oak, and pine forest and high-elevation tussock grasslands, among others, holding high species richness and endemicity of terrestrial vertebrates, showed habitat losses ranging from 30% to 80% of their area. Tropical ecosystems, including tropical rainforest, tropical deciduous forest, mangroves, and wetlands, among others, holding high species richness of terrestrial vertebrates, showed habitat losses ranging from 40% to 90% of their areas (Koleff et al., 2008; Conabio, 2014; SEMARNAT, 2016). Clearly, temperate and tropical ecosystems should have the highest priority for biodiversity conservation in Mexico (Brooks et al., 2002; Koleff et al., 2008; Conabio, 2014).

Our study focused on the spatio-temporal impact of cumulative habitat loss on individual species, using ecological niche modeling projected as species potential and extant distributions (Sánchez-Cordero et al., 2005; Botello et al., 2015a, 2015b). By quantifying habitat loss between different LULC time series, we were able to determine habitat loss trajectories projected in species extant distributions associated with increasing threats on their conservation. Our methodological approach relied on the assumption that ecological niche modeling projected as species potential distribution accurately reflected the real distribution of the endemic species of terrestrial vertebrates. We feel confident of the results as we chose only projected distributions of the endemic species that produced robust models according to published protocols (Liu et al., 2005, 2011; Merow et al., 2013; Soberon and Peterson, 2005). Further, this methodological approach can be applied for comparing our results with other studies elsewhere, as ecological niche modeling is widely used (Peterson et al., 2011). A potential shortcoming is that several endemic species of terrestrial vertebrates showed a low number of independent point occurrences, which can lead to biases or inaccuracies in their distributions, particularly at the ecoregional level (Soberon and Peterson, 2005; Merow et al., 2013). Another assumption in our methodological approach is that areas of habitat loss, including single-crop agriculture and livestock areas, urban areas, and bare soil in the LULC time series land use and vegetation classifications types of INEGI, are unsuitable habitats for the selected endemic species of terrestrial vertebrates to establish reproductive and permanent populations. Of course, there are endemic species of terrestrial vertebrates that occur in these transformed areas, but whether they successfully established reproductive and permanent resident populations in these transformed habitats is unknown for most species (Betts et al., 2019; Fahrig et al., 2019). Thus, we believe that it is more favorable for our conservation exercise to exclude these transformed habitats and adopt a more precautionary perspective in our methodological approach. We acknowledge that even if our methodological approach is incorrect, it does not harm the conservation status of the endemic species of terrestrial vertebrates included in this study (Sánchez-Cordero et al., 2005, 2009; Fuller et al., 2007; Botello et al., 2015a, 2015b).

Species extant distributions of endemic terrestrial vertebrates showed the highest proportion of habitat loss between the LULC 1985 and LULC 1993 time series, followed by the LULC 1993 and LULC 2002 time series (SEMARNAT, 2016) (Figs. 1 and 2). These LULC time periods coincided with high national habitat loss rates; 7.9 million ha of natural habitats were lost from 1970 to 1993, and 3 million ha of natural habitats were lost from 1993 to 2002 (SEMARNAT, 2016). In the following years, habitat loss decreased to lower rates reaching 855,000 ha between 2007 and 2011, partly as a consequence of more efficient Federal and State governments and NGOs policies to prevent deforestation providing sustainable environmental options for stakeholders and landowners, as payment for conserving biodiversity and forested areas

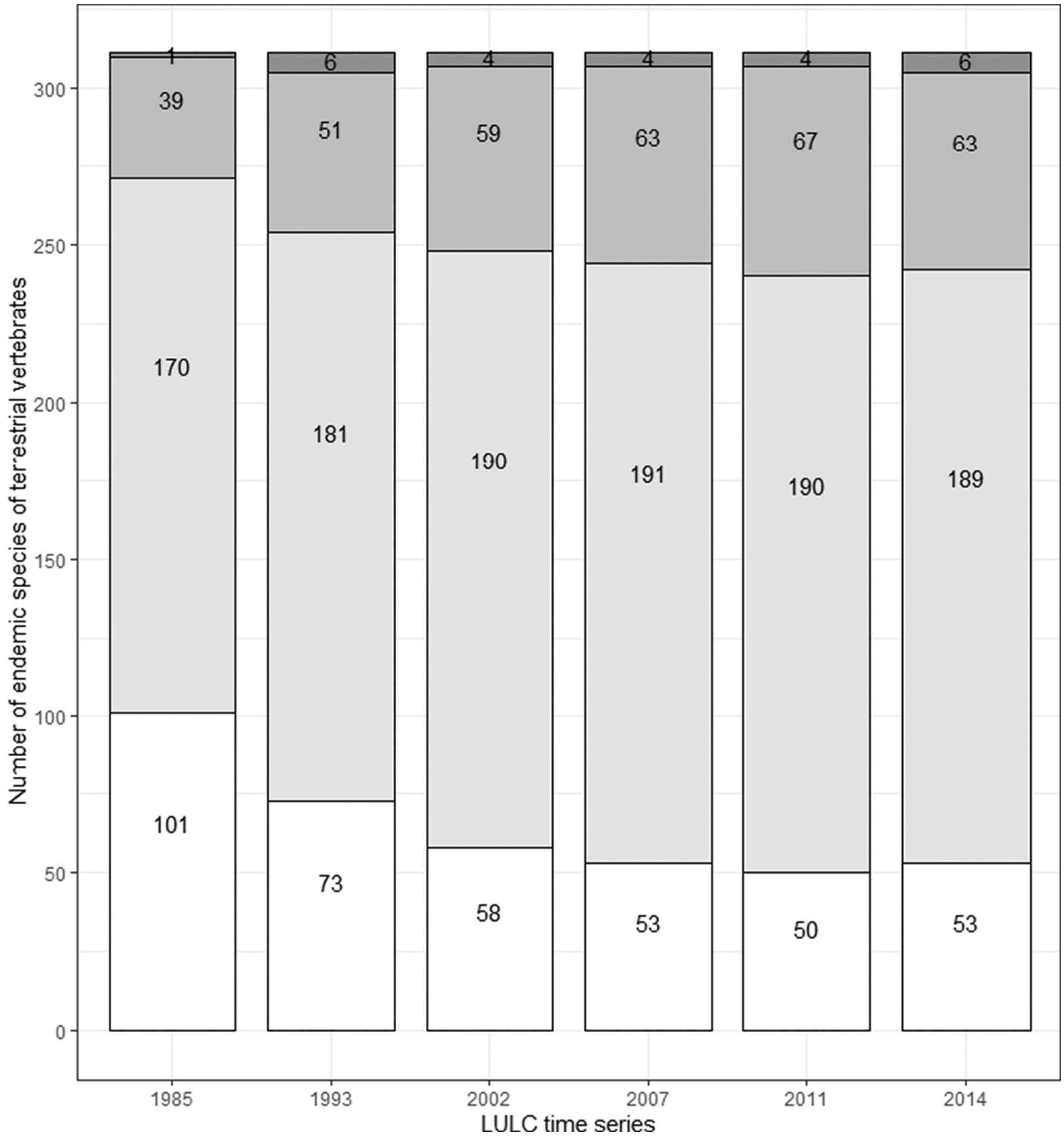

Fig. 2. Number of endemic species of terrestrial vertebrates included in our study, according to the species distribution range reduction (%) due to cumulative habitat loss, in the LULC time series of the INEGI. Color in bars corresponds to the percentage in species distribution range reduction: white <30%; light grey 30–50%, medium grey 50–80%, and dark grey >80%. Numbers in the color of bars correspond to the specific number of endemic species of terrestrial vertebrates (see Material and methods for details).

(Flores-Martínez et al., 2020). The decrease in habitat loss rates after the LULC 2002 time series resulted in a lower proportion of habitat loss in species extant distributions of endemic species of terrestrial vertebrates (Figs. 1 and 2). We observed significant differences in the proportion of habitat loss in species extant distributions of endemic terrestrial vertebrates between LULC 1985 and LULC 2014 time series. For example, 92 species, including 15 species of amphibians, 31 species of birds, 32 species of reptiles, and 14 species of mammals, showed a sufficiently high percentage of habitat loss in their distributions to increase conservation threats (Fig. 2). Moreover, our analyses were restricted to coarse-grained habitat loss in species extant distributions and did not include habitat fragmentation. It has been widely documented that habitat fragmentation is relevant affecting population persistence in small remaining habitat fragments (Betts et al., 2019; Fahrig et al., 2019; Morante-Filho et al., 2018). Thus, it is likely that areas identified as remnant natural habitat in our species extant distribution models included highly fragmented habitats that can lead to local population extirpations (Fig. 3). If so, our methodological approach is underestimating conservation threats of cumulative habitat loss on individual species of the selected endemic terrestrial vertebrates.

Moreover, habitat fragmentation can differentially affect endemic species of terrestrial vertebrates. For example, species showing a low dispersal ability or are habitat specialists are prone to be affected by high habitat fragmentation due to their limited mobility to disperse from one fragment to another. For example, some endemic species of salamanders, lizards, and rodents have either low mobility, are habitat specialists or both, making it difficult to move and adapt from one fragment to another (Hernández-Ordóñez et al., 2019; Anderson Arce-Peña et al., 2019; Russildi et al., 2016; Stuart et al., 2004; Beebee and Griffiths, 2005; Gibbs, 1998; Bowne and Bowers, 2004; Houlahan and Findlay, 2003; Mayani-Parás et al., 2019). This shortcoming in our study can be overcome by conducting detailed fieldwork on specific areas relating fragmentation (and size of fragments) and sampling permanent reproductive populations of endemic terrestrial vertebrate species

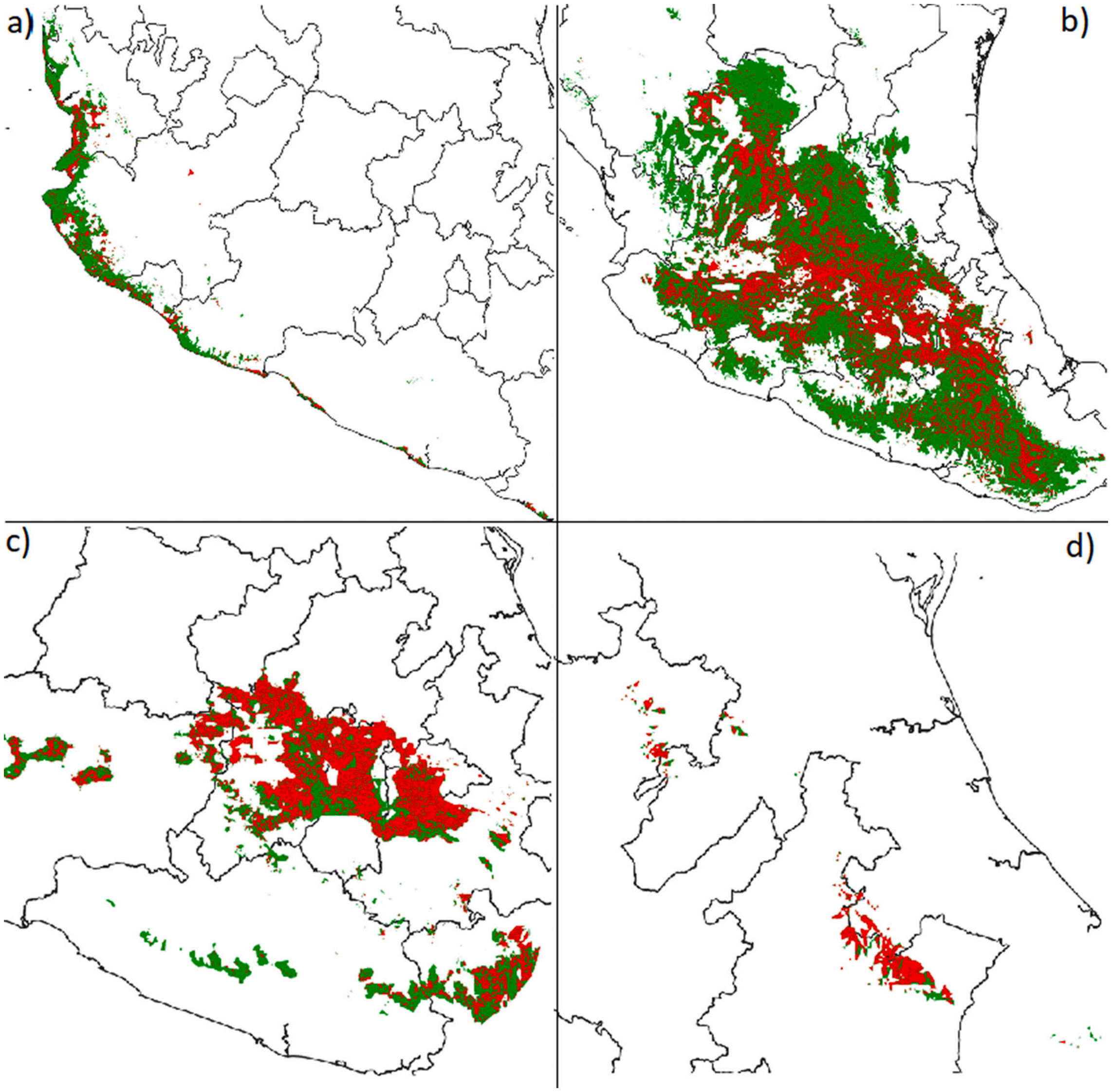

Fig. 3. Impact of regional cumulative habitat loss on four selected endemic species of terrestrial vertebrates included in the category as Least Concerned, according to the IUCN. (a) *Cyanocorax sanblasianus* (bird) showing <30%; (b*) Incilius occidentalis* (amphibian) showing 30–50%; (c) *Cratogeomys merriami* (mammal) showing 50–80%, and (d) *Lepidophyma sylvaticum* (reptile) showing >80% reduction in their distributions, respectively. Red color shows habitat loss in species potential distribution. Green color shows areas holding suitable remnant habitat, depicted as species extant distribution. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

inhabiting these fragments of suitable habitat (Fahrig et al., 2019). Our study can help to identify priority areas of endemic species of terrestrial vertebrates and then produced fine-grained habitat fragmentation maps of these areas for establishing field-sampling protocols.

The IUCN Red List criteria is a worldwide commonly used methodology for assigning species conservation status, and planning and establishing priorities to support species at risk (Rodrigues et al., 2006). The IUCN proposes assigning conservation status based on the percentage of loss in species distribution ranges in the last 10 years (Criterion A). According to the IUCN, only 78 of the endemic species of terrestrial vertebrate are at risk, while 222 species do not merit a risk category, and 11 species have not been evaluated or are under the Data Deficient (DD) category. With the data obtained in this study, if we strictly apply the IUCN Criterion A, that is, only including habitat loss in species extant distributions in the last 10 years (between the LULC 2002 and LULC 2014 time series), only 38 species would be considered at risk (18 vulnerable, 19 endangered and 1 critically endangered), while 222 species would not merit a risk category. Nonetheless, if we include the cumulative habitat loss in the species extant distributions of the LULC 2014 time series, the number of endemic species of terrestrial vertebrates under a risk category increased significantly. For example, one-third of the species lost <30% of their distribution and would not be considered at risk, while half of the species lost between 30% to 50% of their distribution and would be considered vulnerable, one-fourth of the species lost between 50% to 80% and would be considered endangered. Finally, 10% of species would be considered critically endangered since they lost >80% of their distributions (Figs. 2 and 3). In any case, our study raised concerns about the increased conservation threats of the selected endemic species of terrestrial vertebrates due to the cumulative habitat loss significantly reducing their distribution ranges (Figs. 1, 2, and 3).

There were important differences in the regional impact of cumulative habitat loss in species extant distributions. We observed that the percentage of remnant natural habitat loss in species extant distribution modeled in the LULC time series was independent of the species distribution range size. For example, species with small potential distributions could show either high or low reductions in their distributional ranges (Fig. 1). Thus, habitat loss in species potential distributions

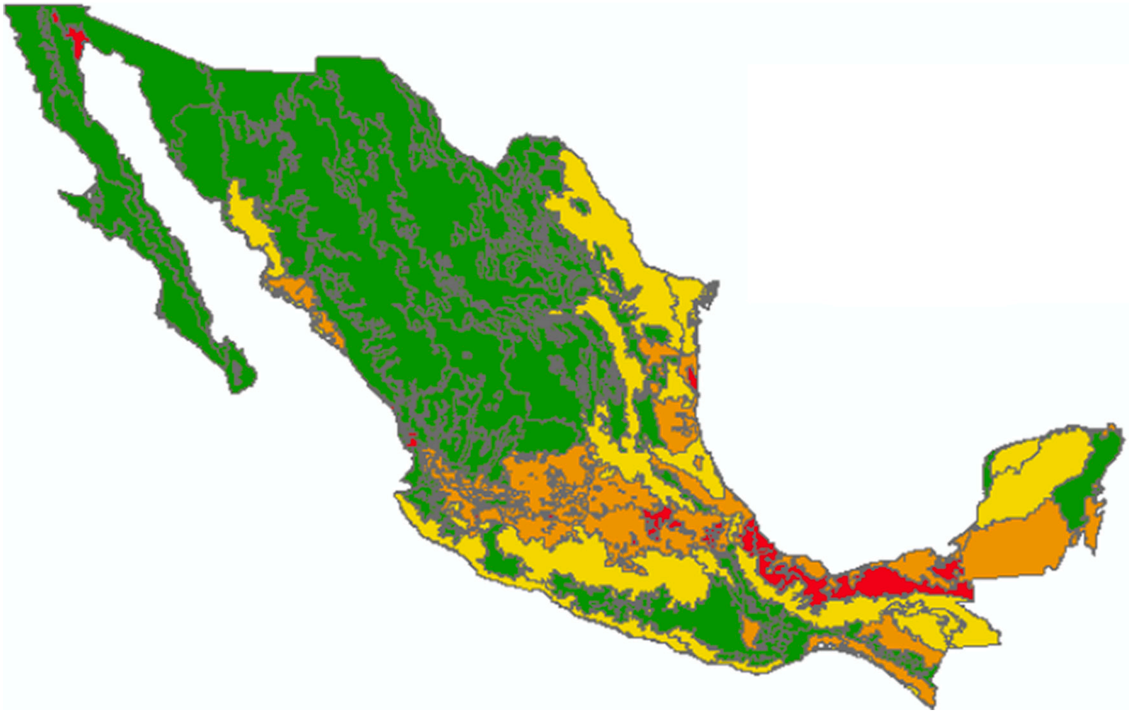

Fig. 4. Average reduction in species range distributions of selected endemic terrestrial vertebrates in ecoregions. Species losing <30% of their distributions (green ecoregions); Species losing 30–50% of their distributions (yellow ecoregions); Species losing 50–80% of their distributions (orange ecoregions), and species losing >80% of their distributions (red ecoregions). The source of names of the ecoregions is included in Methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

appeared to be related to the geographic locations of their distribution ranges in ecoregions, rather than to their distribution range sizes *per se* (Figs. 1 and 2) (Sánchez-Cordero et al., 2005; Fuller et al., 2007; Botello et al., 2015a, 2015b). Assessing habitat loss in species extant distributions in the ecoregions allowed to identify areas where species are most vulnerable, regardless of their distributional range size (Figs. 1 and 4). It appears that for endemic species of terrestrial vertebrates, the location on a particular ecoregion determined species conservation threats. Most of the selected endemic species of terrestrial vertebrates occurred in the Transvolcanic Belt System, followed by the Pacific Coast and Southern Mexico. These areas hold a complex topography and a great diversity of ecosystems (Rzedowski, 1986; Sarukhán et al., 2009), holding high species endemicity (Peterson and Navarro, 2000; Fuller et al., 2007). However, these areas coincided with ecoregions showing high cumulative habitat loss as the Transvolcanic Belt System and the Mexican High Plateau, followed by the Gulf of Mexico Humid Coastal Plains and Hills. Endemic species of terrestrial vertebrates occurring in these ecoregions have lost on average > 50% of their distribution (Fig. 4). It is likely that other faunistic and floristic groups occurring in these ecoregions show similar species conservation threats. The IUCN Red List includes only 84 endemic species of vertebrates of Mexico, but our analyses showed that at least 237 species should be carefully reviewed for consideration in their conservation status. Further, at an ecoregion level, endemic species of terrestrial vertebrates occurring in the ecoregions with high cumulative habitat loss should be considered as critically endangered, in spite of their risk assignment at the national level (Fig. 4). In sum, the cumulative impact of habitat loss should be considered when determining species conservation threats both regionally and nationwide.

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CRediT authorship contribution statement

Fernando Mayani-Parás: Conceptualization, data curation, data analyses, writing draft; **Francisco Botello**: Conceptualization, writing draft; **Saúl Castañeda**: Data curation, and Data analyses; **Mariana Munguía-Carrara**: Writing draft; **Víctor Sánchez-Cordero**: Conceptualization, supervision, and writing draft.

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.

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