Impact of climate change on local tree species richness in Mexico

by

Marlen Acosta Alamo

Submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Biology, Queens College
The City University of New York

Thesis Supervisor: Dr. Jose D. Anadon

Biology Department

Queens College

ABSTRACT

In the past decades, studies related to the implications that a changing climate will have on biodiversity have increased. However, the effects of climate change at community level in tropical and subtropical latitudes are still poorly studied. We analyzed the impact of climate change on tree species richness in Mexico, a megadiverse country with high levels of species richness and endemism. We constructed species distribution models for 1974 tree species, that represent the 96% of the total Mexican tree community. For predicting the species distributions in the future, we used seven bioclimatic variables for a 'business as usual' climate change scenario (RCP 8.5). Our study revealed a decrease on local tree species richness at a 10 x 10 km scale. For Mexico, the mean local species richness will decrease a 14%, from 203 to 174. The maximum local species loss is forecasted for tropical rainforests where all its territory will lose species and the mean species number will decline in a 22%, from 416 to 326. The less affected ecoregion will be the North American deserts where the mean species number will decline in only a 3%, and local tree species richness is projected to increase in 48% of its area. For the endemic trees, Mediterranean California is the ecoregion with highest percentage of area (82%) projected to gain species. The local loss of species in the forests and gain of species in arid regions points towards a savannization of the ecoregions as a response of trees to the climate change. The local change on species richness will contribute to the reshuffling of the Mexican biodiversity, probably modifying the composition of the communities and the ecosystems functioning.

Key Words Climate change, species richness, endemic species, ecoregions, species distribution models.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

Increasing levels of global greenhouse gases emission are linked to the climate changes that Earth is currently undergoing. Since 1970, CO_2 emissions have increased by about 90%, and global mean surface temperature has risen at an average rate of 0.08^0C per decade in the past century (EPA, 2018). Currently in Europe, North America and the Arctic the rates of temperature change are higher than the global average (Smith *et al.*, 2015). In addition, global mean surface temperatures for 2081–2100 are projected to increase between 0.3°C and 4.8°C (IPCC, 2013). As the global climate warms further in the next several decades, the rearrangement of communities caused by the shift of species' ranges will become even more prevalent, together with widespread local extinctions (Wiens, 2016).

Studies related to how trees cope with climate change are frequent in the literature (Lenoir *et al.*, 2009; Ruiz-Labourdette *et al.*, 2012; Monleon and Lintz, 2015; Serra-Diaz *et al.*, 2015; Kerns *et al.,* 2017; Sittaro *et al.,* 2017; Hernandez *et al.,* 2017; Fei *et al.*, 2017; Steinbauer *et al.,* 2018). The case of trees is particularly relevant since they are sessile long-lived organisms that play and important role in ecosystems through carbon sequestration, nutrient cycling, biomass production, and serving as support and shelter for animal communities. Tree species experiencing climate conditions outside their climatic niche could face fates such as the shift of their geographic distribution to track their ecological niche; the shift of their climatic niche to adapt to the new conditions; or their local extinction (Chakraborty *et al.*, 2016).

The shift of tree species geographic range towards higher latitudes and altitudes is one of the most frequent responses to climatic change reported on the literature (Lenoir *et al.*, 2009; Monleon and Lintz, 2015; Kerns *et al.,* 2017; Sittaro *et al.,* 2017; Hernandez *et al.,* 2017). These authors have found that the tree seedlings studied were establishing above the current limit of adults, slowly expanding their populations at the high elevations edges or at northern latitudes.

Regarding the shift of trees' climatic niche to adapt to new conditions, it has been found that young trees' distribution is expanding more in the climatic space than in the geographic space, occupying new portions of climate niche while their geographical range shrinks (Serra-Diaz *et al.*, 2015). It is important to point out that if this retraction of the species distribution ranges comes together with an overall decrease in their abundance, the risk of extinction increases (Lenoir and Svenning, 2014). Reports of species vulnerability to extinction have been made in meta-analyses for plants together with animals (Wiens, 2016; Urban 2015; Schwartz *et al.*, 2006), portraying high risk of species loss for both taxonomic groups, being particularly threatened species with narrow distribution ranges (Schwartz *et al.*, 2006).

Either one of processes described above could potentially affect the species richness of an ecosystem, since richness is the emergent effect of distribution shifts or extinction events. The reduction or replacement of certain species in a community can be consequential because species can have substantially different effects on ecosystem structure, function, and services, and the impacts can have profound implications for the resilience and sustainability of the ecosystems (Fei *et al.*, 2017).

Research efforts related to climate change impact on biodiversity in tropical and subtropical areas are recently increasing, but they are still relatively low in number (Lenoir and Svenning, 2014). Following these authors' recommendations in their paper reviewing the current state of the art on climate-related species range shifts, we consider Mexico as a suitable study region for four reasons. First, it extends through tropical and subtropical latitudes, areas less studied and predicted to experience the disappearance of current climates and the appearance of novel ones (Williams *et al.* 2007). Second, Mexico is one of the 17 megadiverse regions of the world, being one of the five countries with higher number of endemic vascular plants. Third, it counts with seven defined ecoregions ranging from deserts to temperate forests, making it convenient for studying the climate impact on biodiversity throughout an environmental gradient. Fourth, in 2002, only the 33.8 % of the original extension of Mexican forests and jungles remained, with the greatest loss in the tropical areas (Sarukhán *et al.,* 2009), making the country's biodiversity vulnerable to the effects of a changing climate.

To study the effects of climate change on species richness as a measure of biodiversity, statistical modelling is frequently used. Often, researches are based on distribution models of individual species considering only a small group of species (Dyderski *et al*., 2018; Ordonez and Svenning, 2017; Miller and McGill, 2018; Sittaro *et al.*, 2017; Fei *et al.*, 2017; Monleon and Lintz, 2015; Serra-Diaz *et al*., 2015; Thuiller *et al*., 2006 a, b). The consequences of climatic change at community level are, however, less addressed. To model community responses to climatic conditions several strategies have been described (Ferrier and Guisan, 2006). The first strategy, known as 'assemble first, predict later', takes biological data and classifies it generating entities that are modelled as function of environmental predictors. ‘Predict first, assemble later’, also known as Staked-Species Distribution Models (S-SDMs), is the second strategy. In this case, the species are modelled individually as function of environmental predictors, and after the models are stacked and aggregated to obtain the community-level output. The third strategy is ‘assemble and predict together’ or Macroecological Models (MEM) in which all species are modelled at the same time, predicting the richness directly (Guisan and Rahbek, 2011). In our study, we used the second strategy because, in addition to provide individualistic responses of the species to the environment, it allows to analyze presence-only data obtained from different sources (Ferrier and Guisan, 2006).

Predicting how tree richness in Mexico will be impacted by climate change will provide a measure of the potential changes in the country’s biodiversity in the future. By using community level modelling, we will synthesize data on a large number of species that will be more easily interpretable by decision makers (Ferrier and Guisan, 2006). In addition, identifying regions with projected high numbers of species lost or gained in the future decades will be of vital importance for better conservation planning. Our goal is to assess the impact of climate change on local tree species richness, as a proxy of biodiversity, for year 2070 on the Mexican country and its ecoregions.

Our specific objectives are to:

1) Describe the current pattern of total and endemic local tree species richness in Mexico and its ecoregions.
2) Assess the impact of climate change on total and endemic local tree species richness of Mexico for year 2070.
3) Assess the impact of climate change on total and endemic local tree species richness per Mexican ecoregion for year 2070.

2. METHODS

Our general approach was to model the distribution of all the tree species reported for Mexico considering their total geographic ranges on the American continent. By accounting for the species complete distribution, we modelled their total realized niche, preventing bias at range limits in geographic and environmental projections (Broennimann *et al.*, 2006). Once the models were obtained, we focused only on Mexico for the analyses.

2.1 Study area

The study area encompasses the country of Mexico, with an extension of 1 964 375 km^2. Mexico is located in North America, between tropical and subtropical latitudes (32° 43' 06'' North, 4° 32' 27'' South). The most prominent geographic feature of the country is the central plateau dominated by arid and semiarid climate. The central plateau is flanked by mountain chains, the Sierra Madre Oriental on the east and the Sierra Madre Occidental on the west. The highest altitude (5,610 m) in these mountains is registered for the volcanic peak of Citlaltépetl. In Mexico, the mean annual temperature can range from 0^{o}C to 30^{o}C, and the total annual precipitation from less than 100 mm to more than 4500 mm (INEGI, 2017). The wide range of altitude in Mexico, combined with the variety in climatic conditions allow the distinction of seven terrestrial ecoregions with different types of vegetation (Fig.1).

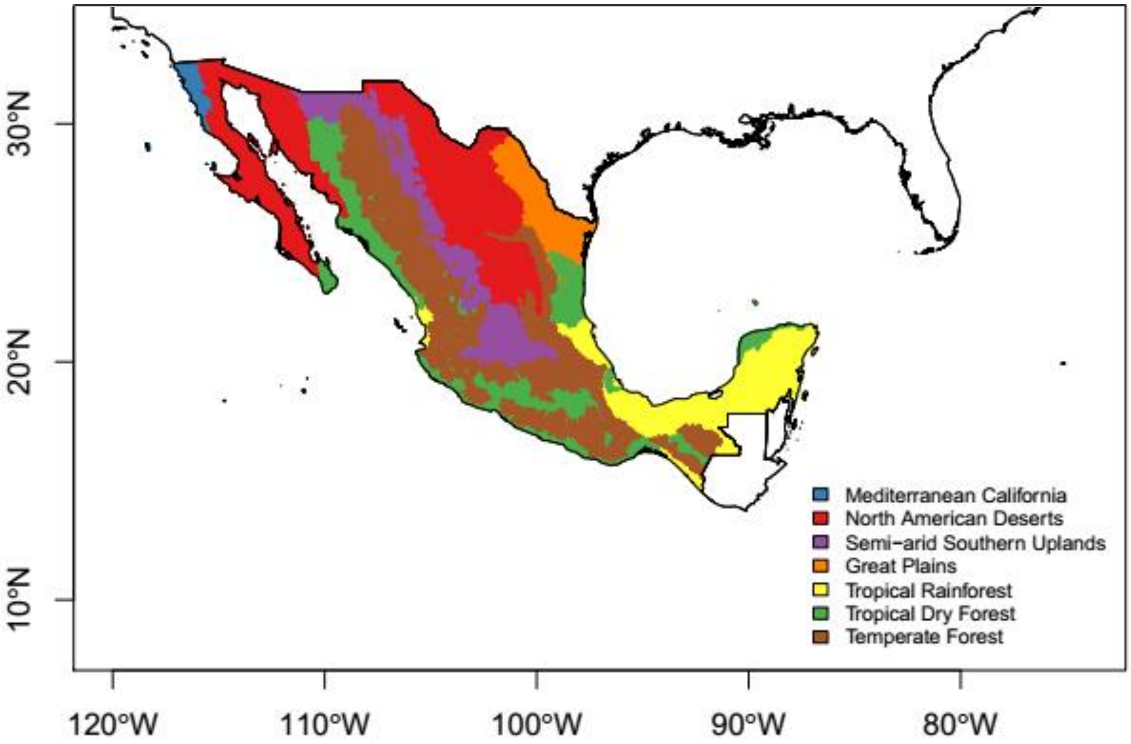

Figure 1. Mexican ecoregions (INEGI, CONABIO and INE, 2008).

2.2 Species occurrence data

The tree species occurrence data used in the present study were obtained from the Mexican National Forest and Soil Inventory (CONAFOR, 2012), and the Botanical Information and Ecology Network (BIEN3, Enquist *et al.*, in prep.). To resolve species names discrepancies between these two data bases, we used the Taxonomic Name Resolution Service (TNRS, 2018).

We downloaded records of tree species reported for Mexico from BIEN3 to check for species that were not included on the Mexican National Forest and Soil Inventory (MNFSI), and to add to the analysis the tree species' occurrence points reported for the

American continent. To download the species records from the BIEN3 data base we used the R package “BIEN” (Maitner *et al.*, 2017).

The two data bases (MNFSI and BIEN3) were merged together, obtaining a total of 2058 tree species. The merged MNFSI-BIEN3 data set was cleaned to remove duplicated records, as well as records were latitude/longitude was not available. To account for possible sampling bias, we applied a spatial thinning method on the R package “spThin” to randomly remove occurrence records, ensuring that not two presence points were closer than a linear distance of 10 km but retaining the largest possible number of records (Aiello-Lammens *et al.*, 2015).

2.3 Climate data

The data for current and future climate were obtained from WorldClim website, version 1.4 (www.worldclim.org, Hijmans *et al.*, 2005). A correlation analysis using a cut off value of 0.70 was performed to narrow down the number of environmental predictors for Mexico as described by Anadon *et al.* (2012), thus avoiding high correlation between variables that produce overfitting of the species distribution models. Seven bioclimatic variables were selected: four related to precipitation (Annual Precipitation, Precipitation of Driest Quarter, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter), and three related to temperature (Mean Diurnal Range, Temperature Seasonality, Minimum Temperature of Coldest Month). The spatial resolution of these bioclimatic layers is 5 arc-minute of a longitude/latitude degree (about 10 km at the equator).

Climatic projections for the year 2070 (average for 2061-2080), were performed using the Representative Concentration Pathway 8.5 (RCP 8.5), provided by the Intergovernmental

Panel on Climate Change (IPCC) on its fifth Assessment Report (IPCC, 2014). The RCP 8.5 is a scenario that assumes that anthropogenic greenhouse gas emissions will continue to rise throughout the 21st century. In addition, this pathway describes a future world with high population and relatively slow income growth with modest rates of technological change and energy intensity improvements (Riahi *et al.*, 2011).

2.4 Species Distribution Models

To carry out our study, we used niche based or species distribution models (SDMs). SDMs software packages take in geographical coordinates of species, relate these to climatic variables and map likely species distributions, under current or possible future conditions, in geographic space (Booth *et al.*, 2014). An individualistic modeling of species distribution was used in our study. This community level approach, known as 'predict first, assemble later' or Stacked -SDM, provides more accurate projections and does not tend to over predict species richness (Baselga and Araujo, 2009). To account for the species total realized niches, the models were fitted and projected to the American continent, and then cropped to the shape of Mexico, our study region (Broennimann *et al.*, 2006).

For SDMs construction, the minimum necessary number of occurrence points per species is three (van Proosdij *et al.*, 2016). From the total of 2058 tree species in this study, 84 had less than three occurrence points, therefore they were excluded from the analysis. For the rest of 1974 species, the MNFSI-BIEN3 data were split in two sets based on a threshold of ten unique occurrence points. The SDMs for species with ten or more occurrence points were fitted to climatic data using the package 'maxnet' (version 0.1.2) that implements MaxEnt using the ‘glmnet’ R package. (Phillips *et al.,* 2017). For species with nine to three occurrence points, we decided to use a more simplistic, rectilinear approach than MaxEnt to avoid overfitting of the models. This simpler approach was the BIOCLIM function on the ‘dismo’ R package (Hijmans *et al*., 2017).

MaxEnt is a general-purpose machine learning method for presence-only modeling of species distributions (Phillips *et al.*, 2006). This method estimates the closest to uniform probability distribution, using the pixels of the study area with known species occurrence records as sample points, and environmental variables as features, allowing the detection of new or relevant response shapes (Merow *et al.*, 2014). BIOCLIM, on the other hand, predicts suitable conditions in an environmental space that represents the range of observed presence values in each environmental dimension. (Phillips *et al.*, 2006 and Booth *et al.*, 2014). Using a simpler approach such as BIOCLIM, reduces overfitting and helps to understand the primary drivers of species distributions. (Merow *et al.*, 2014)

For the SDMs built in ‘maxnet’, default features and regularization parameters were selected. As our data were presence only, we generated 2000 pseudo-absence points for each species from a delimited background, excluding the points where the species was recorded. The delimited background consisted in an area containing the targeted species’ presence points and a 9^0 (999 Km) buffer region around them to encompass all the environmental conditions of locations where the species are likely to reach via dispersion (Merow *et al.*, 2013).

For the SDMs built in BIOCLIM, default parameters were selected as well. This method is based on presence-only data, therefore, there were no pseudo-absence points generated for species modeled using this approach.

The models for each species were created with all presence points available after the thinning process. For fitting the models, we did not consider non-climatic factors such as land use or biological interactions. In addition, we assumed that the current relationship between species distributions and environmental variables is stable (Thuiller *et al.*, 2006 a). Another model assumption was that the trees have unlimited dispersal abilities.

For each species, the model obtained was used to project the species' presence on the Mexican country into the present. We use the clog-log output for model prediction that gives a probability value of suitability estimate between 0 and 1 (Phillips, 2017). Potential tree species distributions in Mexico for the year 2070 were obtained by projecting each of the 1974 individual SDMs to 17 General Circulation Models (Coupled Model Intercomparison Project 5 -CMIP5) under RCP 8.5 (IPCC, 2014).

2.5 Species richness in the present and the impact of future climate change.

We estimate the local species richness value by adding the species' occurrence probability in each map cell. We did not convert the probability values of occurrence of each map cell into a binary statement of presence/absence because this practice has been reported to produce a strong bias in the direction of overprediction (Calabrese *et al.*, 2014). For species richness estimations, we worked with local richness values at a scale of 10 km x 10 km (a map cell). All maps have a resolution of 5 arc-minute of a longitude/latitude degree (about 10 km at the equator).

The 1974 SDMs obtained for the present time, were stacked and summed to obtain one map of the current predicted richness of Mexican tree species in each cell. The 1974 projections corresponding to each one of the 17 CMIP5 Global Circulation Models were stacked and summed, to obtain the predicted richness of tree species in each cell for the 17 future General Circulation Models. These 17 Staked-SDMs were then averaged to obtain one map of the mean future species richness prediction for Mexico.

To calculate the climate change impact on species richness for the year 2070 in Mexico, the Stacked – SDM that predicts the richness of tree species for the present time was subtracted from each of the 17 Stacked - SDMs that predict the richness of tree species for future climatic scenarios (i.e. $\text{future}_{[\,i\,]}$ - present). The differences calculated were averaged to obtain a map of the mean predicted gain/loss of tree species for year 2070.

The three maps obtained (map of current species richness, map of future species richness, and map of mean predicted gain/loss of tree species), were subdivided into the seven Mexican ecoregions to assess the impact of climate change on the tree local richness of each area. We considered ecoregions as the geographic space where the biological units are currently located, that is, we use the present geographic boundaries for the analysis of the local richness in the present and in the future. In that sense, we are using the ecoregion as a geographic rather than a biological unit.

The analysis of the richness was conducted for all the tree species and for the endemic species only. The endemic species list for our study was elaborated by us. By visually inspecting the geographic distribution of the tree species in BIEN3 we categorize species as endemics if they had more than 50% of their presences points reported inside Mexico.

To describe tree species richness patterns in the future and in the present, we considered three parameters: 1) minimum number of local species richness for the country and per ecoregion, 2) maximum number of local species richness for the country and per ecoregion, and 3) the local average richness value. In the assessment of the impact of climate change on total and endemic tree species richness for Mexico and per ecoregion, we calculated the difference between the current and the future mean local species richness. To perform a more intuitive diagnostic of the change of local richness, we considered that cells losing species are those with a decline in more than five percent of their species number, and that cells gaining species are those with an increase in more than five percent of their species number. For the cells that gained or lost five percent or less of their species, we considered that a non-significative change happened.

All analyses were performed in R version 3.3.3 (R Development Core Team, 2017)

3. RESULTS

In the MNFSI-BIEN3 data set, 2058 tree species were registered for Mexico. From the total of species, we modeled 1974 species, 84 were not included in the analysis due to insufficient presence points reported for them. Of the sample modeled, 595 species were identified as endemic.

3.1 Current tree species richness pattern

Total richness

For Mexico, the current local richness (per cell of 10 km x 10 km) ranges from 24 to 770 tree species (Fig. 2A and 2B), with an average of 203 species. When the analysis was performed per ecoregion, the highest species richness values are predicted to be found in the forests (Fig. 2B). The maximum richness value per cell, 770, was found in the tropical rainforest (Fig. 3, first column). This ecoregion has the highest mean number of species per cell (416), followed by tropical dry and temperate forests with local average richness values of 283 and 282 respectively. Semi-arid Southern Uplands has intermediate mean richness, with a value of 123. Great Plains, Mediterranean California, and North American deserts show the lowest local mean richness values, between 81 and 62 species per cell. North American deserts also has the minimum local value of richness reported (24 species).

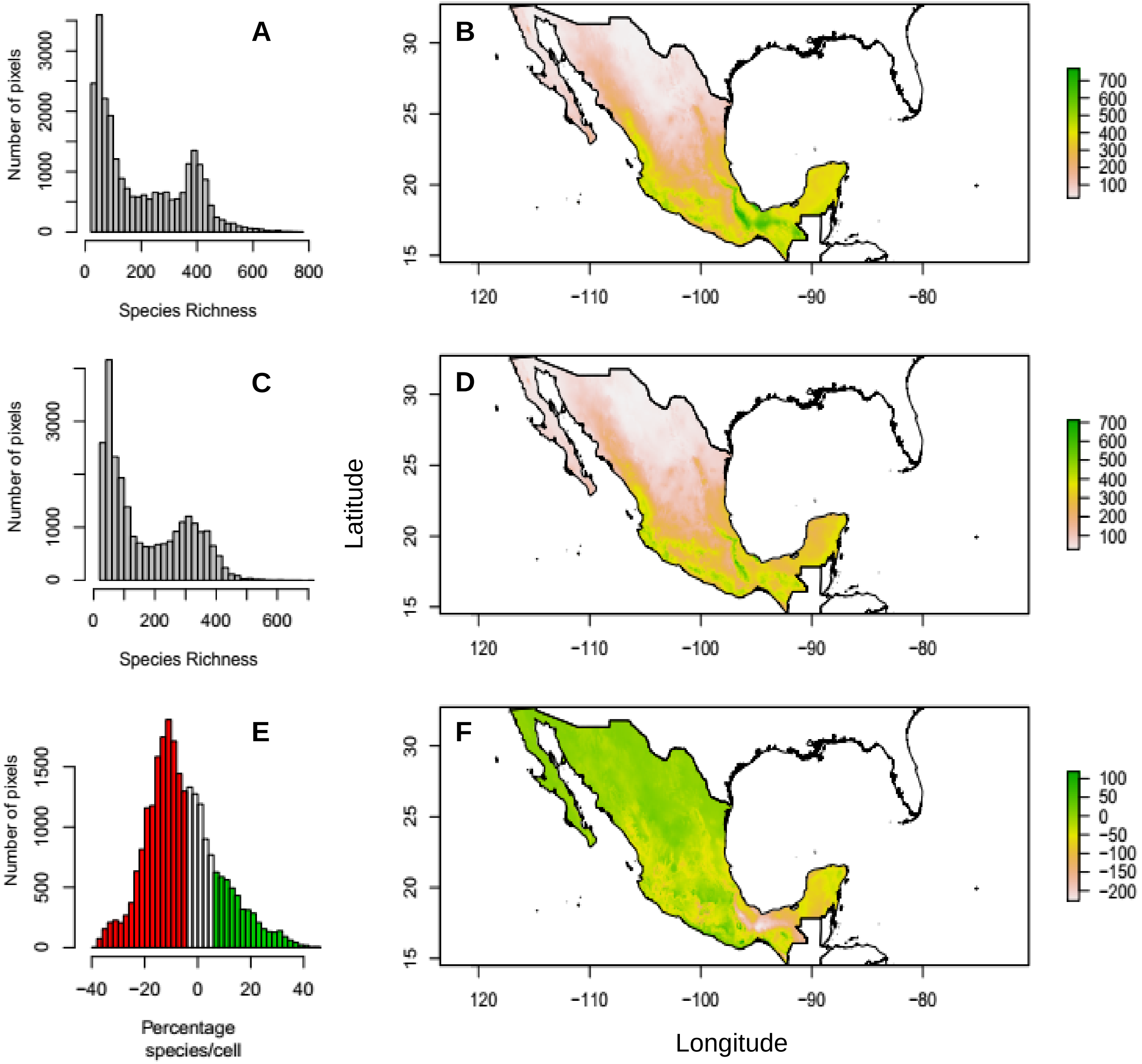

Figure 2. Impact of climate change on local tree species richness in Mexico. A) Current frequency of species richness per cell. B) Current predicted species richness C) Future frequency of species richness per cell. D) Averaged future species richness. E) Percentage of species gained/lost per cell for year 2070 (red color: species loss, green color: species gain, white color: no significative change). F) Averaged predicted gain/loss of total tree species for year 2070.

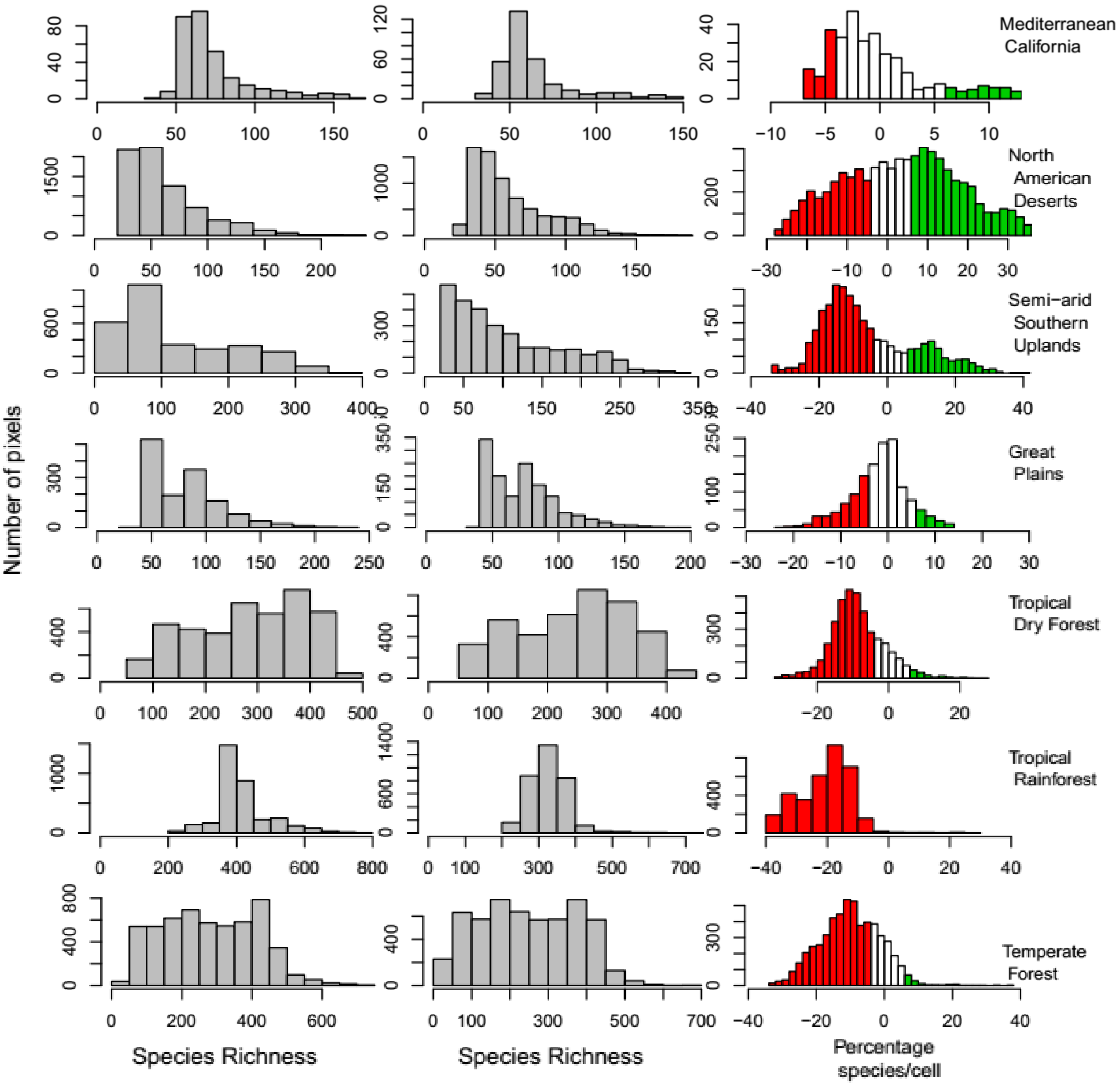

Figure 3. Impact of climate change on local tree species richness per ecoregion. (Red color represents the loss of species, green color represents the gain of species, white color represents non-significative change in local species richness).

Endemic richness

For Mexico, the endemic local richness ranges from two to 187, with a mean value of 61 species. In the analysis per ecoregion, the highest local values of endemic richness are also found on the forests (Fig. 5, first column). In the temperate Forest, species numbers are the highest, ranging from five to 187, with a mean local richness of 100 species. Tropical dry forest and tropical rainforest follow with an average of endemic local richness values of 94 and 84 respectively. On the other hand, the lowest local species richness is reported for Mediterranean California, North American desert, great plains and semi-arid southern uplands, with average values between 15 and 45 species. The minimum number of species per cell is reported for the North American desert (two species).

3.2 Future tree species richness and the impact of the climate change

Total richness

Projections for the Mexican country (Fig. 2C and 2D) forecast a decline in the local tree species number. The richness values per cell are predicted to be between a minimum of 26 species and a maximum of 713. The average local species richness per cell will decrease in a 14.29%, from 203 species to 174 (Table 1). When analyzed the balance of local species lost and gained predicted for year 2070 in the country (Fig. 2E and 2F) we obtained that, in general, there will be a higher number of species lost than gained. Local richness will decrease in more than five percent of its species in more than half of the Mexican territory (Table 1, Fig. 2E). The maximum number of species lost will be 227. Gain of species (more than 5%) will occur only in 19.90% of Mexico. In those cells, the richness increase will range from 1 to 118 species.

Region	Mean species number/cell		Mean loss of species	% of species loss	Cells gaining species (%)	Cells losing species (%)	Maximum species lost	Maximum species gained
	Current	Future						
Mediterranean California	74	64	10	13.51	14.02	4.88	9	7
North American Deserts	62	60	2	3.23	48.12	28.18	61	22
Semi-arid Southern Uplands	123	105	18	14.63	22.54	60.63	90	24
Great Plains	81	74	7	8.64	10.32	20.63	49	9
Tropical Dry Forest	283	243	40	14.13	4.18	69.40	144	65
Tropical Rainforest	416	326	90	21.63	0.56	98.42	227	64
Temperate Forest	282	248	34	12.06	3.64	66.67	181	118
Mexico	203	174	29	14.29	19.90	57.29	227	118

Table 1. Balance of loss and gain of local species per ecoregion and for Mexico. Cells gaining species are those in which the increase in species number is more than 5%. Cells losing species are those in which the decrease in species number is more than 5%.

Our models predicted that, in all ecoregions, the mean local species richness will decrease (Table 1 and Fig.3, second column). In this respect, the most impacted region will be the tropical rainforest, with a decrease of the 22%, from 416 to 326 in the average number of species per cell. In the rest of the ecoregions the percentage of decline of mean species richness per cell will be below 15%, being the less affected the North American desert with a decrease of only 3%.

The analysis of the balance of local species lost and gained (Table 1 and Fig.3, third column) yielded that four out of seven ecoregions are projected to suffer loss in more than half of their map cells. These four ecoregions are the semi-arid southern uplands, the tropical dry forest, the tropical rainforest, and the temperate forest. The most drastically affected ecoregion is the tropical rainforest, where 98% of its territory is forecasted to lose up to a maximum of 227 species. In the 0.6% of the tropical rainforest that will gain species locally, the maximum number gained will be 64. Tropical dry forest, temperate forest and semi-arid southern uplands will lose species in 60-70% of their areas. For the tropical dry forest, the gain of species is reported in only 4% of its area. Temperate forests show the highest number of species gained locally (181), this gain however is a maximum value and will be restricted to 4% of its territory. In the case of the semi-arid southern uplands, although it is projected to lose up to 90 species in 61% of its territory, it is also the second ecoregion with more percentage of area (23%) predicted to gain more than five percent of species per cell.

The three ecoregions where the loss of species is projected to happen in less than half of their territories are the North American deserts, Mediterranean California, and the great plains (Table 1). In the North American desert, it is also reported the highest percentage of territory with a projected increased local species richness (48%), this gain however, will not be greater than 22 tree species in any location. Great Plains and Mediterranean California have the highest percentage of area where the change in local species number will be non- significative with 81% and 69%, respectively (Fig 3, third column). In addition, in the Mediterranean California the percentage of area gaining species is forecasted to be three times greater than that losing species, and the maximum number of local species lost and gained are comparable.

Endemic richness

In the future, endemic species will also show a general decrease in local species richness (Fig. 4C and 4D). For Mexico, the average local richness will decrease a in 13.11%, from 61 in the present to 53 (Table 2). Local richness values are predicted to be between a minimum of 2 species and a maximum of 181. The average future gain/loss of endemics predicted for year 2070 (Fig.4E and 4F) shows that, there will be a higher number of species lost than gained. Local endemic richness will decrease in more than half of the country (55%). The maximum number of species lost will be 49. Gain of species will occur in 26.79% of Mexico. In those cells, the local richness increase will range from 1 to 38 endemic species.

The mean local endemic species richness will decrease in all ecoregions except for Mediterranean California, where it will remain unchanged (Table 2). Regarding this parameter, the most impacted region will be the semi-arid southern uplands, with a decline from 45 to 36 in the average number of species per cell. In the rest of the ecoregions the percentage of decline of mean local species richness will be below 13%.

The analysis of the impact of the climate change on local endemic tree richness per ecoregion (Table 2 and Fig.5, third column), shows species loss in more than half of the cells for four out of the seven ecoregions. These four ecoregions are the semi-arid southern uplands, the tropical dry forest, the tropical rainforest, and the temperate forest. The most drastically affected ecoregion is the tropical rainforest, losing local species in 75% of its area. For this ecoregion, the maximum of local species lost forecasted will be 37.

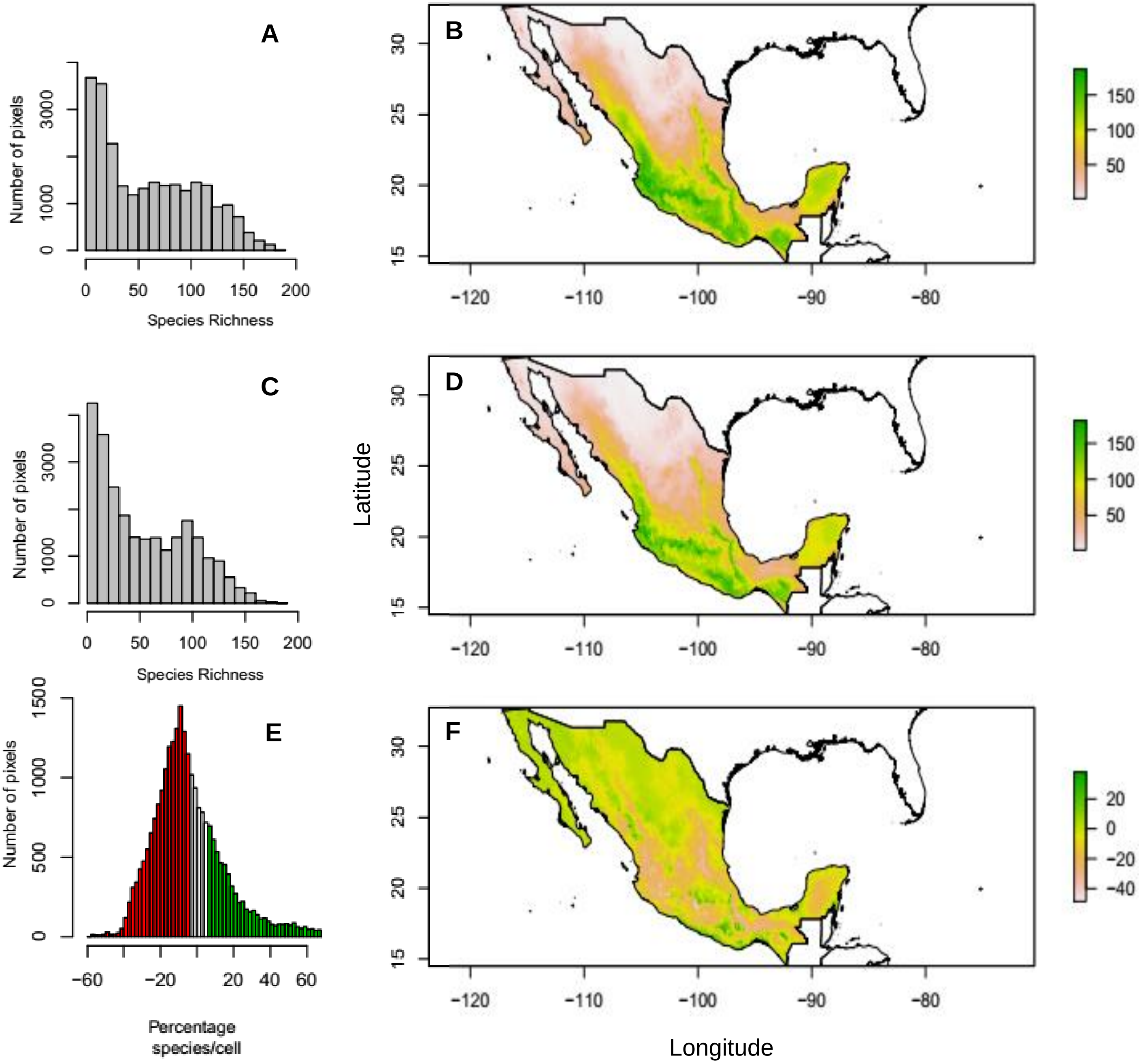

Figure 4. Impact of climate change on local endemic tree species richness in Mexico. A) Current frequency of species richness per cell. B) Current predicted species richness C) Future frequency of species richness per cell. D) Averaged future species richness. E) Percentage of species gained/lost per cell for year 2070 (red color: species loss, green color: species gain, white color: no significative change). F) Averaged predicted gain/loss of endemic tree species for year 2070.

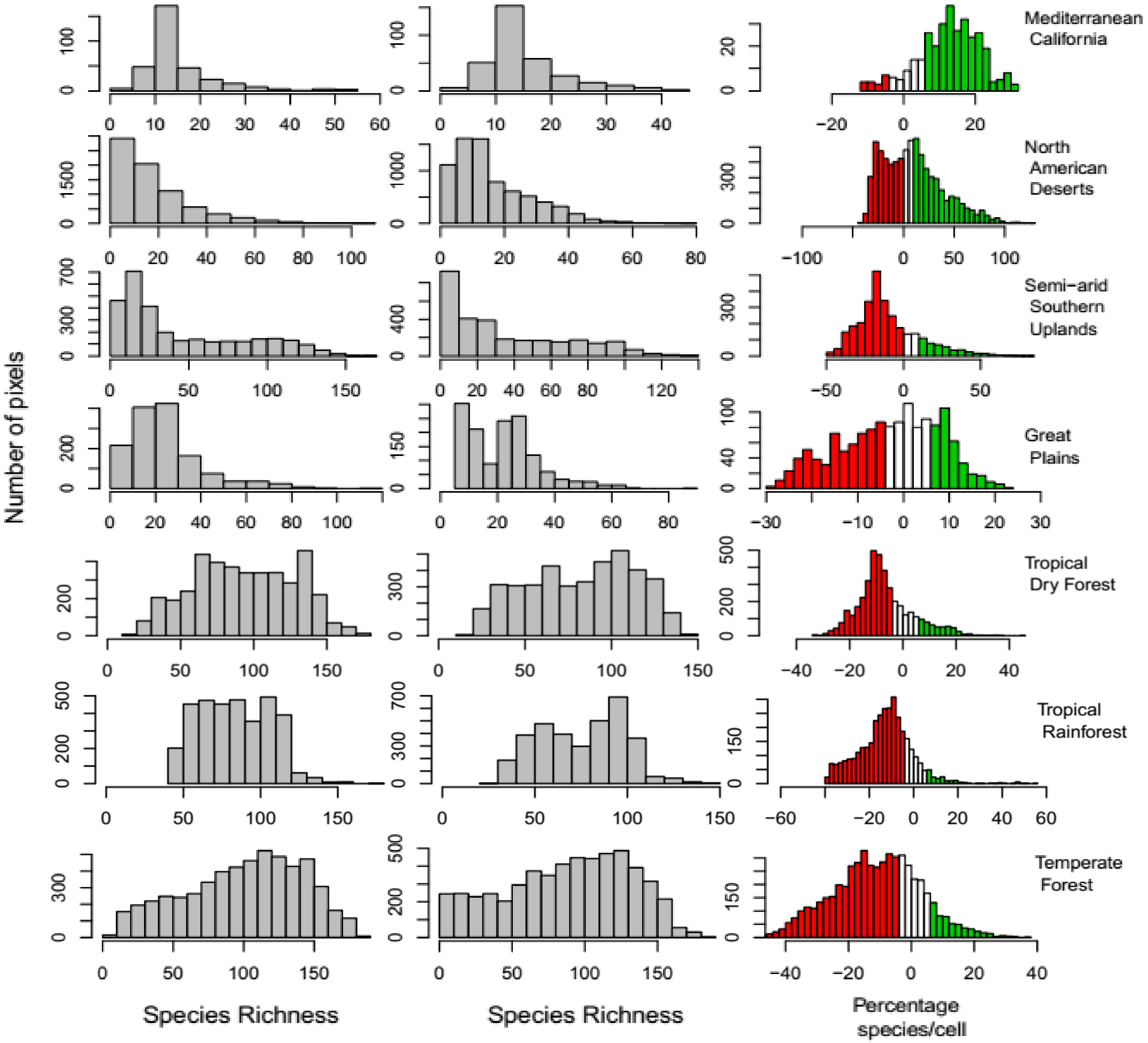

Figure 5. Impact of climate change on local endemic tree species richness per Mexican ecoregion (Red color represents the loss of species, green color represents the gain of species, white color represents non-significative change in local species richness).

Tropical rainforest is also the only ecoregion where the percentage of area gaining endemic species is lower than 10%. In the proportion of the tropical rainforest that will gain species, the maximum number gained will be 29. Tropical dry forest, temperate forest and semi-arid southern uplands will lose species in 60-70% of their areas and will gain species in less than 25% of their areas.

Region	Mean species number/cell		Mean loss of species	% of species loss	Cells gaining species (%)	Cells losing species (%)	Maximum species lost	Maximum species gained
	Current	Future						
Mediterranean California	15	15	0	0.00	82.32	3.35	5	3
North American Deserts	18	16	2	11.11	52.23	34.32	36	8
Semi-arid Southern Uplands	45	36	9	20.00	20.42	67.30	40	8
Great Plains	24	22	2	8.33	27.65	37.54	28	4
Tropical Dry Forest	94	82	12	12.77	13.79	62.07	47	27
Tropical Rainforest	84	76	8	9.52	5.89	74.83	37	29
Temperate Forest	100	88	12	12.00	11.23	62.95	49	38
Mexico	61	53	8	13.11	26.79	55.40	49	38

Table 2. Balance of loss and gain of local endemic species per ecoregion and for Mexico. Cells gaining species are those in which the increase in species number is more than 5%. Cells losing species are those in which the decrease in species number is more than 5%.

North American deserts, Mediterranean California, and the great plains are the three ecoregions forecasted to lose local species in less than half of their territories (Table 2 and Fig.5, third column). In the Mediterranean California, it is also reported the highest percentage of area with a projected increase in local species richness (82%), this gain however, will not be greater than 3 tree species in any location. Great Plains ecoregion has the highest percentage of area where the change in local species number will be non-significative (35%). The north American desert, on the other hand, is projected to gain more than five percent of species in half of its area.

4. DISCUSSION

4.1 Current tree species richness pattern

The highest total species richness is found on the Sierra Madre Mountains and the Yucatan Peninsula, location of the madrean pine-oak woodlands and the Mesoamerican forests, two of the world's biodiversity hotspots. Madrean pine-oak woodlands harbors one-quarter of all Mexico's plant species, and the Mesoamerican forests are the third largest among the world's hotspots (Myers *et al.,* 2000). As expected, the lowest species richness values are reported in arid and semi - arid regions where the reduced water availability and high temperatures usually limit the formation of forests.

The pattern of species richness for the endemic tress is similar, with the highest concentration of species in the biodiversity hotspots area, particularly in the mountainous temperate forests. This result coincides with other studies in Europe, Nepal and Bolivia that have found a positive relationship between endemic vascular plant richness and altitude (Cañadas *et al.*, 2014; Vetaas and Grytnes, 2002; Kessler, 2000). The high levels of species endemism mentioned by other authors (Sarukhán *et al.,* 2009 and Myers *et al*, 2000) are evident in our sample as well, since areas with more than 100 endemic species per cell encompass one quarter of the Mexican territory.

4.2 Climate change and total species richness

4.2.1. Future tree species richness for Mexico

In Mexico, future climate change will produce a decline in the mean local tree species number. In addition, the amount of area projected to lose more than five percent of its species is three times the amount of area predicted to gain more than five percent.

Decreasing or disappearance of areas with suitable climatic conditions for the survival of species is probably the cause of this predicted local loss of tree richness for Mexico. By year 2100, novel and disappearing climates are projected to occur as result of global warming, mainly in tropical mountains and biodiversity hotspots such as Mesoamerica (Williams *et al.*, 2007), producing a decline in the regional capacity for plants species richness (Sommer *et al.*, 2010) and increasing the probability of species extinctions. Wiens (2016), in a metanalysis, found that climate-related extinctions are more common in species from the tropics since their climatic niches are narrow in association with less variation in the daily and seasonal temperatures. It is valid also to consider the probability of further reduction in the species richness due to an extinction debt in portions of ranges still occupied by tree species that would have become climatically unsuitable for them by 2070 (Dullinger *et al.*, 2011).

A contrasting result is offered by Iverson and Prasad (2001) when predicting an increase in average species richness across eastern United Stated linked to climatic change. They found that locations with the lowest species richness in the present were predicted to have additional species in the future, and that this richness increase occurs linearly with the increase temperature of the climate change scenario used.

4.2.2 Future tree species richness per ecoregion.

There is a differential impact of the climate change on the local species richness of the different ecoregions. This impact is projected to be greatest on Mexican forests, evidencing that, in the future, the conditions where the trees' climatic niche is fulfilled will occur in fewer cells than in the present for those ecoregions. As we mentioned in the

Methods section, we are referring to ecoregions as the geographical units rather than the biological ones, and we have not considered the spatial shift of biological units due to climate changes.

The tropical rainforest, currently with the highest mean local richness value, it is also the ecoregion with higher species decrease risk, losing up to 227 species throughout its territory. In addition to our predictions, it is the fact that only 14.3% of the surface of the Mexican tropical rainforest is included on Natural Protected Areas (Cantu Ayala *et al.*, 2013), making the future fate of this ecoregion more preoccupant. The case of the tropical dry forest is not less alarming, being part of the group with highest proportion of area losing tree species and with only 6.6% of its extension included Natural Protected Areas (Cantu Ayala *et al.*, 2013). The local decline in forests tree species richness found in this study points towards a savannization of these areas. This process was previously described by Anadon *et al.* (2014) in their study of transition areas in tropical and subtropical Americas where they found that, for year 2070, forests will decrease in area turning into savannas and causing not only a decline in species richness and overall biodiversity but also affecting systems stability and ecosystems functions and services.

Our results are not isolated findings, other highly biodiverse tropical forests, such as the Amazon’s and Central America’s (Allen *et al.*, 2010), are predicted to suffer background tree mortality produced by drought and increasing concentrations of greenhouse gases linked to future warming. In general, low land forest plants, when compared with highland areas, respond less effectively to climate change velocities (Bertrand *et al.* 2011) because of the greater habitat fragmentation that reduces the chance for short-distance migrations.

On the other hand, a more optimistic view is provided by Huntingford *et al.* (2013), that obtained only in one of the 22 climate models they tested, predictions of tropical trees biomass loss in the Americas by the end of this century, pointing to a resilience capacity not evident in our results. In concordance with Huntingford *et al.*, Malhi *et al.* (2009) predicted that, for the Amazon's rainforest, increasing dry-season water stress will turn the climate more appropriate for a seasonal forest -and not a savanna-, resilient to drought but vulnerable to fires.

For the temperate forest, our findings also show a severe impact of climate change on the local tree species richness of this territory for year 2070. Under climate warming, a significant decrease on climatically suitable areas for cold-adapted species probably will occur (Ruiz-Labourdette *et al.*, 2012). In addition, mountainous species usually face a lack of potentially colonizable area upward. Accompanying the increase in temperatures and the restricted migration space on the mountain tops; drought and severe wildfire are currently producing a tree mortality never registered for the temperate forest on the past century (Millar and Stephenson, 2015), a condition that could be aggravated in the future.

Opposite to our results, Steinbauer *et al.* (2018) found and acceleration in the rate of increase in plant species richness on mountain summits across all Europe. The authors stated that this increase in richness is driven by the accelerated global warming that is producing upward shifts of species ranges in mountains. This discrepancy could be explained by the fact that, in our models, we considered a time span of only 50 years while the study of Steinbauer *et al.* is based on 145 years of observations. It is possible that by year 2070, the Mexican tree species will still be tracking the climate change because there has not been enough time for them to change their range of distribution, therefore not showing an increase in species richness on the Temperate Forest.

In our study, North American deserts are forecasted to moderately gain local species richness in roughly half of its extension. As arid ecosystems are water-limited, this result could be associated to an increase in precipitation that would promote the growth and reproduction of higher plants (Schwinning and Sala, 2004). Anadon *et al.* (2014), predicted a savannization of Chilean and Peruvian deserts that aligns with the increased tree richness found by us for the North American deserts. However, these same authors forecasted a patchy increase in the extent of the North American deserts. Other studies have also predicted significant decrease in tree richness for the deserts of the South West of United States associated with very high summer and mean annual temperature, decreasing in cool season precipitation and increased aridity (Currie, 2001; Munson *et al.*, 2012).

Mediterranean California forms part of the group of ecoregions with less than half of its area losing tree species richness. This ecoregion is also forecasted to maintain the greatest percentage of area where the local species richness change will be non-significative. The expansion of suitable climatic territories for Mediterranean species has been found to cause an increase in the forested area in which such species coexist. (Hernandez *et al.*, 2017). These species tolerant of high temperatures and drought in the summer were projected to increase their range up to a 350% at a constant elevation, under a future scenario with severe changes in human population and CO_2 levels (Ruiz-Labourdette *et al.*,2012). Although we only measured the impact of climate change on species richness, our results support the idea of a not hostile future climate for the Mediterranean ecoregion. A more recent research (Polade *et al.*, 2017), related to hydro-climate changes in the five Mediterranean-climate regions of the world, has found that contrary to the prediction for the other four zones, California's future projections show a general tendency towards increased winter precipitation. These authors claim, however, that this tendency is subtle, and that particularly for northern Baja California (Mexico) the average winter precipitation will decrease in a 10% for late twenty-first century.

Great Plains is predicted to maintain the second greatest percentage of area where the change in local species richness will be non-significative, and it is part of the group of ecoregions that will lose species in less than half of its territory. Semi-Arid Southern uplands, however, forms part of the group of ecoregions with a high proportion of area losing local species richness. To our knowledge, there is a lack of literature addressing the impact of climate change on tree species richness or distribution for these two territories. Arid and semi-arid ecosystems are an extreme in which essential resources such as water are not available. According to Schwinning and Sala (2004) climate change together with human activity will probably reduce the abundance of native species and even produce some local extinctions in these ecoregions, while allowing an increase of the abundance of non-native species, affecting the species richness and composition of the communities.

4.3 Climate change and endemic species richness

In general, local endemic tree species richness showed a similar future decline due to climate change as the entire Mexican tree community. The case of endemic species requires special attention since they occur naturally in restricted environmental and geographic ranges, being more susceptible to extinction produced by climate change. Endemic trees richness has been predicted to severely suffer the consequences of climate change in other highly biodiverse regions of the world such as Namibia with an average loss of 41% endemic tree species by 2050 (Broennimann *et al.*, 2006). In this same region, Thuiller *et al.* (2006 b), assuming full migration like our study, predicted for year 2080 a reduction in endemic tree species' ranges of up to 43% of their current distribution. According to these authors, the strong sensitivity of endemic trees is linked to the stress produced by the severe reduction in precipitation and increase in temperatures forecasted for the period.

In our study, endemic tree richness is projected to suffer the greatest decline in the forests. According to Dirnböck *et al.* (2011), endemic species in mountains will be particularly affected by habitat loss because they frequently are habitat specialists selected for traits advantageous under stable environmental conditions. The only case where our models predicted that the mean endemic species richness would remain the same in the future was for Mediterranean California ecoregion, characterized by rare and locally endemic taxa that survive as small populations. This ecoregion is also predicted to gain more than five percent of species per pixel in more than 80% of its area. This result could be an indicative that the future climate conditions will fall inside the climatic niche of the endemic trees from Mediterranean California.

4.4 Study limitations and future steps

Our study has certain limitations that could influence our model outputs. In constructing our SDMs we considered that all the tree species have the ability for unlimited migration, therefore, we are assuming that there is no disjunction between the velocity of climate change and the ability of trees to track such changes. It is important to mention that studies considering limited migration in trees have found that the species analyzed would lag behind the projected climate change, with migration velocities up to 50% lower than the needed to keep pace with the climate range shift (Nathan *et al.*, 2011; Miller and McGill, 2018; Sittaro *et al.*, 2017, Pearson, 2006; Corlett and Wescott, 2013). The previous statement demonstrates that our predictions are optimistic, and that if we had considered limited dispersal it is probable that our results would be showing an even more critical decline in the local tree species richness.

Another limitation of our study is that we did not include in the models biotic interactions and changes in land use, factors that have been encountered to improve model outputs accuracy and ecological realism (Broennimann *et al.*, 2006). Additionally, we constructed the models with a coarse spatial scale that does not capture topography or "microclimatic buffering" (Willis and Bhagwat, 2009) that could mitigate regional temperature changes and decrease extirpation risks (Lenoir *et al.* 2016). Furthermore, we did not account for the arrival of new tree species from the pool of adjacent countries, a factor that can produce changes in the Mexican species richness.

Currently, the impact of climate change on other important dimensions of the communities such as functional diversity and phylogenetic richness is attracting the interest of biologists (Ordonez and Svenning, 2017; Graham *et al.*, 2017), but is yet a field to explore. Our future steps will be directed toward the prediction of future novel and disappearing tree community assemblages at the taxonomic, functional and phylogenetic levels. Assessing the impact of climate change in the formation of novel (and disappearance of known) community assemblages will allow us to identify possible shifts in ecosystem functioning that could cause ecological disequilibria and long-lasting ecosystem level effects (Ordonez and Svenning, 2017).

5. CONCLUSIONS

- Currently, we identified a total of 2058 tree species for Mexico. We modeled 1974 species from which 595 were classified as endemics.
- The highest local tree species richness is found in the tropical rainforest with a value of 770. The lowest local richness value, on the other hand, is in the North American desert with a value of 24.
- Under future climate change scenario, we have predicted a 14.29% decline in the mean local species richness in Mexico from 203 to 174. The endemic mean local species richness will be similarly affected, decreasing in a 13.11% from 61 to 53.
- The ecoregions most affected by the decrease of local species number are the tropical rainforests, losing species in 98% of its area; and tropical dry forests and temperate forests, projected to lose species in more than 60% if their areas.
- For the tree community, the ecoregion with highest percentage of territory (48%) projected to increase its local species number will be the North American desert.
- For the endemic trees, the Mediterranean California is the ecoregion with highest percentage of territory (82%) projected gain more than five percent of local species number, while the mean local species richness per cell will remain unchanged (15 species), suggesting that future climate change will be favorable for the trees of this area.
- The local loss of species in the forests and gain of species in arid regions such as the desert, supports the idea of a savannization of the ecoregions as a response of trees to the climate change, a process described by other authors in previous studies.

6. REFERENCES

Aiello-Lammens M.E., Boria R.A., Radosavljevic A., Vilela B. and R.P. Anderson. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545.

Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D., Hogg E.H., Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova D., Lim J.-H., Allard G., Running S.W., Semerci A. and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 2(59): 660–684.

Anadón J.D., Sala O.E. and F.T. Maestre. 2014. Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. *J Ecol*, 102: 1363-1373.

Anadón J.D., Giménez A., Graciá E., Pérez I., Ferrández M., Fahd S., El Mouden H., Kalboussi M., Jdeidi T., Larbes S., Rouag R., Slimani T., Znari M. and U. Fritz. 2012. Distribution of Testudo graeca in the western Mediterranean according to climatic factors. *Amphibia-Reptilia* 33: 285-296.

Baselga A. and M.B. Araújo. 2009. Individualistic vs community modelling of species distributions under climate change. *Ecography* 32(1): 55-65.

Bertrand R., Lenoir J., Piedallu C., Riofrío-Dillon G.,de Ruffray P., Vidal C., Pierrat J.C., and J. C. Gégout. 2011.Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479: 517–520.

Booth T.H., Nix H.A., Busby J.R., and M.F. Hutchinson. 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions* 20: 1–9.

Broennimann O., Thuiller W., Hughes G., Midgley G.F., Alkemade J.M.R. and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* 12 (6):1079-1093.

Calabrese J.M., Certain G., Kraan C. and C.F. Dormann. 2014. Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecol. Biogeogr*. 23: 99–112.

Cantu Ayala C.M., Estrada Arellano J.R., Salinas Rodríguez M.M., Marmolejo Moncivais J.G. and E.A. Estrada Castillón. 2013. Gaps and omissions in conservation of mountain ecoregions in Mexico. *Rev. Mex. Cien. For*. 4(17): 10-27

Cañadas E.M., Fenu G., Peñas J., Lorite J., Mattana E. and G. Bacchetta . 2014. Hotspots within hotspots: Endemic plant richness, environmental drivers, and implications for conservation. *Biological Conservation* 170: 282-291.

Chakraborty A., Joshi P.K. and K. Sachdeva. 2016. Predicting distribution of major forest tree species to potential impacts of climate change in the central Himalayan region. *Ecological Engineering* 97: 593–609.

CONAFOR (Forestry National Commission). 2012. National Forest and Soil Inventory, Report 2004-2009, 228 pp., Zapopan, Jalisco, Mexico.

Corlett R.T. and D.A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology and Evolution* 28(8): 482-488.

Curie D.J. 2001. Projected Effects of Climate Change on Patterns of Vertebrate and Tree Species Richness in the Conterminous United States. *Ecosystems* 4: 216–225.

Dirnböck T., Essl F. and W. Grabitsch. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology* 17: 990–996.

Dullinger S., Gattringer A., Thuiller W., Moser D., Zimmermann N.E., Guisan A., Willner W., Plutzar C., Leitner M., Mang T., Caccianiga M., Dirnböck T., Ertl S., Fischer A., Lenoir J., Svenning J.-C., Psomas A., Schmatz D.R., Silc U., Vittoz P. and K. Hülber. 2011. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change* 2: 619–622.

Dyderski M.K., Paź S., Frelich L.E. and A.M Jagodziński. 2018. How much does climate change threaten European forest tree species distributions? *Glob Change Biol*.24:1150–1163.

Enquist B.J., Sandel B., Boyle B., Svenning J.-C., McGill B.J., Donoghue J.C., Hinchliff C.E., Jorgensen P.M., Kraft N.J.B., Marcuse-Kubitza A., Merow C., Morueta-

Holme N., Peet R.K., Schildhauer M., Spencer N., Regetz J., Simova I., Smith S.A., Thiers B., Violle C., Wiser S.K., Andelman S., Casler N., Condit R., Dolins S., Guaderrama D., Maitner B.S., Narro M.L., Ott J.E., Phillips O., Sloat L.L. and ter Steege H. (in prep.). Botanical big data shows that plant diversity in the New World is driven by climatic-linked differences in evolutionary rates and biotic exclusion.

EPA (United States Environmental Protection Agency Website). Visited: 4/15/2018, 11:30AM. https://www.epa.gov/climate-indicators/greenhouse-gases

Fei S., Desprez J.M., Potter K.M., Jo I., Knott J.A. and C.M. Oswalt. 2017.Divergence of species responses to climate change. *Science Advances* 3(5): e1603055.

Ferrier S. and A. Guisan. 2006. Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology* 43, 393–404.

Guisan A. and C Rahbek. 2011. SESAM– a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography* 38: 1433–1444.

Graham L.J., Weinstein B.G., Supp S.R. and C.H. Graham. 2017. Future geographic patterns of novel and disappearing assemblages across three dimensions of diversity: A case study with Ecuadorian hummingbirds. *Diversity and Distributions* 23:944–954.

Hernandez L., Sanchez de Dios R., Montes F., Sainz-Ollero H. and I. Canellas. 2017. Exploring range shifts of contrasting tree species across a bioclimatic transition zone. *Eur J Forest Res* 136:481–492.

Hijmans R.J., Phillips S., Leathwick J. and J. Elith. 2017. Vignette for Package 'dismo'. https://cran.r-project.org/web/packages/dismo/dismo.pdf.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.

Huntingford, C., Zelazowski P., Galbraith D., Mercado L.M., Sitch S., Fisher R., Lomas M., Walker A.P., Jones C.D., Booth B.B.B., Malhi Y., Hemming D., Kay G., Good P., Lewis S.L., Phillips O.L., Atkin O.K., Lloyd J., Gloor E., Zaragoza-Castells J., Meir P., Betts R., Harris P.P., Nobre C., Marengo J. and P.M. Cox. 2013. Simulated resilience of tropical rainforests to CO2-induced climate change. *Nature Geoscience* 6: 268-273.

INEGI (National Institute of Statistics, Geography and Informatics). 2017. Statistic and geographic yearbook of the Mexican United States. Mexico, 1069 pp.

INEGI (National Institute of Statistics, Geography and Informatics), CONABIO (National Commission for the Knowledge and Use of Biodiversity) and INE (National Institute of Ecology). 2008. Terrestrial Ecoregions of Mexico. Scale 1:1000000. Mexico

IPCC (Intergovernmental Panel on Climate Change). 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

IPCC (Intergovernmental Panel on Climate Change). 2013. Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 27 pp.

Iverson L.R. and A.M. Prasad. 2001. Potential Changes in Tree Species Richness and Forest Community Types following Climate Change. *Ecosystems* 4: 186–199.

Kerns B.K, Powell D.C., Mellmann-Brown S., Carnwath G. and J.B. Kim. 2017. Effects of projected climate change on vegetation in the Blue Mountains ecoregion, USA. *Climate Services*. 11 pp.

Kessler M. 2000. Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecology* 149: 181–193.

Lenoir J., Hattab T. and G. Pierre. 2016. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography* 40: 253–266.

Lenoir J. and J.-C. Svenning. 2014. Climate-related range shifts-a global multidimensional synthesis and new research directions. *Ecography* 38: 15–28.

Lenoir J., Gegout G.C., Pierrat G.C., Bontemps J.D. and J.F. Dhote. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). *Ecography* 32: 765-777.

Maitner B.S., Boyle B., Casler N., Condit R., Donoghue II J., Durán S.M., Guaderrama D., Hinchliff C.E., Jørgensen P.M., Kraft N.J.B., McGill B., Merow C., Morueta-Holme N., Peet R.K., Sandel B., Schildhauer M., Smith S.A., Svenning J.-C., Thiers B., Violle C., Wiser S., and B.J. Enquist. 2017. The BIEN R package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol Evol.* 9:373–379.

Malhi Y., Aragão L.E., Galbraith D., Huntingford C., Fisher R., Zelazowski P., Sitch S., McSweeney C. and P. Meir. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *PNAS* 106 (49): 20610–20615.

Merow C., Smith M.J., Edwards T.C. Jr., Guisan A., McMahon S.M., Normand S., Thuiller W., Wüest R.O., Zimmermann N.E. and J. Elith. 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography* 37: 1267–1281.

Merow C., Smith M.J. and J.A. Silander, Jr. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36: 1058–1069.

Millar C.I. and N.L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349 (6250): 823-826.

Miller K.M. and B.J. McGill. 2018. Land use and life history limit migration capacity of eastern tree species. *Global Ecol Biogeogr*. 27:57–67.

Monleon V.J. and H.E. Lintz. 2015. Evidence of Tree Species' Range Shifts in a Complex Landscape. *PLoS ONE* 10(1): e0118069.

Munson S.M., Webb R.H., Belnap J., Hubbard J.A., Swann D.E. and S. Rutman. 2012. Forecasting climate change impacts to plant community composition in the Sonoran Desert region. *Global Change Biology* 18: 1083–1095.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. and J. Kent. 2000. Biodiversity hotspot for conservation priorities. *Nature* 403(6772):853- 858.

Nathan R., Horvitz N., He Y., Kuparinen A., Schurr F.M. and G.G. Katul. 2011. Spread of North American wind-dispersed trees in future environments. *Ecology Letters* 14: 211-219.

Ordonez A. and J.C. Svenning.2017. Consistent role of Quaternary climate change in shaping current plant functional diversity patterns across European plant orders. *Scientific Reports* 7:42988.

Pearson R.G. 2006. Climate change and the migration capacity of species. *Trends in Ecology and Evolution* 21(3): 111-113.

Phillips S.J. 2017. A Brief Tutorial on Maxent. Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2018-February-19.

Phillips S.J., Anderson R.P., Dudík M., Schapire R.E. and M.E. Blair. 2017. Opening the black box: an open-source release of Maxent. *Ecography* 40(7): 887–893.

Phillips S.J., Anderson R.P. and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Polade S.D., Gershunov A., Cayan D.R., Dettinger M.D. and D.W. Pierce. 2017. Precipitation in a warming world: Assessing projected hydro-climate changes in California and other Mediterranean climate regions. *Scientific Reports* 7(10783).

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Riahi K., Rao S., Krey V., Cho C., Chirkov V., Fischer F., Kindermann G., Nakicenovic N. and P. Rafaj. 2011. RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Climatic Change* 109:33–57.

Ruiz-Labourdette D., Nogues-Bravo D., Sainz-Ollero H., Schmitz M.F. and F.D. Pineda. 2012. Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *J. Biogeogr*. 39: 162–176.

Sarukhán, J., Koleff P., Carabias J., Soberón J., Dirzo R., Llorente-Bousquets J., Halffter G., González R., March I., Mohar A., Anta S. and J. de la Maza. 2009. Natural Capital of México. Sinthesis: current knowledge, evaluation and perspectives of sustainability. National Commission for the Knowledge and Use of Biodiversity, Mexico. ISBN: 978-607-7607-09-0.

Schwartz M.W., Iverson L.R., Prasad A.M., Matthews S.N. and R.J. O'Connor. 2006. Predicting extinctions as a result of climate change. *Ecology*: 87(7): 1611–1615.

Schwinning S. and O.E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141(2): 211–220.

Serra-Diaz J.M., Franklin J., Dillon W.W., Syphard A.D., Davis, F.W. and R.K. Meentemeyer R. K. 2015. California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography* 25: 164-175.

Sittaro, F., Paquette, A., Messier C., and C.A. Nock. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Global Change Biology 23, 3292–3301.

Smith S.J., Edmonds J., Hartin C.A., Mundra A. and K. Calvin. 2015. Near-term acceleration in the rate of temperature change. *Nature Climate Change* 5: 333–336.

Sommer J.H., Kreft H., Kier G., Jetz W., Mutke J. and W. Barthlott. 2010. Projected impacts of climate change on regional capacities for global plant species richness. *Proc. R. Soc. B.* 10 pp.

Steinbauer M.J., Grytnes J.-A., Jurasinski G., Kulonen A., Lenoir J., Pauli H., Rixen C., Winkler M., Bardy-Durchhalter M., Barni E., Bjorkman A.D., Breiner F.T., Burg S., Czortek P., Dawes M.A., Delimat A., Dullinger S., Erschbamer B., Felde V.A., Fernández-Arberas O., Fossheim K.F., Gómez-García D., Georges D., Grindrud E.T., Haider S., Haugum S.V., Henriksen H., Herreros M.J., Jaroszewicz B., Jaroszynska F., Kanka R., Kapfer J., Klanderud K., Kühn I., Lamprecht A., Matteodo M., Morra di Cella U., Normand S., Odland A., Olsen S.L., Palacio S., Petey M., Piscová V., Sedlakova B., Steinbauer K., Stöckli V., Svenning J.-C., Teppa G., Theurillat J.-P., Vittoz P., Woodin S.J., Zimmermann N.E. and S. Wipf. 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556: 231–234.

Thuiller W., Lavorel S., Sykes M.T. and M.B. Araújo. 2006 (a). Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12: 49-60.

Thuiller W., Midgley G.F., Hughes G.O., Bomhard B., Drew G., Rutherford M.C. and F.I. Woodward. 2006 (b). Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology* 12: 759-776.

TNRS (Taxonomic Name Resolution Service). 2018. [Internet]. iPlant Collaborative. Version 4.0 [Accessed: 17 Jan 2018]. Available from: http://tnrs.iplantcollaborative.org

Urban M.C. 2015. Accelerating extinction risk from climate change. *Science* 348 (6234): 571-573.

van Proosdij A.S.J., Sosef M.S.M., Wieringa J.J. and N. Raes. 2016. Minimum required number of specimen records to develop accurate species distribution models. *Ecography* 39: 542–552.

Vetaas O.R. and J.-A. Grytnes. 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology & Biogeography* 11: 291–301

Wiens J.J. 2016. Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. Barnosky A, ed. *PLoS Biology* 14(12):e2001104.

Williams J.W., Jackson S.T. and J.E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *PNAS* 104(14): 5738–5742.

Willis K.J. and S.A. Bhagwat. 2009. Biodiversity and Climate Change. *Science* 326 (5954): 806-807.

www.worldclim.org. Accessed on January 2017.