

Response of the endangered tropical dry forests to climate change and the role of Mexican Protected Areas for their conservation

DAVID A. PRIETO-TORRES¹, ADOLFO G. NAVARRO-SIGÜENZA²,
DIEGO SANTIAGO-ALARCON³ and OCTAVIO R. ROJAS-SOTO¹

¹Red de Biología Evolutiva, Instituto de Ecología, A.C., Laboratorio de Biogeografía, carretera antigua a Coatepec No. 351, El Haya, Xalapa, Veracruz 91070, México, ²Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-399, México D. F. 04510, México, ³Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C., Laboratorio de Ecología de Vertebrados e Interacciones Parasitarias, carretera antigua a Coatepec No 351, El Haya, Xalapa, Veracruz 91070, México

Abstract

Assuming that co-distributed species are exposed to similar environmental conditions, ecological niche models (ENMs) of bird and plant species inhabiting tropical dry forests (TDFs) in Mexico were developed to evaluate future projections of their distribution for the years 2050 and 2070. We used ENM-based predictions and climatic data for two Global Climate Models, considering two Representative Concentration Pathway scenarios (RCP4.5/RCP8.5). We also evaluated the effects of habitat loss and the importance of the Mexican system of protected areas (PAs) on the projected models for a more detailed prediction of TDFs and to identify hot spots that require conservation actions. We identified four major distributional areas: the main one located along the Pacific Coast (from Sonora to Chiapas, including the Cape and Bajío regions, and the Balsas river basin), and three isolated areas: the Yucatán peninsula, central Veracruz, and southern Tamaulipas. When considering the effect of habitat loss, a significant reduction (~61%) of the TDFs predicted area occurred, whereas climate-change models suggested (in comparison with the present distribution model) an increase in area of 3.0–10.0% and 3.0–9.0% for 2050 and 2070, respectively. In future scenarios, TDFs will occupy areas above its current average elevational distribution that are outside of its present geographical range. Our findings show that TDFs may persist in Mexican territory until the middle of the XXI century; however, the challenges about long-term conservation are partially addressed (only 7% unaffected within the Mexican network of PAs) with the current Mexican PAs network. Based on our ENM approach, we suggest that a combination of models of species inhabiting present TDFs and taking into account change scenarios represent an invaluable tool to create new PAs and ecological corridors, as a response to the increasing levels of habitat destruction and the effects of climate change on this ecosystem.

Keywords: ecological niche modeling, ecosystems, global climate change, MaxEnt, tropical dry forests

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Introduction

Increasing evidence indicates that the distribution and survival of species, and the ecosystems they inhabit, are affected by climatic change (Root *et al.*, 2003). Rapid increases in temperature and the rate of habitat destruction could easily disrupt connectedness among habitats, leading to their eventual disappearance or potential species extinctions (Parmesan & Yohe, 2003; Root *et al.*, 2003). Thus, forecasting changes in the distribution of threatened species and/or habitats in future scenarios is relevant for conservation practices (Still *et al.*, 1999; Marini *et al.*, 2009; Rebelo *et al.*, 2010). Recent studies have analyzed the potential impact of

climate change on global biodiversity by extrapolating the climate distributional envelopes of current species to future climate scenarios, ultimately raising concerns regarding future changes in the geographical ranges of species, especially those inhabiting mountain biomes (e.g. Huntley *et al.*, 2004; Rebelo *et al.*, 2010; Golicher *et al.*, 2012; Rojas-Soto *et al.*, 2012).

Under climate-change scenarios, species' populations could move from their original ranges to new unoccupied locations, assuming that they are able to track their preferred climatic niches that would change in geographical space over time (Tingley *et al.*, 2009; Sinervo *et al.*, 2010; Feeley *et al.*, 2012; Golicher *et al.*, 2012). However, this dynamic process could also generate local extinctions and highly fragmented populations, particularly for species with low dispersal capacities

Correspondence: Octavio R. Rojas-Soto, tel. +52 (228) 842 1800 ext. 3021, fax +52 (228) 818 7809, e-mail: octavio.rojas@inecol.mx

(Thomas *et al.*, 2004; Rebelo *et al.*, 2010). The way in which a species copes with changes in its environment depends on its natural history, including certain determining characteristics such as the size of its geographic range, dispersal capacity, reproductive rates, and its degree of specialized habitat requirements (Isaac *et al.*, 2009; Feeley *et al.*, 2012). However, given the limited time and financial resources for conserving and managing biodiversity on a species-by-species basis, it is necessary to focus our attention on the conservation of entire ecosystems in order to maintain their ecological integrity (Olden, 2001; Fera & Peterson, 2002; Tylianakis *et al.*, 2010).

Recently, ecological niche modeling (ENM) has increasingly been used to predict ecosystem distributions over time – considering the effects of climate change – based on mapping the location of climatically suitable areas. However, considering that species and ecosystems, as well as their spatial configuration throughout their distribution, are not static in time (Krebs, 1985; Mayer & Rietkerk, 2004; Jentsch, 2007); the community-based modeling of species represents an alternative approach to the statistical analysis of species co-occurrence in environmental space. This approach can help to define biological units or ecosystems by considering the individual requirements and response of each species to local climatic conditions, in order to find ways to make a more efficient use of limited resources (Graham & Dilcher, 1995; Fera & Peterson, 2002; Ferrier *et al.*, 2002; Araújo & Luoto, 2007; Rojas-Soto *et al.*, 2012; Distler *et al.*, 2015). Community-level modeling combines the distributions from several species (i.e. a species model sum) to produce maps of the spatial pattern of biodiversity distribution (Ferrier & Guisan, 2006). It is implicit that statistical patterns of co-occurrence among species capture meaningful biotic interactions that may play an important role in shaping species distributions (Guisan & Zimmermann, 2000; Anderson *et al.*, 2002; Ferrier & Guisan, 2006; Araújo & Luoto, 2007). This perspective is based on the assumption that abiotic factors and biotic interactions have an effect on species and populations at macro- and microecological scales, respectively; thus, the distribution of a particular ecosystem may be reconstructed at a large geographical scale (above 1 km²) using environmental variables (Araújo & Luoto, 2007; Rojas-Soto *et al.*, 2012; Distler *et al.*, 2015), providing a useful basis for modeling community and ecosystem dynamics (Anderson *et al.*, 2002; Fera & Peterson, 2002; Rojas-Soto *et al.*, 2012).

Our study aims at forecasting potential changes on a globally threatened ecosystem, the tropical dry forests (TDFs; Miles *et al.*, 2006; Sanchez-Azofeifa *et al.*, 2013). Neotropical TDFs are found from northwestern Mexico

to northern Argentina and southwestern Brazil, varying in the size of their extent due to high rates of land transformation, degradation, and fragmentation (Pennington *et al.*, 2009; Linares-Palomino *et al.*, 2011). In the Mesoamerican region, TDFs occur in lowlands along the Pacific slope of Mexico and Northern Central America, stretching more or less continuously from southern Sonora (Mexico) to Guanacaste (Costa Rica), and along the Mexican Gulf Coast in more isolated and discontinuous areas (Trejo & Dirzo, 2000; Pennington *et al.*, 2009; Linares-Palomino *et al.*, 2011). Based on recent reviews of biodiversity patterns and conservation priorities, Mesoamerican TDFs are recognized as a terrestrial ecosystem with high levels of species richness, endemism, and habitat specialization (García-Trejo & Navarro-Sigüenza, 2004; García-Marmolejo *et al.*, 2008; Ceballos *et al.*, 2010; Ríos-Muñoz & Navarro-Sigüenza, 2012). Despite the available information on the distribution of TDFs, their conservation status is precarious, as only 5.7% of their current extent is conserved within protected areas (Miles *et al.*, 2006; Sanchez-Azofeifa *et al.*, 2013). Moreover, a large proportion of Neotropical TDFs are at risk due to the impacts of human population growth (e.g. deforestation and land conversion for agriculture) and climate change (Sanchez-Azofeifa *et al.*, 2005; Miles *et al.*, 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Meir & Pennington, 2011; Collevatti *et al.*, 2013).

Given the diversity of TDFs (see Pennington *et al.*, 2009), the potential impact of climate change on this ecosystem is likely to be regionally different (see Meir & Pennington, 2011; Collevatti *et al.*, 2013). Therefore, the goal of this study was to forecast future distributional changes of Mexican TDFs, in order to understand how the geographic distribution of these threatened ecosystems may respond to climate change – considering that ecosystems are not static – in a local scale, and to propose the creation of dynamic protected areas (DPAs) as future conservation strategies. To achieve this goal, we applied a community-level approach to reconstruct the ecological niche models of 30 species of plants and birds associated with TDFs, assuming that species, particularly those that are ecologically restricted, share similar ecological requirements. Subsequently, we projected this reconstruction under climate-change scenarios for the years 2050 and 2070 provided by the Intergovernmental Panel on Climate Change (IPCC, 2013). Finally, considering possible synergistic effects of climate change and anthropogenic impacts, we included as additional analyses the future effects of current land uses and the existing Mexican PAs on the distribution of TDFs, to identify TDFs hot spots that require immediate conservation action.

Materials and methods

Study area

Rather than limiting our study to a single definition of tropical dry forest, our analysis intends to examine the extent of tropical dry forests in a broad sense. We took into account main bioclimatic and phenological characteristics as indicated by several authors (Murphy & Lugo, 1986; Gentry, 1995; Graham & Dilcher, 1995; Sanchez-Azofeifa *et al.*, 2005, 2009). For this study, TDFs are broadly defined as ecosystems typically dominated by deciduous trees (> 50%), existing in regions with a mean annual temperature > 25 °C, a total annual precipitation between 700 and 2000 mm, and with the presence of three or more dry months every year (Sanchez-Azofeifa *et al.*, 2005).

In Mexico, TDFs encompass several vegetation categories, including seasonal and semiseasonal low tropical forest (*selvas baja caducifolia y subcaducifolia*), seasonal and semiseasonal medium tropical forest (*selva mediana caducifolia y subcaducifolia*), and thorny tropical forest (*selvas espinosas*) (Rzedowski, 1978, 1979, 1990; Trejo, 1998; Trejo & Dirzo, 2000; INEGI, 2003, 2013; Challenger & Soberón, 2008; Ceballos *et al.*, 2010; Pérez-García *et al.*, 2012), as well as the complex landscape matrix of associated vegetation types to TDFs such as coastlines, gallery forests, mangroves, and agriculture land (Sanchez-Azofeifa *et al.*, 2009). The available information suggests that Mexican TDFs are spread from their northernmost distributional limit of approximately 29°N in Sonora to the Guatemalan border in the south (Fig. 1), forming a nearly continuous strip with the

largest areas located in western Jalisco and the Santiago and Balsas rivers basins. On the Mexican Gulf coast (or Mexico's Atlantic watershed), these forests are present in more isolated and discontinuous areas in southern Tamaulipas, central Veracruz, and the Yucatán peninsula. Their spatial distribution is characterized by a heterogeneous matrix of different topographic, aspect, climatic, and edaphic conditions (Rzedowski, 1978, 1979). Accordingly, TDFs in Mexico exhibit a considerable spatial variation in structure and plant species composition. Thus, we define TDFs by the deciduousness of their trees, the general physiognomy described above, and their climatic affinities (Trejo, 1999; Trejo & Dirzo, 2000).

Species and occurrence records

We used 30 species – 15 birds and 15 plants – considered to be ecologically associated and dominant species of Mexican TDFs (Rzedowski, 1978, 1979; Linares-Palomino *et al.*, 2011; Pérez-García *et al.*, 2012; Ríos-Muñoz & Navarro-Sigüenza, 2012). Species with two contrasting life forms were included in the case of plants (i.e. trees vs. shrubs) and birds belonging to different trophic guilds (e.g. granivorous, insectivorous, etc.). Also, for both groups, we selected species with dissimilar geographical distributions patterns: those endemics to Mexico or Mesoamerica, those possessing a larger Neotropical distribution, and species that are phylogenetically unrelated (Table 1).

Specimen locality records per species were gathered from the following three sources: (i) collection records available for

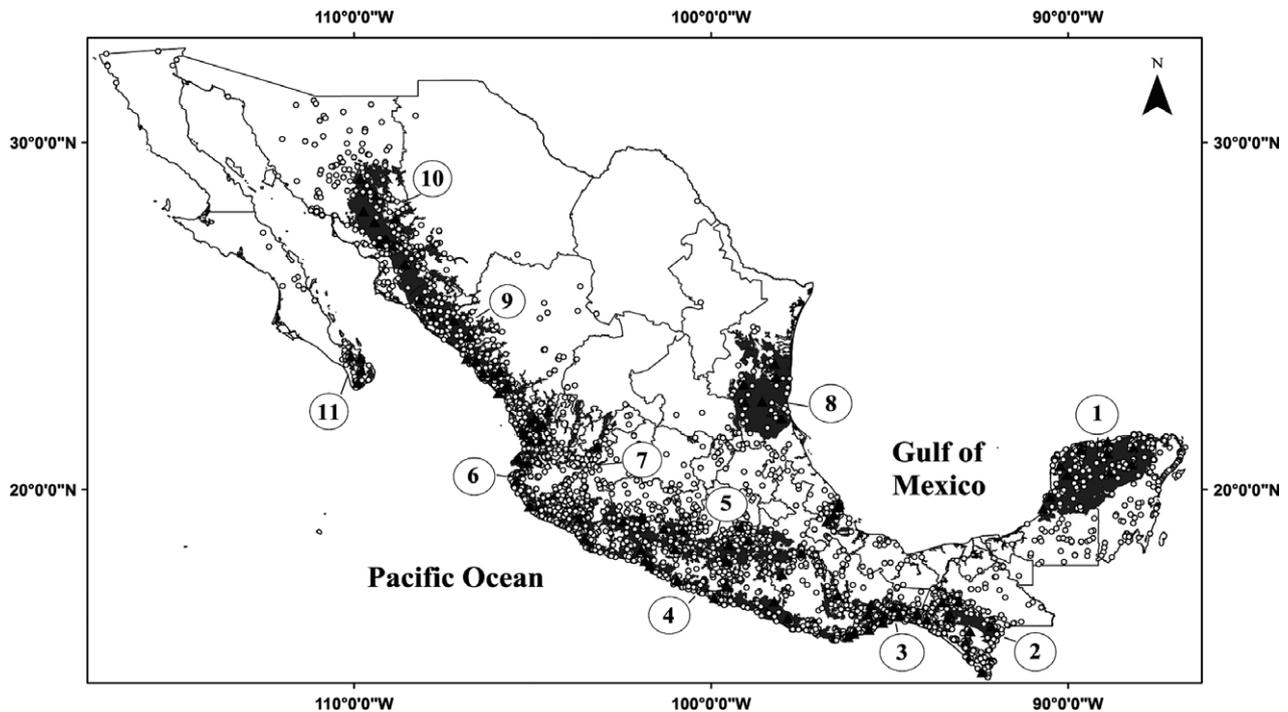


Fig. 1 Unique locality records used for species model performance (white dots). Primary TDFs (gray shading) and known localities of TDFs (black triangles) in Mexico were used to evaluate ENMs of species for the TDFs reconstruction. Numbers correspond to areas: Yucatán forests (1), Chiapas forests (2), Centro American Pacific forests (3), Pacific South forests (4), Balsas river basin forests (5), Jalisco forest (6), Bajío forests (7), Tamaulipas-Veracruz forests (8), Sinaloa forests (9), Sonora forests (10), and Cape forests (11).

Table 1 Species modeled and used for tropical dry forests reconstruction in Mexico. Families and species were assigned according to: IOC World Bird List (Gill & Donsker, 2015), APG III (APG, 2009), and The Plant List (2013)

Species	Records	Habits/life form	Distribution
Birds			
Trochilidae			
<i>Amazilia rutila</i>	1082	Nectarivorous	Mesoamerica
<i>Heliomaster constantii</i>	460	Nectarivorous	Mesoamerica
Caprimulgidae			
<i>Antrostomus ridgwayi</i>	106	Insectivorous	Mesoamerica
<i>Nyctiphrynus mcleodii</i>	30	Insectivorous	Mexico
Cracidae			
<i>Orlatis poliocephala</i>	521	Frugivorous	Mexico
Corvidae			
<i>Calocitta colliei</i>	531	Frugivorous- Insectivorous	Mexico
Passerellidae			
<i>Peucaea humeralis</i>	243	Granivorous	Mexico
<i>P. ruficauda</i>	966	Granivorous	Mesoamerica
Poliophtilidae			
<i>Poliophtila albiloris</i>	576	Insectivorous	Mesoamerica
<i>P. nigriceps</i>	280	Insectivorous	Mexico
Tyrannidae			
<i>Deltarhynchus flammulatus</i>	48	Insectivorous	Mexico
Picidae			
<i>Melanerpes chrysogenys</i>	1092	Insectivorous	Mexico
Psittacidae			
<i>Eupsittula canicularis</i>	924	Frugivorous- Granivorous	Mesoamerica
Strigidae			
<i>Megascops guatemalae</i>	209	Carnivores	Neotropical
<i>M. seductus</i>	44	Carnivores	Mexico
Plants			
Anacardiaceae			
<i>Amphipterygium adstringens</i> (Schltdl.) Standl.	103	Tree	Mexico
Bixaceae			
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	130	Tree	Mexico
Burseraceae			
<i>Bursera fagaroides</i> (Kunth) Engl.	255	Shrub	Mexico
Concolulaceae			
<i>Ipomoea wolcottiana</i> Rose	28	Tree	Mexico
Euphorbiaceae			
<i>Jatropha cordata</i> (Ortega) Müll.Arg.	65	Shrub	Mexico
Fabaceae			
<i>Acacia cochliacantha</i> (Willd.)	277	Shrub	Mexico
<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	109	Tree	Neotropical
<i>Haematoxylum brasiletto</i> H.Karst.	112	Tree	Mesoamerica
<i>Lysiloma divaricatum</i> (Jacq.) J.C. Macbr.	249	Tree	Mesoamerica
<i>L. watsonii</i> Rose	25	Shrub	Mexico
<i>Senna atomaria</i> (L.) H.S. Irwin & Barneby	304	Tree	Mesoamerica
Meliaceae			
<i>Swietenia humilis</i> Zucc.	45	Tree	Mesoamerica
<i>Trichilia hirta</i> L.	119	Tree	Neotropical
Rhamnaceae			
<i>Ziziphus amole</i> (Sessé & Moc.) M.C. Johnst	106	Shrub	Mexico
Rutaceae			
<i>Zanthoxylum fagara</i> (L.) Sarg.	108	Tree	Neotropical

specimens from the ornithological and botanical collections worldwide (see Appendix S1); (ii) the Atlas of the Birds of Mexico (Navarro-Sigüenza *et al.*, 2002, 2003); and (iii) records obtained from fieldwork (only for birds). For both groups of species, records repeated in multiple sources were removed and only unique information of localities was used: all doubtful and ambiguous localities (i.e. information that could not be verified) were omitted. Through this process, a total of 9244 unique occurrence data points (i.e. geographic localities where the species are known to occur) were assembled for the construction of the ecological niche models (Table 1; Fig. 1).

Ecological niche modeling

We obtained ENMs for each of the selected species using MAXENT version 3.3.3k (Phillips *et al.*, 2006), which uses the principle of maximum entropy to calculate the most likely distribution for each species considering two data inputs: localities where each species has been recorded (presence-only data) and digital layers of the climatic variables (Elith *et al.*, 2006, 2011). To characterize the ecological niches, we downloaded interpolated climate data (at 30''-resolution: ~1 km² cell size) from the WorldClim project, which includes a set of 19 climatic variables (Hijmans *et al.*, 2005).

Models were generated using a random sampling of 70% of the locality records as training data and the remaining 30% for model evaluation (testing data). In addition, we ran 1,000 iterations with no extrapolation, to avoid artificial extrapolations from extreme values of the ecological variables (Stohlgren *et al.*, 2001; Elith *et al.*, 2011). All other parameters in MaxEnt were maintained at default settings. We used the logistic response to obtain digital maps containing the values for habitat suitability (continuous probability from 0 to 1; Phillips *et al.*, 2006). The maps obtained were subsequently converted into binary presence-absence data based on the 'fixed omission value 5' (FOV5) threshold value. This threshold can be ecologically interpreted as the identification of pixels predicted to be at least as suitable as pixels where species presence has been previously recorded, rejecting only the 5% of presence records in the model (Pearson *et al.*, 2006; Jiménez-Valverde & Lobo, 2007). For our purposes, this threshold allows us to evaluate species and TDFs distribution by minimizing commission errors in the binary maps.

We evaluated the performance of the MaxEnt model by calculating the commission and omission error values (Anderson *et al.*, 2003), the area under the curve (AUC) of the receiver-operating characteristic (ROC) curve (Elith *et al.*, 2006, 2011), as well as the partial ROC curves test (Peterson *et al.*, 2008). This later criterion is used to solve problems associated with the AUC, avoiding an inappropriate weighing of the omission and commission components of the analysis (Lobo *et al.*, 2008). We calculated partial AUCs using the Tool for Partial-ROC V. 1.0. (Barve, 2008) with 30% of the original data for independent model evaluation and presented the partial ROC results as the ratio of the AUC model to the null expectation ('AUC ratio') following the proposals of Peterson *et al.* (2008, 2011).

Reconstruction of tropical dry forests and spatial analysis

Because there are different degrees of disturbance and human-related modification of the natural environment, the potential TDFs distribution map obtained (hereafter 'modeled TDFs') from the overlap of individual ENMs of species, was compared with the natural vegetation map (hereafter 'primary TDFs map'; INEGI 2003); the later depicts primary forests as the vegetation of certain areas that share similar environmental conditions without human-related modification (INEGI, 2003; see metadata information [<http://www.inegi.org.mx/geo/contenidos/metadatos/ntm.aspx>] for more input on the map). The primary TDFs map was stored in an ASCII 'raster' format and imported to ArcMap 10.0 (ESRI, 2010), with the same pixel size of the environmental layers (~1 km²).

Performance in predicting TDFs distribution was evaluated in terms of omission (underprediction) and commission (overprediction) errors using two approaches (Rojas-Soto *et al.*, 2012): (i) considering the sums of the species models per pixel (adding one model at a time) and its correspondence with the primary TDFs map, and (ii) comparing the distribution of the modeled TDFs with the distribution of 100 TDFs localities that were independently verified (i.e. distinct to different from localities used for individual species modeling) and obtained from collections, herbaria, literature, and fieldwork (Table S1). For this last approach, the coincidence between the modeled TDFs prediction and the independent TDFs' localities was represented in an ecological two-dimensional space using the most important environmental variables identified by a principal component analysis (PCA, results not shown) of the 19 climatic variables for the dataset of the 9244 unique localities (Fig. 1; Table 1) and the Jackknife test calculated by MaxEnt (Table S2). The PCA was performed using SPSS v. 19 for Windows (Nie *et al.*, 1975; Noruésis, 2011).

Finally, we established a decision threshold value above which model outputs were considered as potential TDFs. A set rule does not exist to determine such thresholds because the selection depends on the dataset used and the goals of the analysis. Thus, we assessed the distributional limits based on the proposal of Prieto-Torres and Rojas-Soto (*submit.*), calculating the total prediction percentage (% Prediction = [modeled TDFs / primary TDFs] × 100) and the prediction percentage of independent localities in the two-dimensional space (i.e. the minimum number of species predicted by pixel that coincide with the independent TDFs' localities). Based on these analyses, we decided to use the values equal to or greater than the combination of 10 species models (regardless of species identity), as the threshold for defining the Mexican TDFs distribution, which predicted 78% of the areas on the primary TDFs map and 98% of independently verified TDFs' localities for the present scenario (see Results).

The TDFs distributional areas for current and future projections were calculated (in pixels) for four sets of species models (10, 15, 20, and 25 species combined). Also, we calculated the mean and range of elevation for the geographical TDFs' distribution for each set of species models. In addition, information regarding current land use from INEGI (2013) and the extent of natural protected areas (CONANP, 2011) was projected onto the maps. The vectorial data of vegetation and

current land use maps (scale of 1 : 250 000) of INEGI (2013) were generated from photointerpretation of satellite images Landsat TM5 (from 2011). This procedure was supported and validated with fieldwork performed during 2012, and it included the information on location, distribution, and extent of different plant communities (including intact and modified areas) and agricultural uses (see metadata information [<http://www.inegi.org.mx/geo/contenidos/metadatos/ntm.aspx>] for more information about the maps). To assess the effect of deforestation, we only considered natural (intact) forest, whereas disturbed areas (urban areas, deforested areas, farming areas, and pastureland for cattle ranching) were not included (INEGI, 2013).

Scenarios of future global climate change

In ENM algorithms, the relative magnitude of environmental variables derived from one training dataset can be 'projected' to another set of environmental data, which enables the modeling of species distribution under different climate conditions, such as future climate simulations (VanDerWal *et al.*, 2009; Gasner *et al.*, 2010; Golicher *et al.*, 2012). Despite the potential problems associated with the use of global climate-change scenarios at local scales, ENMs have been widely used for studying the effects of future climate change on species and ecosystem distributions, as they represent alternative future scenarios and demonstrate the potential threats to species of conservation concern (Araújo & Luoto, 2007; Ponce-Reyes *et al.*, 2012; Rojas-Soto *et al.*, 2012; Bedia *et al.*, 2013).

With the goal of predicting general future tendencies, we evaluated the possible conservation impacts of climate change for the Mexican TDFs based on two Representative Concentration Pathway scenarios (RCP 4.5/ RCP 8.5; IPCC, 2013), which were downloaded from the WorldClim website (http://www.worldclim.org/cmip5_30s) as digital layers based on the same bioclimatic variables used to generate the species distribution models. The climatic models used herein represent two moderate scenarios of emissions for different greenhouse gases (e.g. CO₂, methane, nitrous oxide, etc.), which serve as proxies for a wide range of scientific and socioeconomic data, such as population growth, air pollution, land use types, and energy sources (Van Vuuren *et al.*, 2011; IPCC, 2013). The RCP 8.5 is the scenario with the highest predicted greenhouse gas emissions compared with RCP 4.5. Although both assume an increasing human population, RCP 8.5 shows a relatively slow income growth and modest improvements in technology and energy intensity use; this leads to a higher demand for energy derived from fossil fuels and increasing greenhouse gas emissions in the long term, considering an absence of climate-change mitigation policies (Riahi *et al.*, 2011; IPCC, 2013). Thus, our results under this scenario may be interpreted as pessimistic.

For each scenario, we used climate projections from global climate models (GCMs) developed by two different approaches: (i) Commonwealth Scientific and Industrial Research Organization and Bureau of Meteorology (ACCESS 1.0) and (ii) Model for Interdisciplinary Research On Climate (MIROC5). These two approaches show improvements in the

estimation of precipitation values, zonal-mean atmospheric fields, equatorial ocean subsurface fields, and the simulation of El Niño-Southern Oscillation (see Watanabe *et al.*, 2010; Bi *et al.*, 2013). We predicted the persistence of TDFs ecological niche in 2050 and 2070 and generated two maps representing the potential distribution of Mexican TDFs, under the RCP4.5 (optimistic) and RCP8.5 (pessimistic) scenarios, for each year. Eight consensus maps were obtained for the modeled forecasts for every plant and bird species (for the 2 years, the two scenarios, and the two approaches). However, due to limited space, only ACCESS 1.0 RCP 4.5 and RCP 8.5 maps are shown here as an example (interested readers can directly request the additional maps from the corresponding authors).

Finally, shifts in the relationships between the probability of TDFs occurrence for each combination of models (occurrence probability or 'OP') and elevation were explored by comparing the centroids of the scatter plots of pixels. The TDFs' occurrence probabilities of 'n' combined models were calculated following the formula: OP = predicted area as TDFs/ modeled area. As the data from the suitability probabilities were strictly bounded, the variance was nonconstant and errors were non-normal. We fitted generalized linear models (GLMs) for proportion data to assess the variable of elevation among scenarios, along with a two-parameter logistic function that is the equivalent of an analysis of covariance with binomial errors (Crawley, 2007). GLMs analyses were conducted with the R software (R-Core-Team, 2012) using the mgcv library.

Results

Species models and TDFs reconstruction

We obtained 30 models that predicted the potential geographic distribution of each species based on environmental variables that define the ecological niche boundaries (Table S2). All ENMs generated for the selected species showed high values for the AUC test (0.926–0.990) and AUC ratios (1.23–1.93; $P < 0.01$), with a mean omission rate of only 4.65% (Table S2), indicating that the models of the species' ecological niches were adequate.

The overlaps of the individual species maps were used to create consensus TDF maps with a gradient of geographic predictions, which varied according to the number of species used for the reconstructions (Fig. 2a). These reconstructions matched the primary TDFs map (Fig. 1) and identified four major regions holding important TDF extents: a continuous strip along the Pacific coast, from Sonora to Chiapas (including the Cape region in southern Baja California, the Bajío region and the Balsas river basin in central Mexico), and three discontinuous areas in the Yucatán peninsula, central Veracruz, and southern Tamaulipas. We observed that omission errors increased when the number of modeled species increased, without any

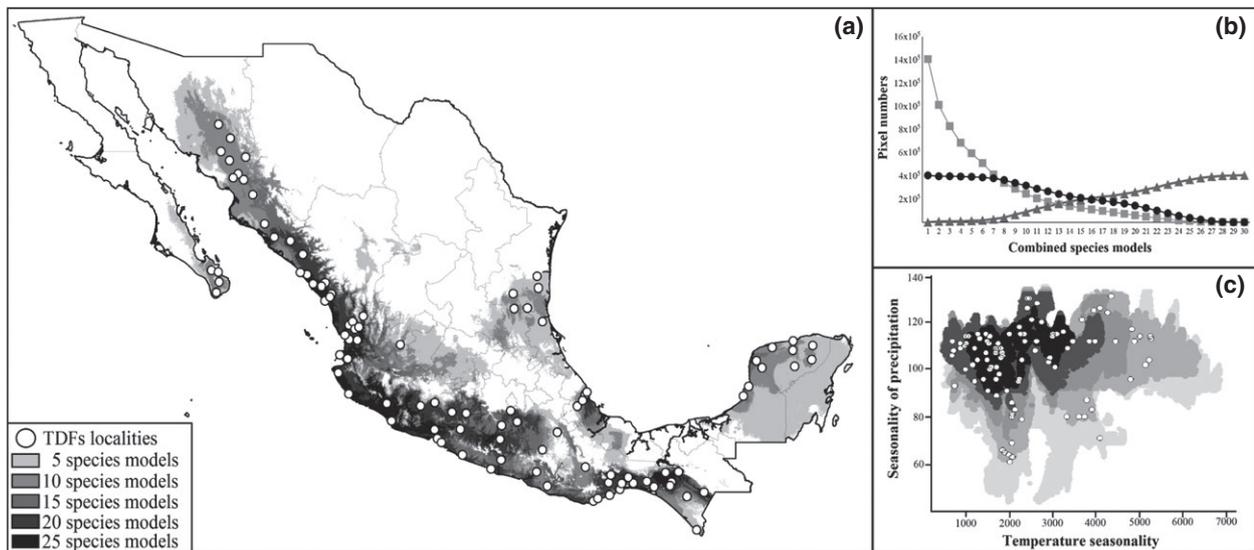


Fig. 2 Consensus maps of TDFs in Mexico obtained by the sum of the predicted ENM's maps of the modeled species. (a) Map of Mexican TDFs reconstruction with accumulation of modeled species. (b) Number of pixels evaluated on the basis of TDFs ranges predicted by the sum of species sets (circles), including the omission values (triangles) and commission values (squares) for each set. (c) Two-dimensional ecological comparison (seasonality of precipitation [coefficient of variation] vs. temperature seasonality [standard deviation *100]) of modeled TDFs for species groupings. White dots represent the known TDF localities used for evaluation.

asymptote in the trend line (Fig. 2b). The opposite pattern was observed for commission errors, which decreased with increasing number of species (Fig. 2b). This generalization was independent of the set of species used by pixel to reconstruct the TDFs distribution maps. Our comparison of TDFs prediction with the 100 independently verified localities, using the two-dimensional perspective, showed that 50% of the localities were predicted with the sum of the ENMs of 25 species, 69% with the sum of 20 models, 98% with the sum of 10 models, and 100% of the localities with the sum of 5 models (Fig. 2c).

We observed that percentage of predicted primary TDFs tends to decrease as the number of predicted species' models increases, with ~96% of areas predicted with the sum of 5 species models, ~78% with the sum of 10 models, ~52% with 15 models, and < 36% when we using 20 or more species models. However, based on comparison with surrounding ecosystems (Chalenger & Soberón, 2008), we observed that the proportion of modeled area obtained corresponding to TDFs increases when the number of combined species' models also increases, resulting in a smooth change in the slope from the overlap of 10 species (regardless of species identity; Fig. S1). These results suggest that although the combination of more models predicts smaller TDFs areas (Fig. S1a), such areas are more ecologically related to our understanding of TDFs, and at the same time indicate the existence of ecotones around its borders (Prieto-Torres & Rojas-Soto *submit*; Fig. S1b,

c). Taken together, we established a threshold of the combination of ≥ 10 species models per pixel to predict the TDFs distribution, which is also the point at which commission values fall below the predicted pixel values for TDFs. Furthermore, omission and commission values reach equilibrium (i.e. their trend lines cross) at approximately 13 species models (Fig. 2b).

Models projecting Mexican TDFs showed areas of overprediction, particularly in the northern part along the Cape Region (Baja California), the Sonora-Sinaloa region, the Bajío Region, and the southern Pacific Coast (Fig. 2a). However, based on the overlap with other ecosystems (mainly temperate forests [$\sim 22\%$]; Fig. S1b, c), this result implies similar climatic conditions at their ecotones; hence, we consider that this combination of models represents both an effective alternative to defining distributional association patterns and probable species exchanges among ecosystems (Prieto-Torres & Rojas-Soto *submit*; see Discussion).

Impacts of deforestation and PAs on the potential TDFs' distribution

Predicted and remnant areas of the potential distribution model of TDFs located within protected areas throughout Mexico are detailed in Table 2. The modeled area included fragments of natural forests within protected areas ($\sim 50\,000\text{ km}^2$), resulting in an important reduction of $\sim 91\%$ of the original ecological niche model (Table 2). Intensive deforestation and land

Table 2 Current and projected distribution of tropical dry forests (TDFs) in Mexico. Results are shown based on MaxEnt algorithm for current and two climate-change scenarios (RCP 4.5 y RCP 8.5), two approaches (ACCESS and MIROC5), and considering four sets of species (10, 15, 20, and 25; see 'Methods'). For each combination, the data correspond to the predicted TDFs extent (number of pixels), proportion of vanishing TDFs, intact TDFs (proportion), TDFs extent (proportion) included in the currently PAs, and mean elevation (m above sea level)

Approach	Climate-change scenario	Set of species	TDFs extent	% Predicted primary TDFs*	Prop. vanishing TDFs†	Intact area (proportion)‡	TDFs extent in protected areas		Elevation
							Modeled area (proportion)	Intact area (proportion)	
Current		10	561 721	78.06	–	243 973 (0.43)	49 778 (0.09)	30 752 (0.06)	730 (0–2857)
		15	335 275	51.99	–	134 871 (0.40)	33 008 (0.10)	19 923 (0.06)	726 (0–2800)
		20	204 058	35.49	–	77 433 (0.38)	19 543 (0.10)	11 277 (0.06)	634 (0–2800)
		25	47 503	9.53	–	16 769 (0.35)	5972 (0.13)	3483 (0.07)	523 (0–2205)
2050									
ACCESS	RCP 4.5	10	595 874	70.09	0.06	278 572 (0.47)	56 182 (0.09)	34818 (0.06)	881 (0–2930)
		15	306 464	44.14	–0.09	136 627 (0.42)	29 484 (0.10)	17 920 (0.06)	818 (0–2800)
		20	143 769	23.66	–0.30●	59 303 (0.41)	16 549 (0.12)	10 098 (0.07)	668 (0–2573)
		25	20 714	3.58	–0.56●●	11 612 (0.38)	4443 (0.21)	2910 (0.14)	488 (0–1820)
	RCP 8.5	10	656 017	67.57	0.17	291 693 (0.44)	64 695 (0.10)	38 984 (0.06)	994 (0–3097)
		15	339 447	40.27	0.01	150 832 (0.44)	35 437 (0.10)	21 404 (0.06)	954 (0–2800)
		20	158 842	21.90	–0.22●	65 912 (0.41)	19 133 (0.12)	11 583 (0.07)	807 (0–2800)
		25	26 853	4.41	–0.43●●	9556 (0.36)	3654 (0.14)	1983 (0.07)	682 (0–2283)
MIROC5	RCP 4.5	10	594 471	71.00	0.06	263 162 (0.44)	57 644 (0.10)	33 977 (0.06)	855 (0–2800)
		15	329 156	44.04	–0.02	139 336 (0.42)	32 355 (0.10)	19 209 (0.06)	859 (0–2800)
		20	187 005	27.11	–0.08●	76 435 (0.41)	20 880 (0.11)	12 583 (0.07)	765 (0–2800)
		25	38 921	6.69	–0.18●●	14 711 (0.38)	45 782 (0.15)	3452 (0.09)	654 (0–2573)
	RCP 8.5	10	565 799	66.33	0.01	242 422 (0.43)	53 003 (0.09)	30 886 (0.05)	933 (0–2873)
		15	321 391	41.97	0.04	138 188 (0.43)	31 653 (0.10)	18 975 (0.06)	888 (0–2800)
		20	180 664	25.91	–0.11●	73 536 (0.41)	19 903 (0.11)	11 825 (0.07)	794 (0–2800)
		25	36 098	5.95	–0.24●●	13 043 (0.36)	5068 (0.14)	2909 (0.08)	753 (0–2573)
2070									
ACCESS	RCP 4.5	10	638 089	66.58	0.14	291 478 (0.46)	65 434 (0.10)	40 981 (0.06)	963 (0–2939)
		15	324 469	42.24	–0.03	144 181 (0.44)	32 657 (0.10)	19 430 (0.06)	901 (0–2800)
		20	154 178	23.44	–0.24■	62 359 (0.40)	17 407 (0.11)	10 355 (0.07)	789 (0–2573)
		25	26 339	4.66	–0.45■	9439 (0.67)	4084 (0.16)	2274 (0.09)	607 (0–2400)
	RCP 8.5	10	591 483	45.42	0.05	267 960 (0.45)	55 248 (0.09)	33 556 (0.06)	1264 (0–3097)
		15	278 395	28.40	–0.17	127 788 (0.46)	30 239 (0.11)	18 469 (0.07)	1083 (0–2800)
		20	112 795	14.39	–0.45■	48 624 (0.43)	15 220 (0.13)	9239 (0.08)	861 (0–2800)
		25	14 302	1.66	–0.70■	6264 (0.44)	3828 (0.27)	2344 (0.16)	607 (0–2300)
MIROC5	RCP 4.5	10	602 713	71.48	0.07	268 030 (0.44)	57 648 (0.10)	34 424 (0.06)	881 (0–2939)
		15	318 215	42.62	–0.05	139 273 (0.44)	31 175 (0.10)	18 837 (0.06)	850 (0–2800)
		20	164 806	23.99	–0.19■	66 854 (0.41)	18 378 (0.11)	10 927 (0.07)	766 (0–2573)
		25	26 690	4.51	–0.44■	9646 (0.36)	4004 (0.15)	2183 (0.08)	692 (0–2400)
	RCP 8.5	10	552 613	50.39	–0.02	248 847 (0.45)	52 300 (0.09)	30 605 (0.06)	1157 (0–3017)
		15	323 900	35.48	–0.03	143 895 (0.44)	32 511 (0.10)	19 105 (0.06)	1015 (0–2800)
		20	174 063	21.37	–0.15■	74 054 (0.43)	20 494 (0.12)	12 312 (0.07)	891 (0–2800)
		25	27 518	3.27	–0.42■	10 113 (0.37)	4436 (0.16)	2533 (0.09)	916 (0–2800)

*% Predicted Primary TDFs show the coincidence among the current TDFs' distribution and the projections across the years.

†Propo. Vanishing TDFs: Bold numbers indicated the increase on average of distribution area for the 2050 (3.0–10.0%) and 2070 (3.0–9.0%) projections using 10 species sets. Black symbols represent the average percentage of the TDFs area that will be lost for years 2050 (points) and 2070 (square) when using sets of 20 (one symbol) and 25 (two symbols) species.

‡Intact Area: Bold numbers represent the TDFs extent predicted to survive or remain intact given the current land use practices and protected areas system.

use changes reduced ~61% of the predicted potential geographic range of TDFs, which is particularly severe in the Yucatán peninsula, Chiapas, the last fragment of Centro American Pacific forest (corresponding to southern Mexico), Mexican Pacific lowlands, Balsas forests, Jalisco, and Bajío Regions. Overall, an important reduction of 94% of the area for the TDFs' distribution model was identified when the effect of deforestation was combined with the exclusion of forest remnants located beyond PAs boundaries (Table 2). Remarkably, ~84% of intact forested areas (intact) predicted by the model were located outside the limits of PAs.

Scenarios of future global climate change

The projection and sum of the ENMs of all 30 species for the 2050 and 2070 climate-change scenarios showed that the current distribution of TDFs would be significantly modified (including its transitional areas [ecotones]). The two climate-change scenarios are similar in their predicted qualitative patterns, although the pes-

simistic scenario predicts larger increases in TDFs distribution. In general, the TDFs located in the northern portion of the Sonoran and Cape Region, the southern Pacific Coast, and the Balsas Region will tend to reduce their area (Fig. 3). In contrast, we observed TDFs to increase in area and relocate into new and higher areas for the years 2050 and 2070 in the Tamaulipas-Veracruz region and the Yucatán peninsula (reduced for the 2070, Fig. 3c, d). We found that in future scenarios, the suitable areas predicted by models tend to significantly increase in elevation (Fig. 4). On average, there is a shift over ~200 m in elevation between the range of the present scenario (730 ± 589 m) and the two climate-change scenarios (ACCESS 2050 = 937 ± 664 m; ACCESS 2070 = 1113 ± 659 m; Fig. 4).

Table 2 shows the current and future predictions based on MaxEnt under RCP 4.5 and RCP 8.5 climate-change scenarios, as well as the synergistic effects of climate change and deforestation. The following patterns emerge from these predictions when TDFs species were modeled: (i) the coincidence between current TDFs'

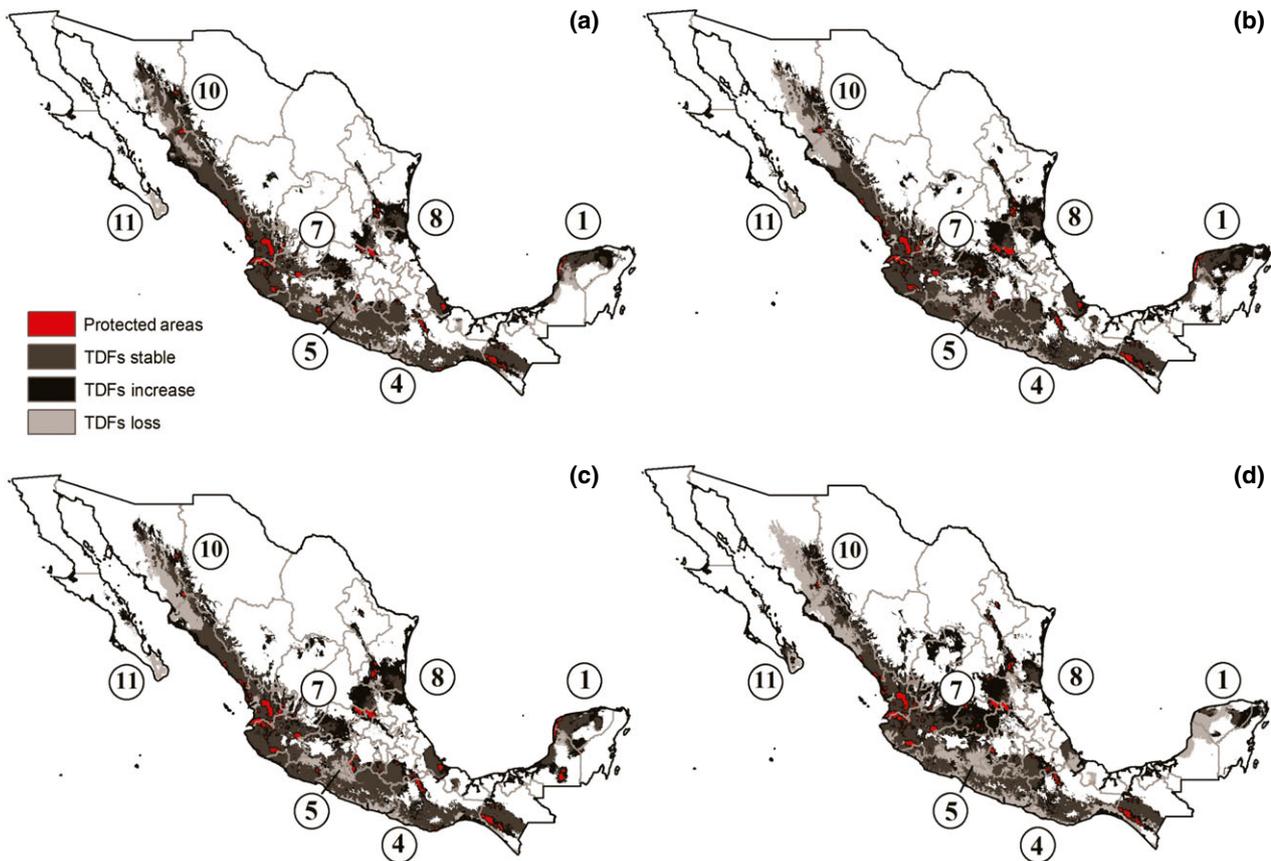


Fig. 3 Mexican TDFs area projected to 2050 (a,b) and 2070 (c,d) under RCP 4.5 (a–c) and RCP 8.5 (b–d) future climatic scenarios by MaxEnt with the ACCESS 1.0 global climate model for the 30 modeled species. In both scenarios, we observed a reduction in the predicted geographic distribution for Mexican TDFs in the Yucatán (1), Pacific South (4), Balsas river basin (5), Tamaulipas-Veracruz (8), Sinaloa (10), and Cape (11) forests. Important modifications (increase or displacement) in the distribution of TDFs were observed for the forests of Yucatán (1, which will be reduced for the 2070 year; Bajío (7); and Tamaulipas-Veracruz (8) forests).

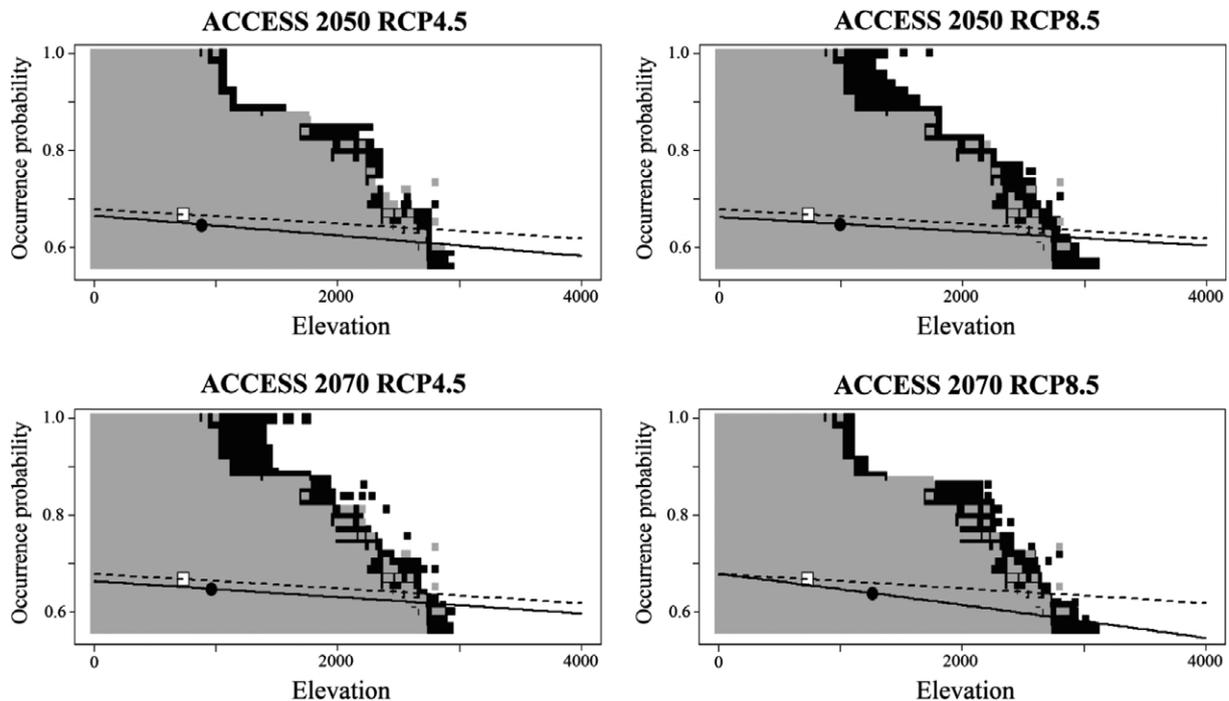


Fig. 4 Generalized linear models and scatter plots for elevation and occurrence probability (current [gray] and future [black]) TDFs distribution for climate-change scenarios (ACCESS 1.0 2050 and 2070). Centroids and linearized coefficients for the scatter data are represented for the current distribution (square and dotted line) and future scenarios (circles and solid line). Regression models for occurrence probability (OP) follow a two-parameter logistic function: $y = \frac{e^{a+bx}}{1+e^{a+bx}}$; whereas linearized coefficients ($a+bx$) for the present scenario were (OP) = $0.7432 - 0.00006629$ (elevation), ACCESS 2050 RCP 4.5 (OP) = $0.6815 - 0.00008805$ (elevation), ACCESS 2050 RCP 8.5 (OP) = $0.6702 - 0.0000632$ (elevation), ACCESS 2070 RCP 4.5 (OP) = $0.6748 + 0.00007144$ (elevation), and ACCESS 2070 RCP 8.5 (OP) = $0.7447 - 0.000014$ (elevation). In both scenarios, we observed that TDFs will move toward higher elevations, occupying higher areas above the average of current elevational distribution (see also Table 2).

distribution and future projections tended to decrease with time; (ii) TDFs distribution area will increase by 3.0–10.0% by 2050 and 3.0–9.0% by 2070 on average, when we used scenarios modeled with MAXENT and sets of 10 species; (iii) TDFs will be reduced by ~18–35% (2050) and 26–50% (2070) in areas under scenarios modeled using sets of 20 and 25 species, respectively; (iv) in general, TDFs will occupy higher regions above the current average elevational distribution, in particular along the northern portion of the Sonora and Sinaloa region (Figs 3 and 4); and (v) out of the TDFs extent predicted to survive, only 42% will remain intact given current land use practices (anything except conserved natural forest; INEGI, 2013) and only ~7.0% will remain under protection (Table 2; Fig. S2).

Discussion

Prediction of ecosystem shifts based on the ecological niches of species

Ecological niche modeling has increasingly been used to predict potential species distributions and effects of

climate change over time on the geographical ranges of species (Hannah *et al.*, 2007). Applications of ENMs for conservation purposes are frequently based on mapping the location of climatically suitable areas into the future (Hannah *et al.*, 2007) or investigating the historical distribution of ecosystems by modeling entire vegetation communities or biomes (Werneck *et al.*, 2011, 2012). However, attempts to forecast the distribution of entire ecosystem based on randomly chosen training points of pre-established ecosystem boundaries may produce misleading results due to the potential mismatch between individual species distributions and ecosystem boundaries (Woodward *et al.*, 2004; Collevatti *et al.*, 2013). The dominant species normally used to define vegetation types may also occur in other communities. Thus, the auto-ecological niche of species could be a more appropriate approach in an ecosystem context (Rojas-Soto *et al.*, 2012; Collevatti *et al.*, 2013) because it considers the individual requirements and response of each species to local climatic conditions (Graham & Dilcher, 1995; Guisan & Zimmermann, 2000; Feria & Peterson, 2002; Huntley *et al.*, 2004).

In this study, we modeled the distribution of Mexican TDFs using a limited number of bioclimatic variables and a set of 30 co-distributed TDF's plants and birds. Our approach includes the assumption, to some extent, that species share similar ecological requirements, particularly those that are ecologically restricted (Feria & Peterson, 2002; Ferrier & Guisan, 2006; Araújo & Luoto, 2007; Rojas-Soto *et al.*, 2012), and that communities and ecosystems are not static in either time or in space (Krebs, 1985; Mayer & Rietkerk, 2004; Jentsch, 2007). The obtained results showed different accumulation patterns for species' models throughout the geographic and ecological space, which supports the idea that communities comprise species groups that change gradually from one place to another (Krebs, 1985; Jentsch, 2007). This dynamic spatial-temporal process of species accumulation patterns is potentially explained by diverse evolutionary histories in different geographic regions (Thompson, 2005; Distler *et al.*, 2015).

The estimation of the Mexican TDFs' extent based on the 10 species threshold showed overprediction (commission errors) when we considered the pre-established limits from the primary TDFs map. However, the overlap observed among the compared ecosystems (Fig. S1) indicated that there are transitional areas along the TDFs borders with its neighboring vegetation, especially with temperate forest and xerophyte scrub forest, suggesting that there is likely a larger climatic expanse that would support TDFs than previously reported. These transitional areas are important because they might encompass the individual responses of each modeled species to ranges of temperature and precipitation values along the ecotones. Our models considered communities to be associations of interacting species, where natural borders in transitional areas between ecosystems are fuzzy. Thus, the dynamic response of species under current and future distributional association patterns must be considered to maintain functional processes in ecosystems (Tylianakis *et al.*, 2010; Rojas-Soto *et al.*, 2012). Such an approach will aid in the efforts to prioritize conservation areas, thereby providing projections on species' adaptive responses across environments (Smith *et al.*, 2001; Araújo, 2002; Distler *et al.*, 2015).

Impacts of deforestation and PAs

We recognize that many different approaches may exist for the interpretation of the current extent of tropical dry forests (Sanchez-Azofeifa *et al.*, 2009). Although a thorough discussion on the precision and errors associated to the INEGI (2013) map used or the deforestation analysis is beyond the scope of this study, we contend

that using this information provides testable predictions in the reconstruction of the current distribution of this ecosystem at the geographical scale used. Our results showed similar tendencies of reduction as has been reported in previous works about land cover and conservation in Mexican and Neotropical TDFs (e.g. Trejo & Dirzo, 2000; Castillo *et al.*, 2005; Miles *et al.*, 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sanchez-Azofeifa *et al.*, 2013). Thus, we consider that our results can contribute to developing more efficient strategies of conservation and management.

The main lesson emerging from our results is that environmentally suitable areas for TDFs will be reduced, mainly due to the deforestation and expansion of the agricultural frontier (Trejo & Dirzo, 2000; Castillo *et al.*, 2005; Miles *et al.*, 2006; Sanchez-Azofeifa *et al.*, 2009; Portillo-Quintero & Sánchez-Azofeifa, 2010). The TDFs have been the preferred zones for agriculture and human settlement in Mesoamerica, the Caribbean, and South America (Murphy & Lugo, 1986; Miles *et al.*, 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sanchez-Azofeifa *et al.*, 2013) and are among the most heavily utilized, disturbed, and least conserved of the large tropical ecosystems (Sanchez-Azofeifa *et al.*, 2005, 2009). In the year 1990, only 27% of Mexico's original TDF land cover remained intact as conserved mature or secondary forest, and in certain regions nearly 60–71% of the original vegetation has been lost due to agriculture and cattle ranching (Trejo & Dirzo, 2000; Castillo *et al.*, 2005; Sanchez-Azofeifa *et al.*, 2009; Portillo-Quintero & Sánchez-Azofeifa, 2010). These land uses and modification rates may be particularly severe for TDFs' species, where anthropogenic activities (i.e. agricultural practices, presence of roads, urban settlements) may create barriers that prevent species movement, reducing connectivity between predicted distribution areas (Ochoa-Gaona & González-Espinosa, 2000; Trejo & Dirzo, 2000; Challenger & Soberón, 2008). Moreover, such factors can have strong effects on pollinator foraging patterns, as well as on plant–pollinator interactions, and plant reproduction (e.g. Quesada *et al.*, 2009). Our results support Janzen's original contention that TDFs are the most threatened major tropical habitats (Janzen, 1988), where mitigation measures are required to slow down the ongoing erosion of biodiversity (Miles *et al.*, 2006; Maass *et al.*, 2010; Sanchez-Azofeifa *et al.*, 2013).

The PAs have been a main instrument of ecosystem conservation and have contributed to stopping ecosystem degradation and to maintaining essential ecological processes (Hannah *et al.*, 2007; Ceballos *et al.*, 2010; Maass *et al.*, 2010). However, it is important that the current Mexican PA system may be insufficient to stop these degradation processes (Figueroa & Sánchez-Cordero, 2008). We observed only ~10% (~6% of intact

areas) of the potential distribution area of TDFs (Table 2) under a protected category (whether federal, state, municipal, social, or private), which showed pronounced gaps in TDFs protection. Additionally, it is important to note that PAs are also subject to multiple threats, being vulnerable to the management of their surrounding areas and even within the same PA due to human populations living within its borders (Maass *et al.*, 2010). Thus, the management of PAs must also extend to the wide area of influence and incorporate not only the conservation focal sites, but also surrounding areas under a social scope that considers restoration and sustainable development, for instance, the 'Ejidos' Conservation Areas' (Castillo *et al.*, 2005; Maass *et al.*, 2010).

Promoting the creation of new protected areas and ecological corridors within fragmented dry forest landscapes, and engaging local communities in sustainable dry forest management initiatives should be more seriously considered as a high priority measure for the mitigation of overall tropical deforestation (Castillo *et al.*, 2005; Maass *et al.*, 2010; Portillo-Quintero & Sánchez-Azofeifa, 2010). Investing in efforts to identify priority areas for conservation are needed in order to increase regional connectivity among PAs and to permit the tracking of changes in species' habitats (Hannah *et al.*, 2007; Ceballos *et al.*, 2010). Our study can serve as a starting point for improving the protection of Mexican TDFs; in particular, considering the TDFs strip along the Pacific coast, where anthropogenic pressures in lowland areas are strong (Trejo & Dirzo, 2000). Maintaining the current protection of TDFs that are currently located in PAs (Fig. 3), the TDFs areas most at risk from human activity and with high biodiversity values (hot spots) should be assigned the highest priority for future conservation efforts (Bezaury-Creel *et al.*, 2009; Ceballos *et al.*, 2010).

Scenario of future global climate change

When considering the effect of climate change, the climatically suitable areas for TDFs distribution will increase in both area (3.0–10.0% by 2050 and 3.0–9.0% by 2070 [Table 2]) and elevation (shifting over ~200 m above the average of current elevational distribution; Fig. 4). Our model projections are consistent with previously observed trends for the predicted migrations of communities to higher elevations (Villers-Ruiz & Trejo, 1997, 1998). These results reinforce the widely accepted idea that significant changes in the ranges of mountain biota will occur during the twenty-first century due to climate change (Villers-Ruiz & Trejo, 1997; Nogués-Bravo *et al.*, 2007; Gasner *et al.*, 2010; Forero-Medina *et al.*, 2011). Previous studies have predicted that at least 13% of the temperate forests in Mexico will be lost

due the effects of climate change, where, for example, migrations (ca. 200 m uplift from the current average) of cloud forest are forecasted for higher elevations (Villers-Ruiz & Trejo, 1997, 1998; Ponce-Reyes *et al.*, 2012; Rojas-Soto *et al.*, 2012).

We predicted the future disappearance of TDFs in regions such as the Cape and Balsas river basin regions (with highest elevation of 700–900 m), where an increase in temperature combined with a reduction in precipitation could increase the length of the dry season (Villers-Ruiz & Trejo, 1997; Golicher *et al.*, 2012), which is the key factor in determining the distribution of TDFs and xerophyte scrub forests (Trejo, 1998, 1999). Humidity is the key limiting factor of TDFs due to their geographical position because humidity is retained in the surrounding high mountains (Trejo, 1998). Thus, TDFs species will be pushed toward higher elevations to track their climatic niches, which could produce local extinctions or drastic contractions in the distribution of habitat specialists such as *Ortalis poliocephala* (Peterson *et al.*, 2002), and lizards of the genus *Sceloporus* (Reptilia: Phrynosomatidae) (Sinervo *et al.*, 2010), as cited in two studied examples.

It is very difficult to know how species will respond to climates that do not exist at present because the impacts on reproductive success and successful colonization depend on many factors, such as the size of its geographic range, dispersal capacity, reproductive rates, and its degree of specialized habitat requirements (Isaac *et al.*, 2009; Feeley *et al.*, 2012). Peterson *et al.* (2002) showed that under different assumptions of dispersal ability, the species' distributional areas expand and contract with different frequencies: under the assumption of no dispersal ability, the numbers of species suffering extreme reductions in their distributional areas (closed to 90%) are higher. Thus, as the species will respond in an independent manner to climate change, we can assume that under new climates, some species will be able to persist and extend their distributions, some others might experience drastic reductions (increasing their extinction risk), and some others could remain unaffected (Peterson *et al.*, 2001, 2002; Sinervo *et al.*, 2010; Feeley *et al.*, 2012).

Colonization in response to climate change is evident with directional changes in species' compositions over time (Bush *et al.*, 2004; Pennington *et al.*, 2009; Urrego *et al.*, 2010; Werneck *et al.*, 2011, Werneck *et al.*, 2012). For instance, lowland species may slowly become more abundant at higher elevations, while highland species may decrease in abundance or disappear altogether in response to global warming (Bush *et al.*, 2004; Urrego *et al.*, 2010). Recent studies for modern tropical plant communities have shown

consistent and directional changes in the composition of tree species, where the relative abundance of lowland species has increased in most plots at higher elevations (Sinervo *et al.*, 2010; Feeley *et al.*, 2011a,b; Feeley, 2012). Taken altogether, it is suggested that many tropical species are potentially shifting their geographic distributions in response to increases in temperature, but it remains unknown whether species will be capable of moving fast enough to keep pace with current and future climate changes (Sinervo *et al.*, 2010; Feeley *et al.*, 2012). The current existence of segregated TDFs in higher elevations (above 1800 m asl) in the states of Querétaro, Nayarit, Oaxaca, and Puebla (Pérez-García *et al.*, 2012) provides support to the elevational shift for this biome, given that different variants of this vegetation type show particular physiological and phenological adaptations allowing them to be resilient to changes in soil moisture (Trejo, 1999; Thuiller *et al.*, 2004).

Finally, it is important to note that although we observed matching among individual species models and their projections, this tends to decrease in the future (particularly when sets of ≤ 15 species were modeled [Table 2]). These results show that the specific impacts of climate change on TDFs are not uniform across its distribution and illustrate the differing magnitude of effects that may be expected for the richness values of particular regions. Previous studies in Mesoamerican ecosystems showed that both temperature (increase) and precipitation values (decrease) could lead to a widespread reduction of current potential species richness (Peterson *et al.*, 2002; Golicher *et al.*, 2012). Although extinctions and drastic range reductions in Mexico are predicted to be relatively few (mainly in the Chihuahuan desert and northwestern coastal plain), species turnover in some local communities, such as southern Oaxaca and in the Cape region, is predicted to be high at $\sim 40\%$ (Peterson *et al.*, 2002; Sinervo *et al.*, 2010; Golicher *et al.*, 2012). It is expected that as climatic conditions change, new natural communities with unknown ecological properties may arise (Peterson *et al.*, 2002; Sinervo *et al.*, 2010; Golicher *et al.*, 2012). For instance, Correa-Metrio *et al.* (2012) showed that despite apparent strong resilience of vegetation in lowland Central America to pulses of temperature during the last 86 000 years, novel plant associations emerged parallel with exceptionally high rates of ecological change. Thus, to protect the biodiversity of TDFs, future conservation efforts should concentrate on identifying new conservation areas (or ecological corridors) that consider the likely future environmental changes, including potential transitional areas with the surrounding ecosystems, in an effort to avoid species extinctions and to conserve the

ecological integrity of ecosystems (Araújo, 2002; Hannah *et al.*, 2007; Tylianakis *et al.*, 2010; Collevatti *et al.*, 2013).

Final considerations

PAs are a useful conservation tool as a response to climate change; however, there is a major need to upgrade PAs under a dynamic approach that considers future scenarios in order to respond to changing distributional patterns and increasing levels of habitat destruction (Dudley & Parish, 2006; Bezaury-Creel *et al.*, 2009; Ceballos *et al.*, 2010). To address this problem, we propose the creation of dynamic protected areas (DPAs). Such conservation areas will combine the protection of current focal habitat ranges along with areas (e.g. corridors) derived from the future projections of ENMs, which can be upgraded as more precise climate-change scenarios become available. Such strategies will aid in developing reliable adaptation and mitigation strategies to conserve the biodiversity of focal ecosystems. Our proposal of DPAs will concomitantly integrate climate-change scenarios within present conservation strategies and the shifting dynamics of populations throughout an ecosystem's distribution and its transitional areas (Araújo, 2002). Therefore, the selection of new PAs could satisfy representation targets for both current and future distributional ranges at once (Hannah *et al.*, 2007). Adding new areas to conserve both present and future ranges of species represents a less costly strategy (in area and resources) than using a two-step process (i.e. representation of current ranges and afterward addressing the consequences of climate change; Hannah *et al.*, 2007).

This study represents a first assessment of the implications that global climate change can have for the biological diversity of the Mexican TDFs. Diverse modeling approaches have been used to the same end in others studies (e.g. the geographical simulations [Lindgren, 1998;], regression tree analysis [Iverson *et al.*, 1999;]), and Dynamic Global Vegetation Models [DGVMs; Prentice *et al.*, 2007; Scheiter *et al.*, 2013]) for other taxa, ecosystems, and regions. However, at present, the relative predictive abilities of each approach have not been compared. The approach we proposed can be used to produce synthetic models of the combined effects of climate change and other threats (e.g. deforestation) on ecosystems, allowing us to understand and integrate our biological knowledge with the social and ecological drivers that determine their change. Additionally, we suggest that future investigations should take advantage of current NASA monitoring efforts (using MODIS Terra and Aqua satellites) to perform an automated spatiotemporal sampling, in

order to advance our understanding on the degree of fragmentation and level of conservation of Mexican TDFs or any other ecosystem under study. Given the frequency of land cover data collection by these two satellites, we expect that the current map will serve as a baseline for updates at regular time intervals, enabling extrapolation of these studies to larger regions. Future research must be directed to generate additional information along these lines to improve the information of ecosystems for their sustainable management and protection.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Percentage of prediction and overlap of modeled tropical dry forests (TDFs) in comparison with the Mexican ecosystems proposed by Challenger & Soberón (2008): (a) Percentages of prediction of primary TDFs maps; (b) Proportion of modeled area predicted considered as TDFs; and (c) Relation between the numbers of species predicted by pixels and each ecosystem type. Colors correspond to: TDFs (brown), Temperate Forests (blue), Xerophyte Scrub Forests (yellow), Wetland Forests (orange), Grassland (green), Cloud Forests (grey), and Mangrove Swamp (purple). Proportions of pixels by ecosystems were calculated following the proposed by Prieto-Torres & Rojas-Soto (*submit*).

Figure S2. Intact areas of Mexican TDFs projected to 2050 (c, b) and 2070 (c,d) under RCP 4.5 (a–c) and RCP 8.5 (b,d) future climatic scenarios given current land use practices (not natural forests; INEGI, 2013).

Appendix S1. Ornithological and botanical collections of international museums that kindly provided data included.

Table S1. Localities records of tropical dry forests (TDFs) in Mexico were used to evaluate ENMs of species for the prediction of TDFs.

Table S2. Percentage of contribution of each environmental variable used and validation values obtained for the species models generated.