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Habitat suitability models to make conservation decisions based on areas of high species richness and endemism

Nathalie S. Hernández-Quiroz[1], Ernesto I. Badano[1*], Felipe Barragán-Torres[2], Joel Flores[1], Carmelo Pinedo-Álvarez[3]

[1] IPICYT/División de Ciencias Ambientales, Camino a la Presa San José 2055, Colonia Lomas 4ª Sección, C.P. 78216, San Luis Potosí, SLP, México.

[2] CONACYT-IPICYT/División de Ciencias Ambientales, Camino a la Presa San José 2055, Colonia Lomas 4a Sección, C.P. 78216, San Luis Potosí, SLP, México.

[3] Facultad de Zootecnia y Ecología, Universidad Autónoma de Chihuahua, Periférico Francisco R. Almada Km 1, C.P. 31453, Chihuahua, Chih., México.

* Corresponding author: ernesto.badano@ipicyt.edu.mx / telephone: +52 444 8342049 / Fax: +52 444 8342010 / ORCID: 0000-0002-9591-0984

Abstract

Biodiversity positively relates with the provisioning of ecosystem services and preserving areas with elevated diversity of highly-functional species could help to ensure human well-being. Most studies addressed to make these decisions use maps relying on species occurrences, where sites containing several species are proposed as priority conservation areas. These maps, however, may underestimate species richness because of the incompleteness of occurrence data. To improve this methodology, we propose using habitat suitability models to estimate the potential distribution of species from occurrence data, and later shaping richness maps by overlapping these predicted distribution ranges. We tested this proposal with Mexican oaks because they provide several ecosystem services and habitat suitability models of species were calibrated with MaxEnt. We used linear regressions to compare the outputs of these predictive maps with those of maps based on species occurrences only and, for both mapping methods, we assessed how much surface of sites with elevated richness and endemism of oaks is currently included within nature reserves. Both mapping methods indicated that oak species are concentrated in mountain regions of Mexico, but predictive maps based on habitat suitability models indicated higher oak richness and endemism that maps based on species occurrences only. Our results also indicated that nature reserves cover a small fraction of areas harboring elevated richness and endemism of oaks. These results suggest that estimating richness across extensive geographic regions using habitat suitability models quickly provides accurate information to make conservation decisions for highly-functional species groups.

Keywords: conservation priority areas; forest conservation; *Quercus*; oaks; species distribution models

Introduction

Biodiversity conservation is critical because the interaction of biotic communities with their physical habitat result in several ecosystem services that support human well-being (Cardinale et al. 2012). Paradoxically, species extinction rates due to human activities currently are 1000 times higher than those due to natural causes and, during this century, they are predicted to increase ten times because of the accumulation of human impacts on natural ecosystems (De Vos et al. 2015). Reducing this extensive loss of biodiversity to ensure the provisioning of ecosystem services requires developing methodologies able to quickly provide accurate information to decision makers about what geographical areas must be prioritized for conservation.

As the provisioning of ecosystem services is positively related with biodiversity (Díaz et al. 2006; Mace et al. 2012), it can be proposed that sites containing elevated richness of highly-functional species should be the target of conservation actions. Previous studies have assessed species richness across extensive geographical regions by counting the incidence of species within operative spatial units (e.g., political subdivisions of countries or latitude-longitude quadrants), where the output of this procedure are maps highlighting those spatial units where several species concur (Kerr 1997; Peterson and Navarro-Sigüenza 1999; Peterson et al. 2000; Orme et al. 2005; Torres-Miranda et al. 2011; Miguel-Talonia et al. 2014; Mokany et al. 2014; Jenkins et al. 2015). Nevertheless, species inventories used to build these maps are often incomplete, especially if they come from botanical collections instead of systematic sampling systems (Hortal et al. 2007; Caley et al. 2014). Thus, this mapping method may underestimate species richness across spatial units because the resulting maps do not include all sites where the different species are actually present (Hurlbert and White 2005; Hurlbert and Jetz 2007). In consequence, this may lead to misleading conservation decisions for biodiversity.

This methodology, however, can be improved if species distribution ranges are estimated with probabilistic models instead of directly inferring them from extent-of-occurrence data. In the case of plants, habitat suitability models based on environmental variables have been proved to be useful to estimate their potential distribution ranges (Cruz-Cárdenas et al. 2014; Martínez-Pastur et al. 2016; Ramírez-Albores et al. 2016). Indeed, robust models to predict the distribution of plant species can be constructed with presence-only records obtained from literature and botanical collections, which are the same data used to build the extent-of-occurrence richness maps described in the former paragraph (Elith et al. 2011). These models assume that, if no dispersal limitation and no biotic interactions are considered, plant species will only occur in sites where the physical habitat matches with the survival requirements of its fundamental niche (Elith et al. 2006). Thus, the probability of finding a given plant can be estimated as a function of the environmental variables that define the different habitats across the target region (Elith et al. 2006; Phillips et al. 2006; Hirzel and Le Lay 2008). If this methodology is used to make biodiversity conservation decisions, those sites where several species overlap elevated occurrence probabilities should be prioritized.

We focused on Mexican oaks (*Quercus* spp., Fagaceae) to test this proposal. We did it because this plant group provides critical ecosystem services that support human well-being in this country. Oaks have elevated ecological, cultural and economic value in Mexico because they have been used as source of food, medicines and raw materials from pre-Columbian times (Luna-José et al. 2003). About 30 million people in Mexico currently depend on oak forests for freshwater supply, while they also are important carbon sinks (García-Coll et al. 2004; Muñoz-Piña et al. 2008). Further, Mexico is the most important diversification center of oaks (Nixon 2006). This country harbors a third of the oak species described to date (161 of 450 species), form which 56% are endemic (Valencia 2004), and their forest provide habitat for an elevated diversity of native plants and animals (Koleff et al. 2009).

In this study, we used habitat suitability models to estimate the distribution ranges of as many Mexican oaks as possible and overlapped these models to shape a species richness map based on occurrence probabilities. This map was compared with an extent-of-occurrence richness map to determine how much the outputs of these two methods differed. Further, as more than the half of Mexican oaks are endemic, we also built these maps by considering endemic species only. After that, we assessed whether high-richness and high-endemism areas predicted by these maps are currently included within natural reserves.

Methods

To estimate the distribution ranges of oaks, we searched for occurrence data of all species reported in Mexico. These searches were conducted in Global Biodiversity Information Facility (available at http://gbif.org; consulted on August 2016) because this database includes corroborated species reports from herbaria and scientific publications. Occurrence data were visualized in Quantum GIS 2.18 (available at https://www.qgis.org) and species records located outside Mexico were removed. We also removed points located within cities because these occurrences can be subsidized by man (e.g., parks and botanical gardens) and may not reflect the habitat requirements of species (Sax et al. 2013; Ramírez-Albores et al. 2016).

We later gathered the environmental variables associated to each occurrence point of oaks using the climatic layers of WorldClim 2.0. These layers interpolate climatic data between 1950 and 2000 and provide the values of 19 bioclimatic with a spatial resolution of 1-km^2 per pixel (Fick and Hijmans 2017). Due to the elevated spatial resolution of these layers, for each oak species we looked for occurrence points located less than 1.5 km from each other and only retained one of them to avoid overfitting the habitat suitability models (Elith et al. 2006). Bioclimatic variables were complemented with topographic variables obtained from the geodatabases of National Institute of Statistics and Geography (consulted on September 2016 at http://www.inegi.org.mx), which provided data of elevation, slope aspect, ground inclination and soil type for each occurrence point. The datasets containing the depurated occurrence points of the different oak species and their respective environmental variables are available as supplementary material in the Zenodo repository (http://doi.org/10.5281/zenodo.1133339).

MaxEnt 3.4 was used to build the habitat suitability model of each oak. Although other computer programs are also available for modeling habitat suitability and estimate the distribution ranges of plant species, MaxEnt has been proven to perform better when presence only data is available, as in our case (Elith et al. 2011). This software produces robust models if more than 30 occurrence points are available for each species (Wisz et al. 2008; Elith et al. 2011) but, despite our efforts for gathering this amount of data for all Mexican oaks, this condition was satisfied by 59 species (37 oaks endemic to Mexico, see Table 1). Thus, the richness maps only considered these species. Further, because the inclusion of redundant environmental variables in these models may lead to overpredict species distribution ranges, we checked for cross-correlation between all pairs of variables within the dataset of each oak species (Beaumont et al. 2005; Elith et al. 2011). For this, we run Spearman correlation tests in R 3.4 (available at https://www.R-project.org) and look for relationships with correlation coefficients above 0.70 (Warren et al. 2008). When a variable was related with several others, we retained that variable with higher correlation coefficients with most the other (Elith et al. 2011; Cruz-Cárdenas et al. 2014).

We used the bootstrap resampling algorithm of MaxEnt to calibrate the habitat suitability model of each species, which randomly resampled 100 times the 75% of its occurrence data (training points). The remaining 25% of the dataset was used to test the accuracy of the model (test points) by computing the area under receiver operating characteristic curves (AUC). These curves were built by plotting the fraction of test points correctly classified by the model (true positives) against the fraction of test points incorrectly classified by the model (false positives). AUC varies between 0 and 1, where values below 0.5 indicate that the model cannot differentiate between random occurrences and occurrences due to the environmental factors, while values close to 1 indicate that the distribution of the target species is strongly correlated with the environmental variables (Fielding and Bell 1997, Elith et al. 2006).

The habitat suitability model of each species was geographically visualized in Quantum GIS 2.18 as a map of occurrence probabilities with a resolution of 1-km^2 per pixel. As these probability values varied between 0 and 1, it was necessary to set a criterion defining what pixels had elevated likelihood of containing each species. For this, we reclassified the pixels of maps in probability quartiles (0.00-0.25, 0.25-0.50, 0.50-0.75, 0.75-1.00) and superimposed the occurrence points of the respective species. After that, we counted the number of true occurrences within each quartile. For all species, the largest number of occurrence points was contained in the third quartile and, therefore, we assumed that species are more likely to occur in pixels with occurrence probabilities above 0.5. In this way, the potential distribution range of each oak was redrawn by removing those pixels with occurrence probabilities below 0.50.

To determine what areas may contain elevated oak richness, we overlapped the estimated distribution ranges of the 59 species and superimposed on them an UTM-scaled grid of 27.7 x 32.5 km (about 0.25° latitude x 0.33° longitude). This grid represents a spatial scale 1:50000 that divides the continental surface of Mexico in 2312 cells of about 900 km^2 each. The richness map based on occurrence probabilities (hereafter, probability-based map) was shaped by counting the number of oak species overlapping their distribution ranges within each grid-cell. This map was compared with a richness map shaped with extent-of-occurrence data only (hereafter, occurrence-based map). This latter map was constructed by plotting occurrence points of oaks on the former grid and counting the number of species contained within each cell. To simplify the comparisons between these maps and better visualize areas containing elevated number of oaks, their grid cells were classified into richness categories that increased every ten species (i.e. 1-10 species, 11-20 species, and so on). After that, we focused on endemic species and repeated the same procedures described above to identify areas containing elevated oak endemism.

Simple linear regressions were used to compare the outputs these two mapping methods. In these analyses, values of oak richness and endemic species within the cells of occurrence-based maps were regressed against the respective values predicted by probability-based maps. The resulting regression functions should have intercepts close to 0 (zero) and slopes close to 1 (one) if both methods indicate similar values of oak richness and endemic species across grid cells (i.e., their outputs are spatially correlated). Otherwise, if values of richness and endemic species differ across cells of occurrence-based and probability-based maps, the parameters of regression functions should deviate from these theoretical values. To perform these comparisons, we computed the 95% prediction intervals of regression functions and assessed whether they contained a theoretical linear curve with intercept 0 and slope 1.

To assess whether those grid cells that contain elevated richness and endemism of oaks are currently protected, we superimposed the polygons of natural protected areas on the probably-based and occurrence-based maps. As protected areas of Mexico can belong to either the federal government or local state governments, we considered both types of reserves. Polygons of reserves were obtained from the National Commission for the Knowledge and Use of Biodiversity (available at http://www.biodiversidad.gob.mx; consulted on March 2017) and, for each grid cell of our maps, we computed the fraction of them contained within these reserves. All data analyzed in this study are included in the interactive maps of the online supplementary material.

Results

The habitat suitability model of each oak species required a specific set of environmental variables to calibrate it, and the contribution that each of these variables made to the model was exclusive of each oak species. The environmental variables used to calibrate habitat suitability models varied between seven and thirteen across the different oak species (Table 1). The bioclimatic variables more commonly retained in these models were mean temperature of the driest quarter of the year (93.2% of models), temperature seasonality (91.5% of models), mean diurnal range of temperature (89.8% of models), precipitation of the wettest quarter of the year (88.1% of models), precipitation of the driest quarter of the year (84.7% of models) and precipitation seasonality (69.5% of models) (see Table 1). Among the topographic variables, elevation was always correlated with bioclimatic variables and, therefore, it was never included in the models. The other topographic variables (slope aspect, ground inclination and soil type) were retained in all habitat suitability models (Table 1). Environmental variables of each model explained more than 99% of its total variance, but the individual contribution of each variable to explain variance largely differed among oak species (Table 1).

From these models, the distribution ranges of oaks estimated by only considering occurrence probabilities above 0.5 contained, in average, 57% of the real occurrence points of each species. These distribution ranges were mainly extended on the four most important mountain ranges of Mexico, including Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur, and the Trans-volcanic Mexican Belt (the interactive maps of oak distribution ranges that are available as supplementary material in the Zenodo repository; http://doi.org/10.5281/zenodo.1133339). Climate in these regions is temperate, but a few oak species were also predicted to spread towards warmer valleys that occur across the coasts of the Pacific Ocean and the Gulf of Mexico (e.g., *Quercus aristata*, *Quercus cedrosensis*, *Quercus glaucescens*, *Quercus glaucoides*, *Quercus elliptica*, *Quercus magnoliifolia*, *Quercus* *oleoides*, *Quercus peduncularis*, *Quercus polymorpha*, *Quercus tuberculata* and *Quercus xalapensis* - see the interactive maps of oak distribution ranges that are available as supplementary material in the Zenodo repository; http://doi.org/10.5281/zenodo.1133339).

The probability-based map of species richness that resulted from overlapping these distribution ranges predicted that 18 grid cells can potentially contain more than 30 oak species, while no grid cell of the occurrence-based map reached this richness level (Fig. 1 - see also the interactive maps of species richness that are available as supplementary material in the Zenodo repository; http://doi.org/10.5281/zenodo.1133339). The number of grid cells in all other richness categories was also higher in the probability-based map than in the occurrence-based map (cells with 1-10 species: 967 vs. 730; cells with 11-20 species: 419 vs. 62; cells with 21-30 species: 216 vs. 3; Fig. 1). Richness values of grid cells from the occurrence-based map were positively related with those predicted by the probability-based map for the same cells ($F_{(1, 2310)} = 1718.694$, $p < 0.001$, $r^2 = 0.427$). The intercept and the slope of this regression function were -0.195 and 0.230, respectively, but the 95% prediction intervals of this function did not contain the theoretical curve with intercept 0 and slope 1 (Fig. 1).

The number of grid cells in all richness categories decreased when the probability-based and the occurrence-based map were built with endemic oaks only (Fig. 2 - see also the interactive maps of species richness that are available as supplementary material in the Zenodo repository; http://doi.org/10.5281/zenodo.1133339). Nevertheless, all richness categories had higher frequencies in the probability-based map than in the occurrence-based map (cells with 1-10 species: 966 vs. 596; cells with 11-20 species: 376 vs. 8; cells with more than 20 species: 25 vs. 0; Fig. 2). Richness values of these two maps were also positively corelated ($F_{(1, 2310)} = 1675.302$, $p < 0.001$, $r^2 = 0.420$), following a linear function with intercept of -0.077 and slope of 0.204. However, the theoretical curve with intercept 0 and slope 1 was not contained within the 95% prediction intervals of this regression function (Fig. 2).

In the maps described above, we considered that conservation actions must be focused on those grid cells from the upper richness categories – i.e., cells with more than 20 species. Thus, we assessed how much surface of these cells is contained within nature reserves of Mexico. This country has 182 reserves belonging to the Federal Government and 370 reserves belonging to state governments, which cover a total of 948,259 km^2 (48% of the continental surface of Mexico). The probability-based map that included all oak species predicted that 224 grid cells (210600 km^2) can contain more than 20 species, but also indicated that only 18% of this surface is currently protected (Fig. 1 - see also the interactive maps of species richness that are available as supplementary material in the Zenodo repository; http://doi.org/10.5281/zenodo.1133339). The respective occurrence-based map indicated that just three grid cells (2700 km^2) have over 20 different oaks and less than 10% of this surface is protected (Fig. 1). For endemic oaks, the probability-based map predicted 25 grid cells with more than 20 endemic species (22500 km^2), but less than a fourth of this surface (5211 km^2) is located within protected areas (Fig. 2 - see also the interactive maps of species richness that are available as supplementary material in the Zenodo repository; http://doi.org/10.5281/zenodo.1133339). This later assessment was not performed on the occurrence-based map because all grid cell contained less than 20 endemic oaks (Fig. 2).

Discussion

Habitat suitability models indicated large variability in the type of environmental variables that influence the occurrence of different oak species across Mexico. Indeed, when the same variable was included in different models, there were large discrepancies in the power with which that variable explained the potential distribution of different oak species. These results suggest that the oak species included in this study have well-differentiated survival requirements, which contradicts the widely accepted hypothesis that phylogenetically close species should have ecological niches largely overlapped (Losos 2008). This elevated diversity of survival requirements, however, agrees with the proposal that the huge diversification of the genus *Quercus* in Mexico resulted from niche differentiation processes that adapted these species to the wide variety of climatic conditions that occurs across this country because of its irregular topography (Hipp et al. 2017).

The probability-based map indicated that about 70% of the continental surface of Mexico meets the survival requirements of oaks. Nevertheless, a note of caution must be introduced before analyzing the patterns of richness and endemism that resulted from this procedure. This is because we estimated the distribution ranges of oaks with bioclimatic and topographic variables, while we did not consider other factors than can also influence their distribution, such as anthropogenic impacts and dispersal limitations. For example, the expansion of the agricultural frontier in Mexico over the past four centuries has progressively denuded more than 50% of native forests (Ricker et al. 2007; Rosete-Vergés et al. 2014). In consequence, our habitat suitability models may predict elevated occurrence probabilities of oaks within operative spatial units where forest are no longer present. Thus, our approach can be useful to identify high-richness and high-endemism areas of plant species but making conservation decisions with this information is still requiring field vegetation samplings addressed to verify whether the target species are actually present within these areas.

The elevated values of oak richness and endemism predicted by the probability-based maps, as compared with those of occurrence-based maps, reinforce the suggestion that this latter procedure can misestimate species richness (Hurlbert and White 2005; Hurlbert and Jetz 2007). However, it is important to note that probability-based maps may also overrate species richness at some operative spatial units because they do not consider potential dispersal limitations of plants. This is particularly important for oaks because they are zoochoric trees that depends on small vertebrates (e.g., rodents and birds) for acorn secondary dispersion (Steele and Smallwood 2002; Ramos-Palacios et al. 2014), but the movement of these animals may be constrained by natural barriers, such as deserts, mountain ranges and man-disturbed areas (e.g., agricultural fields and urbanized areas). Therefore, probability-based maps may predict the occurrence of some oak species into spatial units that they have not reached yet, which in turn could inflate local richness. In our case, these potential biases are likely to be small because we used true occurrences of oaks to validate the probability-value thresholds that determine the boundaries of their distribution ranges, but this caveat should be considered before making conservation decisions for other pant groups.

Probability-based maps also indicated that the areas concentrating elevated richness and endemism of oaks (i.e., grid cells with more than 20 species) are mainly located in montane regions of Mexico. This concurs with general suggestion that oaks dominate temperate forest of this country (Rzedowski 1978; Martínez 1981; Zavala-Chávez 1989; Valencia 2004; Romero-Rangel et al. 2015). Although our results indicate that these regions harbor several nature reserves, they also indicate that just a small fraction of the areas with high richness and endemism of oaks are currently protected. This could be attributed to the lack of knowledge about functional value of this plant group, as well as the elevated priority that governments give to the preservation of zones with elevated aesthetic and recreational value for people (Toledo 2005). Indeed, despite the elevated cultural value that oaks have in Mexico, the elevated endemism of this group, and the strong threats they face due to the advance of deforestation, no single oak species is currently included in the official list of endangered species of this country (NOM-059-SEMARNAT 2010), and there is no single reserve specifically addressed to preserve these trees (Arriola-Padilla et al. 2014). Our probability-based maps then allow proposing that, after verifying the presence of oaks in those grid cells predicted to contain elevated richness and endemism of this group, protected areas that partially cover them must be expanded to better protect the elevated diversity of Mexican oaks. Further, as several of these grid cells fully dropped outside protected areas, the establishment of new reserves must be also considered.

Conclusions

The habitat suitability models of oaks developed in this study allowed to estimate the patterns of richness and endemism of this group across the country. Despite the potential limitations that we identified for the resulting probability-based maps, our results suggest that this procedure can provide reliable information about what regions contain elevated richness and endemism of species. This methodology can facilitate decision-making regarding what areas must be prioritized to preserve diversity of highly-functional species and their associated ecosystem services. Further, this procedure can also be employed to identify whether nature reserves protect species diversity within a given region. In our case, the results indicate that extensive areas of highly-rich oak forests are unprotected.

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Supplementary material

Supplementary material of this study is freely available at the Zenodo repository under the following doi: http://doi.org/10.5281/zenodo.1133339. These materials include a Microsoft Excel file (SM 01-Oak occurrences.xlsx) that contains the occurrence points used to calibrate the habitat suitability models of the 59 oak species. The repository also contains interactive maps indicating the predicted and observed distributions of the 59 Mexican oak species (SM 02-Estimated oak distribution ranges.kmz), as well as the probability-based and occurrence-based maps of oak richness and endemism (SM 03-Oak richness maps.kmz). These maps projections are provided in KMZ format to make them easy to visualize in Google Earth (freely available at www.google.com/earth).

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Figure captions

Fig. 1. Probability-based (A) and occurrence-based (B) maps of species richness including the 59 oaks for which habitat suitability models were calibrated (scale 1: 50000; each grid cell covers about 900 km^2). The figure shows the four most important mountain ranges that harbor temperate forests in Mexico (black boundaries) and the areas addressed to preserve nature (blue boundaries). Mountain ranges are Sierra Madre Oriental to east, Sierra Madre Occidental to west, Sierra Madre del Sur to south, and the Trans-Volcanic Belt that runs from east to west across meridional Mexico.

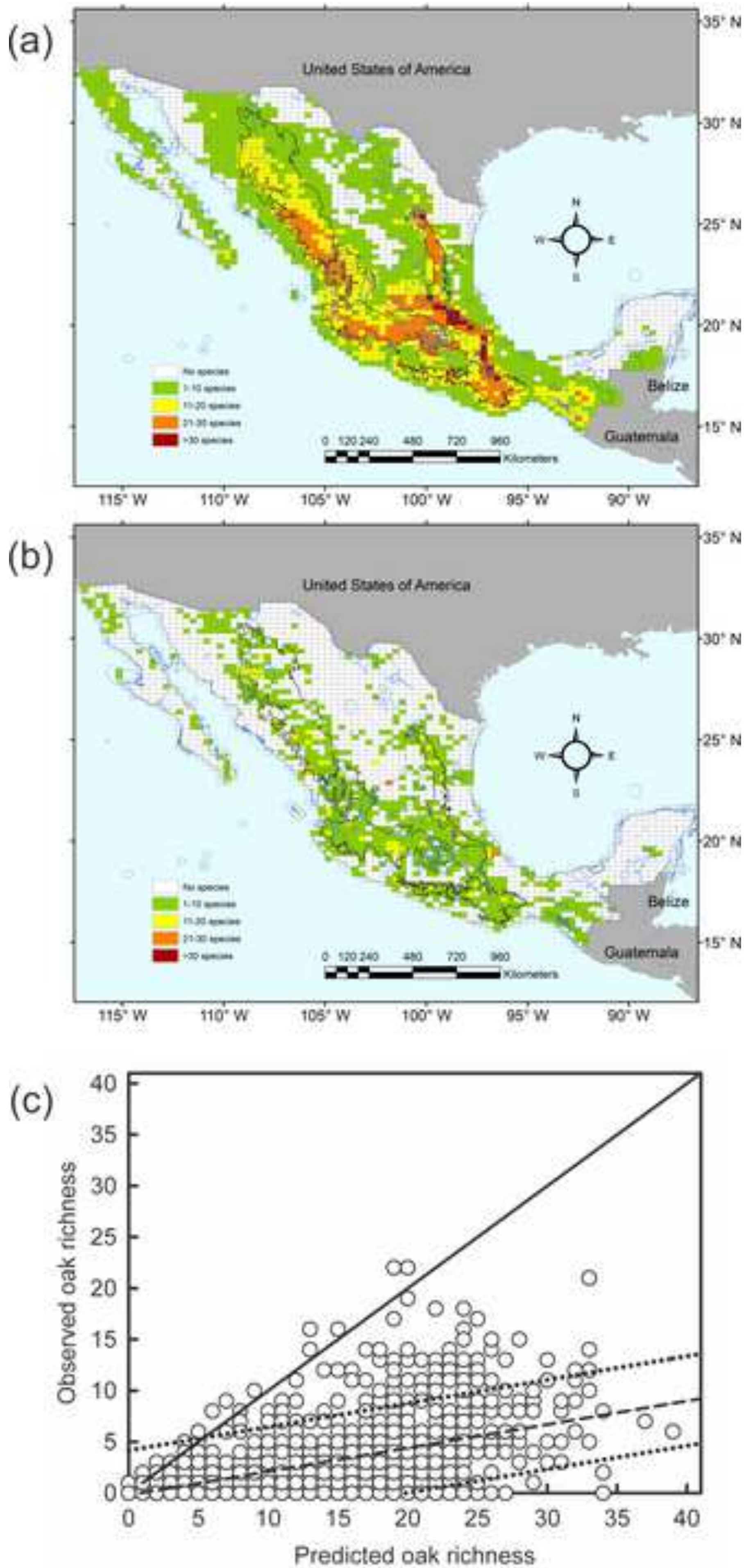
Fig. 2. Probability-based (A) and occurrence-based (B) maps of species richness that only included the 39 endemic oaks for which habitat suitability models were constructed (scale 1: 50000; each grid cell covers about 900 km^2). The figure shows the four most important mountain ranges that harbor temperate forests in Mexico (black boundaries) and the areas addressed to preserve nature (blue boundaries). Mountain ranges are Sierra Madre Oriental to east, Sierra Madre Occidental to west, Sierra Madre del Sur to south, and the Trans-Volcanic Belt that runs from east to west across meridional Mexico.

Table 1. Mexican oak species included in this study (endemic species are indicated with asterisks). The table indicates the number of occurrence points used to develop the habitat suitability model of each species (N), the number of environmental variables included in the model (VAR) and its AUC value, and the cover of the predicted distribution range (km^2). The following columns indicate the percent variance (%) explained by each variable into the model, while the last column of the table indicates the total variance of the model explained by these variables (Var). Bioclimatic variables are: mean diurnal range of temperature (B01), isothermality (B02), temperature seasonality (B03), maximum temperature of the warmest month (B04), minimum temperature of the coldest month (B05), temperature annual range (B06), mean temperature of the wettest quarter of the year (B07), mean temperature of the driest quarter of the year (B08), mean temperature of the warmest quarter of the year (B09), mean temperature of the coldest quarter of the year (B10), annual precipitation (B11), precipitation of the wettest month (B12), precipitation of the driest month (B13), precipitation seasonality (B14), precipitation of the wettest quarter of the year (B15), precipitation of the driest quarter of the year (B16), precipitation of the warmest quarter of the year (B17) and precipitation of the coldest quarter of the year (B18). Topographic variables are: slope aspect (T01), ground inclination (T02) and soil type (T03).

Species name	**N**	**VAR**	**AUC**	**km^2**	**Bioclimatic variables**																		**Topographic variables**			**Var**
					B01	**B02**	**B03**	**B04**	**B05**	**B06**	**B07**	**B08**	**B09**	**B10**	**B11**	**B12**	**B13**	**B14**	**B15**	**B16**	**B17**	**B18**	**T01**	**T02**	**T03**	
*Quercus acutifolia**	127	9	0.97	71586	2.5		55.8					22.2						4.3		1.3	2.2		3.2	4.8	3.6	99.9
*Quercus affinis**	63	10	0.98	28467	4.8	3.8	10.4					20.9						1.0	1.0	39.6			1.1	13.5	3.8	99.9
*Quercus albocincta**	43	8	0.99	38286	2.6		34.1					6.0							33.4	0.9			2.9	16.0	4.1	100
*Quercus aristata**	33	11	0.99	11427	0.9		15.5	5.5				2.5					16.4		38.8	0.6		2.1	2.9	4.0	10.8	100
Quercus arizonica	94	10	0.96	44233	4.4		21.1					2.8		29.5				3.6	20.9	2.8			1.2	8.3	5.4	100
*Quercus canbyi**	68	8	0.98	24959	7.1						4.7							2.1	21.7	39.9			1.0	16.4	7.0	99.9
Quercus candicans	153	10	0.97	51311	2.9		33.4					23.0							23.0	2.6	1.0	0.7	1.4	4.4	7.7	100
Quercus castanea	340	11	0.94	112006	7.4				13.0					8.5			1.4		36.2	1.3	1.9	10.7	1.1	15.3	3.3	100
*Quercus cedrosensis**	33	9	1.00	8889	1.6							0.1	27.8				51.1	1.6		1.0			2.3	10.6	4.0	100
Quercus chihuahuensis	107	10	0.95	91543	5.1		27.9					1.8		9.4				8.4	27.0	1.6			2.7	11.4	4.6	99.9
*Quercus conspersa**	87	10	0.96	72495	3.5		50.7					6.6						4.4	2.7	1.2	4.0		3.2	18.3	5.4	100
*Quercus conzattii**	31	13	0.98	27575	5.5	6.1						3.5	27.8	2.5				3.6	8.7	5.9	2.1	1.9	3.3	13.5	15.6	100
Quercus crassifolia	252	10	0.95	99158	2.2		21.4					37.5						3.9	16.1	6.5	1.2		1.3	5.7	4.1	99.9
*Quercus crassipes**	128	11	0.97	34801	0.8	1.2	36.7					20.7						3.3	1.6	0.8	1.1		1.4	2.1	30.3	100
Quercus depressipes	34	8	0.97	50734			9.4					12.7		34.9				3.0	18.3				4.6	6.6	10.4	99.9
*Quercus deserticola**	84	11	0.96	59915	1.0		40.8					25.5						7.0	4.0	0.9	4.1	0.6	2.2	5.2	8.7	100
*Quercus durifolia**	72	9	0.96	59174			16.5		29.2			12.6						1.3	19.5	3.3			1.6	5.4	10.5	99.9

*Quercus eduardii**	132	9	0.97	51751	8.1		41.1					21.9						10.9	4.4		4.7	1.6	3.9	3.5	100
Quercus elliptica	106	9	0.96	65261	1.9		27.4					9.4						40.5	2.3	0.9		1.4	11.3	5.0	100
Quercus emoryi	57	10	0.96	82595	4.4		12.2					2.1		34.6			0.9	24.6	2.2			2.4	6.3	10.3	100
*Quercus frutex**	35	11	0.99	25018	2.0	3.3	36.9					39.1					0.9	1.4	1.2	2.0		2.2	4.4	6.6	100
*Quercus gentry**	73	11	0.97	49521	0.8		15.9					8.6					11.6	24.6	2.5	0.7	3.8	1.6	18.3	11.7	100
*Quercus glabrescens**	40	10	0.96	40594	0.9		29.6					17.8					2.6	1.3	6.0	4.5		4.6	18.9	13.9	100
*Quercus glaucenscens**	43	9	0.96	50242	2.9		36.8					2.9						18.8	1.6	1.1		4.3	14.0	17.5	99.9
*Quercus glaucoides**	115	9	0.95	74263	2.8		40.0					3.6						3.8	1.7	17.7		2.1	25.4	3.0	100
*Quercus greggii**	69	9	0.99	11365	1.6		16.6					32.1					20.2	5.5	6.0			0.9	11.7	5.4	100
Quercus grisea	84	13	0.95	63956	3.4		5.4	18.9				9.8		19.3			1.6	3.8	0.7	12.0	1.9	2.7	8.4	12.0	99.9
Quercus hypoleucoides	45	9	0.98	16753	2.3		21.7					1.7		19.1			10.5		24.8			2.7	14.1	3.1	100
Quercus intricata	31	11	0.98	28738	1.8		7.4		12.4			5.8		0.1			31.2	13.7	5.1			3.4	9.6	9.6	100
*Quercus jonesii**	100	10	0.96	49464	3.7		12.2					19.2					6.8	25.7	4.6		10.0	3.9	7.4	6.3	99.8
*Quercus laeta**	253	11	0.94	128777	5.4		6.0			20.0		10.2	25.8					8.2	4.8		5.5	2.6	9.3	2.3	100
Quercus lancifolia	49	9	0.97	29063			24.3			12.7		10.6						17.9	3.7	5.8		1.7	14.1	9.2	100
Quercus laurina	227	10	0.96	63337	3.1		42.2					34.0					1.7	4.6	1.8	1.6		1.7	4.9	4.3	99.9
*Quercus magnoliifolia**	191	10	0.96	77416	3.6		52.6					3.9						7.0	12.2	3.4	1.4	1.3	10.3	4.3	100
*Quercus mexicana**	110	8	0.96	47456	2.4		30.5					37.8					11.2	2.5				0.9	8.7	6.0	100
*Quercus microphylla**	66	10	0.97	48792	1.2		29.9			2.4		48.4						3.0	0.5	1.9		2.0	2.4	8.3	100
Quercus oblongifolia	56	11	0.97	26805	1.2		19.3					2.4		18.1			13.4	1.1	1.1		23.9	1.0	11.9	6.6	100
*Quercus obtusata**	272	11	0.95	96300	3.5		37.4					21.6					12.3	9.3	3.2	1.8	2.3	1.3	4.0	3.3	100
Quercus oleoides	41	11	0.98	27008	48.4		2.7			3.2	4.6	0.9					4.1	13.0		1.4		2.3	8.2	11.1	99.9
Quercus peduncularis	115	9	0.95	87250	3.3		37.1					9.0						24.0	2.0	1.4		1.1	13.7	8.5	100
*Quercus peninsularis**	31	7	1.00	3357			3.4				88.7						2.2		1.6			1.0	1.7	1.5	100
Quercus polymorpha	125	10	0.98	34073	11.9		7.0				11.0	13.9					8.5	9.5	19.5			0.9	15.3	2.5	100
*Quercus potosina**	56	11	0.98	29686	4.0		24.7			1.0		32.5						5.6	3.7	6.7	7.1	2.4	3.1	9.1	99.9
*Quercus pringlei**	51	9	0.97	21940	3.9		8.2					21.7					21.5	11.3	16.5			1.8	10.2	4.9	100
*Quercus resinosa**	67	10	0.97	65144	8.7		29.7					6.5						13.7	11.1	5.2	8.1	2.5	8.7	5.9	100
*Quercus rhysophylla**	40	7	0.99	18006						15.9	1.3					14.2	27.2					4.2	30.6	6.7	100
Quercus rugosa	306	11	0.94	84898	2.3		18.6					40.3					2.9	15.8	1.4	2.4	1.1	1.3	8.4	5.5	100
Quercus sapotifolia	42	9	0.99	26305	11.1		17.7			11.4		15.4					9.0	16.7				3.7	9.0	6.0	100
*Quercus sartorii**	64	8	0.99	29142	12.7		12.3					16.3					21.3	15.4				1.1	15.9	5.0	100
*Quercus scytophylla**	84	9	0.95	65551	3.7		3.3					19.3						46.7	5.5	0.9		3.8	13.0	3.8	100
*Quercus sebifera**	38	8	0.98	34702			17.8			15.5		18.0					9.7	8.5				3.4	15.6	11.5	100
Quercus sideroxyla	149	10	0.96	53217	1.9	7.0	17.7		9.6			31.3						21.2	6.2			1.6	2.1	1.5	100
*Quercus striatula**	36	9	0.99	14346	5.0		19.2		2.2			46.3			1.9		14.0					1.1	1.9	8.4	100
*Quercus subspathulata**	40	9	0.97	41099	1.5		9.8					4.3						36.0	9.9	0.6		6.3	15.0	16.6	100
Quercus toumeyi	38	10	0.99	11784	2.7		5.2		33.4			1.4					13.5	2.3			32.8	1.2	2.4	5.0	99.9
*Quercus tuberculata**	76	10	0.96	51373	3.2		24.5	2.7				7.5					11.7	12.3	2.7			2.3	28.5	4.5	99.9
*Quercus urbanii**	40	9	0.95	42260	3.8		22.0					18.4					12.5		9.1		2.2	4.3	19.0	8.8	100
Quercus viminea	86	9	0.95	69662	6.4		23.0					8.8					4.4	25.0	2.3			1.4	20.0	8.6	99.9
*Quercus xalapensis**	103	11	0.97	31867	5.9	1.8	7.4	3.5				10.8					2.1	0.9	41.5			0.9	17.5	7.7	100

Figure 1


(a)
United States of America
Belize
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35° N
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0 120 240 480 720 960
Kilometers
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(b)
United States of America
Belize
Guatemala
35° N
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110° W
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100° W
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0 120 240 480 720 960
Kilometers
N
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(c)
Observed oak richness
Predicted oak richness
0
5
10
15
20
25
30
35
40

Figure 2

Click here to download Figure Figure 2-Hernandez-Quiroz et al.tif