Suitable climatic habitat changes for Mexican conifers along altitudinal gradients under climatic change scenarios

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Abstract. The high biodiversity of the Mexican montane forests is concentrated on the Trans-Mexican Volcanic Belt, where several Protected Natural Areas exist. Our study examines the projected changes in suitable climatic habitat for five conifer species that dominate these forests. The species are distributed sequentially in overlapping altitudinal bands: *Pinus hartwegii* at the upper timberline, followed by *Abies religiosa*, the overwintering host of the Monarch butterfly at the Monarch Butterfly Biosphere Reserve, *P. pseudostrobus*, the most important in economic terms, and *P. devoniana* and *P. oocarpa*, which are important for resin production and occupy low altitudes where montane conifers merge with tropical dry forests. We fit a bioclimatic model to presence–absence observations for each species using the Random Forests classification tree with ground plot data. The models are driven by normal climatic variables from 1961 to 1990, which represents the reference period for climate-induced vegetation changes. Climate data from an ensemble of 17 general circulation models were run through the classification tree to project current distributions under climates described by the RCP 6.0 watts/m^2 scenario for the decades centered on years 2030, 2060 and 2090. The results suggest that, by 2060, the climate niche of each species will occur at elevations that are between 300 to 500 m higher than at present. By 2060, habitat loss could amount to 46–77%, mostly affecting the lower limits of distribution. The two species at the highest elevation, *P. hartwegii* and *A. religiosa*, would suffer the greatest losses while, at the lower elevations, *P. oocarpa* would gain the most niche space. Our results suggest that conifers will require human assistance to migrate altitudinally upward in order to recouple populations with the climates to which they are adapted. Traditional in situ conservation measures are likely to be equivalent to inaction and will therefore be incapable of maintaining current forest compositions.

Key words: assisted migration; conifer species; drought stress; forest conservation; forest management; Random Forests; suitable climatic habitat; xeric limit.

Introduction

Mexico is one of the five countries with the greatest biodiversity worldwide (Ramamoorthy et al. 1993). It presents the largest number of pine species (Styles 1993), mainly distributed throughout the mountain ranges of

the country (Perry 1991). The Trans-Mexican Volcanic Belt (TMVB), a high-altitude plateau that contains the highest volcanic peaks of the country (timberline at 4000 m above sea level [m a.s.l.] with the highest peak at 5,675 m a.s.l., Neyra-Jáuregui 2012), is a region located in central Mexico, along an east-west geographic distribution axis (between 19° and 20° N; see Fig. 1), on which is concentrated a large number of endemic conifer species. The conifer species of main ecological and economic importance are distributed sequentially from high

to low altitudes on the TMVB as follows: (1) the timberline species, *Pinus hartwegii* (3,000–4,000 m a.s.l.; Lauer 1978), (2) *Abies religiosa* (2,400–3,600 m a.s.l.), which comprises the dense forest where the Monarch butterfly (*Danaus plexipus*) overwinters at the Monarch Butterfly Biosphere Reserve (MBBR; Oberhauser and Peterson 2003, Sáenz-Romero et al. 2012a), (3) the most economically important species, *P. pseudostrobus* (2,200–2,900 m a.s.l.; Sáenz-Romero et al. 2012b), (d) *Pinus devoniana* (also known as *Pinus michoacana*), which develops a juvenile grass stage and provides some resistance to drought (1,600–2,450 m a.s.l.; Sáenz-Romero and Tapia-Olivares 2008), and (5) *Pinus oocarpa*, which inhabits the lowest altitudinal limit of the pine–oak forest, and becomes interspersed with the tropical dry forests (1,100–1,600 m a.s.l.; Sáenz-Romero et al. 2006). The latter two species are both very important for resin production (Leyva-Ovalle et al. 2013, Quiroz-Carranza and Magaña-Alejandro 2015). Moreover, the most important Mexican Protected Natural Areas (PNA) of high-altitude vegetation is found in the TMVB, covering the highest volcanoes (for elevations see Fig. 1; Neyra-Jáuregui 2012). Finally, this region contains one of the best examples of sustainable pine–oak forest management conducted by the Purépecha Ethnic group at Nuevo San Juan Parangaricutiro (NSJP) and Cherán, Michoacán

state, whose communal forest management model is considered ecologically and economically equitable (Bray et al. 2005, Orozco-Quintero and Davidson-Hunt 2010).

Despite the enormous conservational and economic importance of the TMVB, the region is threatened by many factors, one of the most prominent of which is the impact of climatic change. Concentrations of greenhouse-effect gases in the atmosphere reached unprecedented global levels in 2017 of above 405 ppm of CO_2 (WMO 2018), and are likely to produce an increase in the global mean annual temperature of 1.5°C by 2030 (IPCC 2018, Hansen et al. 2019). In many regions of the world, this temperature increase will be accompanied by a precipitation decrease of up to 30% (IPCC 2013). For Mexico, the reduction of precipitation has been estimated at an average of 9.0% by the decade centered on the year 2060 (Sáenz-Romero et al. 2010).

This combination of temperature increase and precipitation decrease will cause more frequent, more severe, and hotter droughts that will act to induce forest decline (Allen et al. 2015), since the plastic response of tree populations to a changing climate will eventually be exhausted (Alfaro 2014, Allen et al. 2015), particularly for the populations at the xeric limit*s* of the species (lower altitudinal limit, or southern margin in the Northern Hemisphere; Mátyás 2010, Mátyás et al.
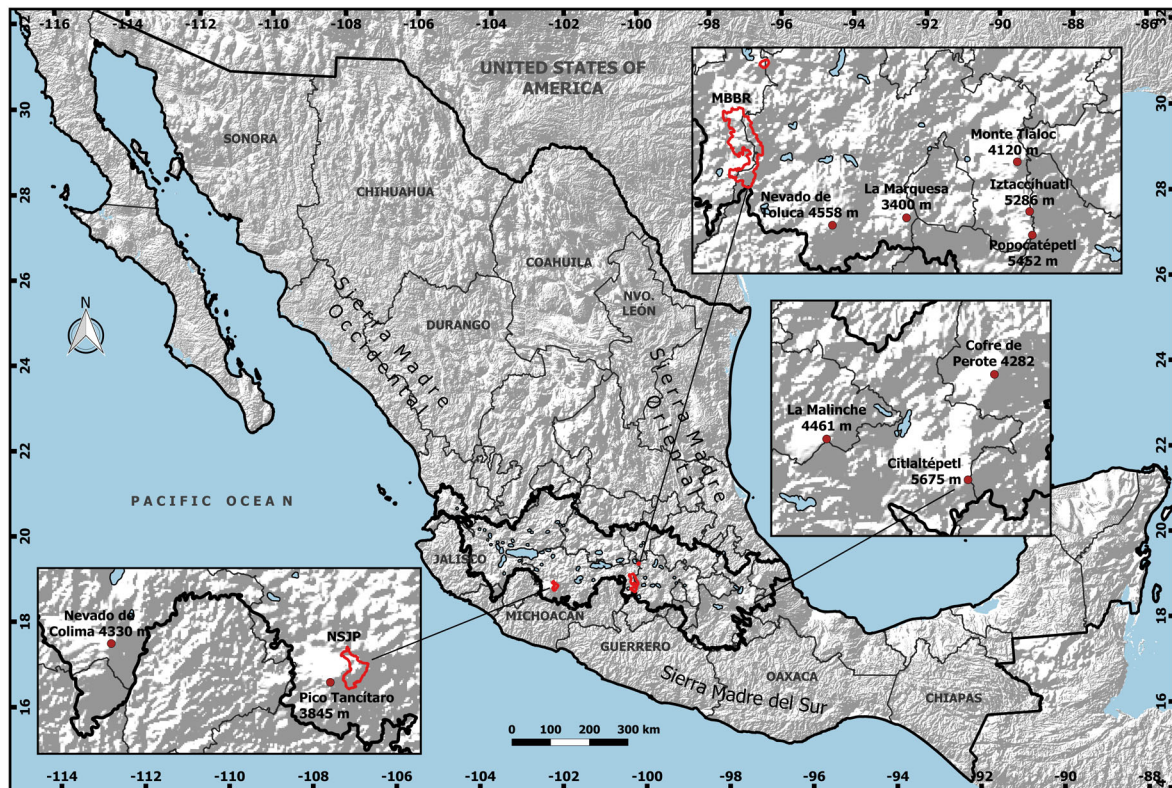

Fig. 1.   Mexico political divisions, prominent geographical regions, and Trans-Mexican Volcanic Belt (TMVB; black contour), indicating the Monarch Butterfly Biosphere Reserve (MBBR; red contour) and the Native Indigenous Community of Nuevo San Juan Parangaricutiro (NSJP; red contour), and major volcanoes (red dots) with their altitudes (m above sea level).

2010). There is no doubt that forest decline is now an ongoing process in several parts of the world (Allen 2010). Some examples of this are *Populus tremuloides* in the Rocky Mountains, USA (Rehfeldt et al. 2009), *Cedrus atlantica* in the Moyen Atlas mountain range, Morocco (Mátyás 2010), and *Fagus sylvatica* in southwestern Hungary (Mátyás et al. 2010).

In Mexico, *Abies religiosa* trees of the TMVB with symptoms of decline have been documented (Flores-Nieves et al. 2011; severe defoliation), along with the decline of *Pinus pseudostrobus* trees at the xeric limit of the species distribution (López-Toledo et al. 2017).

Vegetation models that consider climatic change in order to predict the geographic distribution of biomes suggest that the Mexican conifer forest will lose 92% of its suitable climatic habitat in the TMVB and 85% in the Sierra Madre by the end of the current century (Rehfeldt et al. 2012). Other projections made for several Mexican conifer species suggest that current habitats will not only be reduced, but will shift to higher altitudes, appear in other localities and even perhaps disappear altogether (Gómez-Mendoza and Arriaga 2007, Ledig et al. 2010, Gómez-Díaz et al. 2011, Sáenz-Romero et al. 2010, 2012a, 2015, Gutiérrez and Trejo 2014, Pérez-Miranda et al. 2014, Cruz-Cárdenas et al. 2016).

The problem is not only the reduction in area of suitable climatic habitat. Within the suitable climatic habitat projected to be maintained for the species as a whole, a decoupling will occur between forest tree populations and the climate to which they are genetically adapted. There is experimental evidence from provenance tests showing that several Mexican conifers have populations that are genetically differentiated for quantitative traits as an adaptation to the relatively narrow intervals of the environment occupied by the species as a whole. This is the case for the five conifer species of the present study: *Pinus hartwegii* (Loya-Rebollar et al. 2013), *Abies religiosa* (Ortiz-Bibian et al. 2017), *P. pseudostrobus* (Sáenz-Romero et al. 2012b), *P. devoniana* (Sáenz-Romero and Tapia-Olivares 2008), and *P. oocarpa* (Sáenz-Romero et al. 2006).

Aims of this research

There is no doubt that the suitable climatic habitat for each species will be displaced to higher altitudes in the TMVB (Sáenz-Romero et al. 2012a). Unfortunately, there is increasing evidence that the speed at which plant species can migrate to higher altitudes by natural means in response to the ongoing climatic change is much slower than will be necessary to maintain the coupling between the plant populations and their suitable climate (Peñuelas et al. 2007, Lenoir et al. 2008, Jump et al. 2009). This necessitates the establishment of programs of human assistance to re-couple these populations to the climatic habitat for which they have evolved. This assisted migration would consist of collecting seeds, producing seedlings in a nursery and conducting massive plantations at sites where the suitable climatic habitat of

the seed source is projected to occur in the near future (Rehfeldt et al. 2002, Tchebakova et al. 2005, Castellanos-Acuña et al. 2015, Sáenz-Romero et al. 2016). In some cases, assisted migration will involve replacing provenances of the same species; in others, for example, at the xeric limit and beyond the upper altitudinal limits of a given species, assisted migration will imply species replacement. The former replacement might be viewed as customary artificial reforestation programs; the latter, however, is the subject of great controversy, especially in ecologist and conservationist circles.

In this study, we determine contemporary and future climatic niches suitable for five conifer species that occur along the elevational gradients of the TMVB: *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana*, and *P. oocarpa*. We examine the suitable climatic habitat lost, maintained and added for each species, and discuss the management challenges for both commercial forestry operations and biodiversity conservation that will be imposed by the projected impacts of climatic change.

In support of the previous excellent and pioneering climate niche modeling available for Mexican forest species, e.g., the research of (although this list is by no means exhaustive): Téllez-Valdés and Dávila-Aranda (2003), Téllez-Valdés et al. (2006), Gómez-Mendoza and Arriaga (2007), Gómez-Díaz et al. (2011), we aim to provide for five coniferous species of the TMVB: (1) more maps of the contemporary and future habitat distribution, in sufficient detail for future use in forest management decisions, (2) more accurate projections, given the statistical robustness provided by Random Forest when using species absence data points in addition to presence data, (3) updated projections using modern projected greenhouse-effect concentration scenarios, such as the RCP 6.0 watts/m^2 and an ensemble of global circulation models.

Materials and Methods

Presence data input: Mexican Forest Inventory

We constructed our species presence database from field observations of *P. hartwegii* Lindl., *Abies religiosa* (Kunth) Schltdl. and Cham., *P. pseudostrobus* Lindl., *P. devoniana* Lindl., and *Pinus oocarpa* Schiede. The data were taken from a subset of 6,674 observations of the presence of conifers from the Mexican National Forest and Soil Inventory (MexFI), produced by the Mexican National Forestry Commission (CONAFOR 2004–2009). The data set of observations produced for each species with these procedures is listed in the results section; Table 1.

Absence data input

We sampled sites with absences of the species from a subset of the MexFI data with ~13,000 plots containing species other than conifers. To ensure that our sample of

TABLE 1. Number of observations, number of "forests," expansion factor used on climatic limits, out-of-bag error, error of omission, and error of commission for each species.

Species	No. observations	No. forests	Hypervolume expansion factor (SD)	Out-of-bag error	Error of omission	Error of commission
Pinus oocarpa	1,118	10	1.25	0.056	0.004	0.091
P. devoniana	269	35	1.25	0.054	0.008	0.084
P. pseudostrobus	429	14	1.25	0.057	0.004	0.092
Abies religiosa	128	25	1.25	0.018	0.000	0.031
P. hartwegii	34	35	1.50	0.074	0.029	0.622

Note: Errors of fit are presented as proportions.

distant absence observations was representative of the vegetation of Mexico, we also used systematic sampling of point locations within the digitalized map of the Biotic Communities of North America (Rehfeldt et al. 2012). The technical procedures, described in detail in Rehfeldt et al. (2006) and also used by Ledig et al. (2010), involved the use of ARCMAP software to obtain a systematic sample of point locations from each polygon on the map and assign an elevation to each point from the digitized elevation model of GLOBE Task Team (1999).

Climate data input for the bioclimatic model

The climate of each species presence or absence data point was estimated by interrogating the spline climate model (built on the ANUSPLINE software; Hutchinson 2004) developed originally by Rehfeldt (2006) and Rehfeldt et al. (2006, 2018), and expanded for Mexico in Sáenz-Romero et al. (2010) for 1961–1990 normals. We use normals of this period to represent a reference climate from which global warming is occurring (Rehfeldt et al. 2018). A complete list of climatic variables is provided in Appendix S2.

Bioclimatic model

Our statistical models are built on the framework of Iverson and Prasad (1998) and closely parallel those of Rehfeldt et al. (2006). We use the Random Forests classification tree (Breiman 2001) to predict the presence–absence of *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana*, and *P. oocarpa* from climate variables. The model thus predicts the habitat realized for the contemporary climate, which is referred to as the climate profile (see Rehfeldt et al. 2006). The Random Forests algorithm, available in R (R Development Core Team 2004), constructs a set of regression or classification trees from an input data set. The trees in their aggregate are called "forest" (Liaw and Wiener 2002).

For classification trees, Breiman (2001) recommends that the number of observations within classes be approximately equal. To satisfy this recommendation, we used the sampling protocol of Rehfeldt et al. (2009) to draw the species data set from our database. In each data set,

40% of the observations were those for which the species was present, weighted by a factor of two. An additional 40% were drawn from the pool of observations lacking the species that occurred within a 32-variable hypervolume, the dimensions of which corresponded to the climatic limits for each species within the TMVB. Each dimension of the hypervolume was expanded somewhat (Table 1) such that most of the absence observations would be the most difficult to separate from the presence observations. The remaining 20% were selected from a pool of data points lacking the species and located outside this hypervolume. Multiple forests were constructed (Table 1) such that all of the observations within the hypervolume would be used in the analysis. Results are presented as averages across the forests.

Mapping realized contemporary 1961–1990 climatic habitat

Pixels of ~1 km^2 (30 arc seconds) resolution comprised the terrestrial portion of our geographic window, defined as the Trans-Mexican Volcanic Belt (TMVB; Gómez-Tuena et al. 2007). By using the digitalized elevations of GLOBE Task Team (1999), we estimated the climate of each pixel from the spline surfaces of Sáenz-Romero et al. (2010). The climate of each pixel was then run through the bioclimatic model using the R program (modules randomForest and yaImpute), with each tree of each forest providing a vote as to whether a given pixel fell within the realized climatic habitat of *Pinus oocarpa*, *P. devoniana*, *P. pseudostrobus*, and *Abies religiosa*; a pixel was assumed to have a suitable climate when receiving a majority (>0.5) of favorable votes; such threshold has been used to display suitable climatic habitat (Sáenz-Romero et al. 2010, 2012a, 2015). To compensate for the low number of observations for *P. hartwegii* and, therefore, a high probability of there being suitable habitat that is not occupied, a pixel was classified as having a suitable climate when it received a favorable vote of > 0.4.

Prediction of future suitable habitats

We projected the 1961–1990 climatic habitat into a future climate space for the decades centered on 2030, 2060, and 2090 using the climate grids (Rehfeldt et al.

2018) for an ensemble of 17 general circulation models, and the scenario 6.0 W/m^2 of the representative concentration pathway (RCP). We considered that ensemble to represent one of many climates and their impacts that should occur later in this century. Since our objective is to aid present forest management decision-making, we focus our discussion on 2060, viewing 2030 as being too soon to achieve any substantial result of alternative forest management, and 2090 as being too distant for projections to be reliable.

Results

Bioclimatic model

The number of presence data points obtained from MexFI varied among species, ranging from 1,118 for *P. oocarpa* to only 34 for *P. hartwegii* (Table 1).

The 32-variable model produced a classification error (also known as out-of-bag error, OOB) across the different number of "forests" created for each species. As the variables were eliminated in a stepwise fashion according to their importance, this error fluctuated until stabilizing just prior to an exponential increase. The most parsimonious model was judged to be at the point where culling an additional variable resulted in a sudden increase in the mean OOB error from across all "forests." We chose a model with six variables for *P. oocarpa* and *A. religiosa*, seven each for *P. devoniana* and *P. pseudostrobus*, and 10 for *P. hartwegii*. The lowest classification error was for the six-variable model of *A. religiosa* (0.018), while the highest error was for the 10-variable model of *P. hartwegii* (0.074) (Table 1).

Error of commission; i.e., predicting the presence of a species when it is absent, was important only for *P. hartwegii* (0.622), which had the highest proportion of such errors (Table 1). Omission errors near zero (Table 1) are suggestive of overfitting, as zero error in biological data is implausible. Using the average prediction from multiple forests, however, compensates for the effects of overfitting when the models used.

The climatic variables of major importance used to generate the bioclimatic model of each species are listed on Table 2.

Mapping of the 1961–1990 climate profile

High precision of the bioclimatic models is demonstrated by superimposing the locations inhabited by each species on predicted distributions. Nearly all of the data points occur in grid cells for which the bioclimatic model predicts that climate is very likely to be suitable for each

TABLE 2. Acronyms, definition, and ranking of climatic variables of greatest relevance to the climate profile of each species.

Acronym	Climatic variable definition	P. oocarpa	P. devoniana	P. pseudostrobus	A. religiosa	P. hartwegii
SUMP	summer precipitation; sum of precipitation Jul–Aug	1		7		6
MAPDD5	(MAP × DD5)/1,000		1			
MMAX	mean maximum temperature in the warmest month			1		1
MTWM	mean temperature in the warmest month	4	3		1	3
SPRP	spring precipitation; sum of precipitation Apr–May	2	6	2		2
TDIFF	MTWM − MTCM	5	2		5	9
GSPMTCM	(GSP × MTCM)/1000				2	
WINP	winter precipitation; sum of precipitation of Nov–Feb	3	7	3		7
PRATIO	GSP/MAP				3	
MAP	Mean annual precipitation (mm)		4			
MMIN	mean minimum temperature in the coldest month		5	4		
SDI	(GSDD5 × 0.5)/GSP				4	
DD5	degree-days > 5°C	6				4
GSDD5	degree-days > 5°C accumulated within the frost-free period					10
MAPMTCM	(MAP × MTCM)/1000			5		
MTCM	mean temperature in the coldest month					5
MTCMMAP	MTCM/MAP			6		
GSPMTCM	(GSP × MTCM)/1000				6	
MAT	mean annual temperature (°C)					8
GSP	growing season precipitation, Apr–Sep					

Note: 1 = most relevant, to 10 = least relevant.

species (probability ≥ 50% for *P. oocarpa*, *P. devoniana*, *P. pseudostrobus*, and *Abies religiosa*, 40% for *P. hartwegii*). No data points reside in grid cells that receive votes < 50% or < 40% for these species, respectively. In the following section, we present the modeling and mapping results according to the altitudinal distribution of these species.

Of these five species, *P. oocarpa* and *P. devoniana* have the broadest suitable climatic habitat distribution in Mexico (Table 3). *Pinus oocarpa* extends similarly from the northwest of the Sierra Madre Occidental in southern Sonora, until reaching the northern and southern mountains of Chiapas (Appendix S3: Fig. S1). The suitable climate for *P. devoniana* occurs mainly in the Trans-Mexican Volcanic Belt (TMVB; Table 3, Appendix S3: Fig. S2). *Pinus pseudostrobus* has the second largest suitable area in the TMVB (Table 3), occurring at moderately high elevations and along the flanks of the volcanoes (Appendix S3: Fig. S3). *Abies religiosa* and *P. hartwegii* have the most restricted areas of suitable climatic habitat (Table 3; Appendix S3: Figs. S4 and S5, respectively). The narrowest distribution is for *P. hartwegii,* since its climate occurs in the upper part of the highest volcanoes of the TMVB, forming the timberline.

Future suitable habitat

Table 3 summarizes the lost, maintained, and added areas (expressed as percentage of the 1961–1990 reference period distribution) of suitable climatic habitat at both country and TMVB scales, for three future periods: the decades centered in the years 2030, 2060, and 2090. For all species, the results show that the area lost will far exceed that added and that this discrepancy will increase over time.

Countrywide and within the TMVB, by 2060, the species that is projected to lose the most suitable climatic habitat are *A. religiosa* (>75%), *P. hartwegii* (>68%), and

P. oocarpa (>52%). *Pinus pseudostrobus* should lose 52% and *P. devoniana* is the species with the lowest loss (<46%). On the other hand, the species that are projected to gain the most area, because their suitable climate appears in new localities, are *P. oocarpa* (11% countrywide and 25% in the TMVB), followed by *P. devoniana* (12% and 16%, respectively), and *P. pseudostrobus* (4% and 9%, respectively). *Pinus hartwegii* and *A. religiosa* are the species with the lowest quantity of new suitable areas (<5%; Table 3).

As the results suggest, for all species, new areas with favorable climate added will advance toward the slopes and highest volcanoes of the TMVB (Figs. 2–6). Some of the new areas for *P. oocarpa* will be located at Tancítaro peak (Fig. 2F), the western edge of the MBBR (Fig. 2B), as well as in the lower parts of the natural protected area of La Marquesa (Fig. 2C). New suitable areas for *P. devoniana* are similar to those of *P. oocarpa* (see Fig. 3B, C, F). For *P. pseudostrobus*, the area added should be mainly in the upper parts of the TMVB volcanoes (Fig. 4A, C).

For *Abies religiosa*, a very worrisome issue is the projected dramatic reduction within the area of the MBBR, especially in the southwestern portion of the Reserve (Fig. 5F). New suitable areas should be added mainly toward the summits of the TMVB volcanoes at elevations exceeding 4000 m a.s.l. (Fig. 5B, E). The suitable climate of *Pinus hartwegii* currently located in the Sierra Madre Oriental (Fig. 6A), like Tancítaro peak (Fig. 6E) would disappear completely. Its suitable climate is projected to appear in the snow-capped mountains at elevations greater than 4,300 m a.s.l., such as the volcanoes Nevado de Colima (Fig. 6F), Nevado de Toluca, Popocatepetl, Iztaccihuatl (Fig. 6B), Pico de Orizaba, and Cofre de Perote (Fig. 6C).

Fig. 7 illustrates both the altitudinally separate and overlapping distributions of the five conifer species studied along altitudinal gradients of the TMVB, as well as the trend of net reduction of suitable climatic habitat as

TABLE 3. Countrywide and Trans-Mexican Volcanic Belt projected lost, maintained, and added suitable climatic areas for 2030, 2060, and 2090, in comparison to area predicted for 1961–1990.

| | | Future predicted area (percent change of 1961–1990) | | | | | | | | |
| | Current (km²) 1961–1990 | Lost | | | Maintained | | | Added | | |
Species		2030	2060	2090	2030	2060	2090	2030	2060	2090
Countrywide										
Pinus oocarpa	228,669	−33	−52	−67	67	48	33	+9	+11	+12
P. devoniana	135,095	−31	−46	−58	69	54	42	+12	+12	+11
P. pseudostrobus	105,787	−66	−52	−68	34	48	32	+4	+4	+3
Abies religiosa	47,359	−62	−77	−88	38	23	12	+2	+2	+1
P. hartwegii	4,037	−57	−73	−87	43	27	13	+3	+4	+5
Trans-Mexican Volcanic Belt										
Pinus oocarpa	37,344	−32	−62	−73	68	38	27	+26	+25	+25
P. devoniana	41,470	−29	−43	−54	71	57	46	+13	+16	+16
P. pseudostrobus	40,072	−33	−52	−66	67	48	34	+7	+9	+7
Abies religiosa	33,695	−60	−75	−86	40	25	14	+1	+1	+1
P. hartwegii	3,255	−51	−68	−85	49	32	15	+3	+5	+6
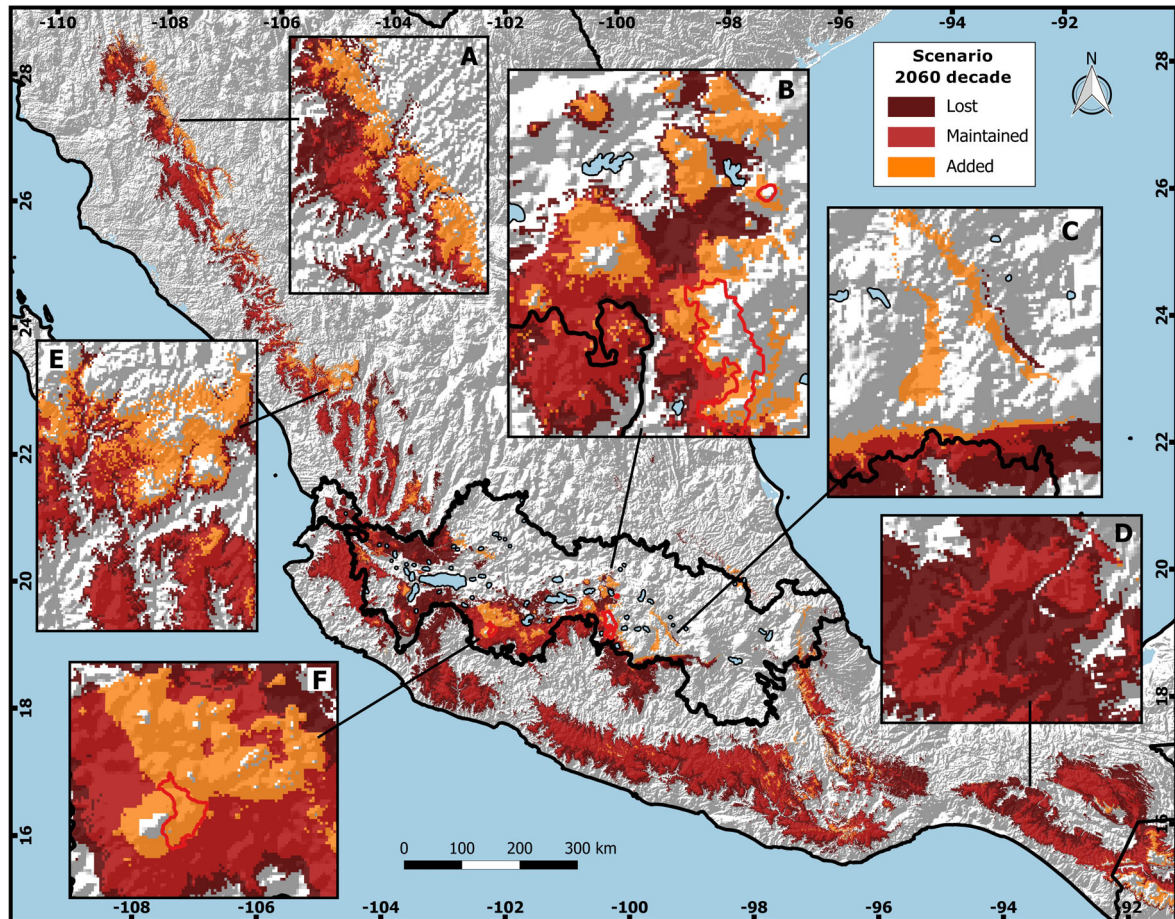
Fɪɢ. 2.　Mapped prediction of the climatic habitat of *Pinus oocarpa* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel B shows the Monarch Butterfly Biosphere Reserve (red contour). Panel F shows the forest of the Native Indigenous Community of Nuevo San Juan Parangaricutiro (red dotted contour), Michoacán state.

these species shift toward higher altitudes. Note that the two species occupying the highest elevations, *Abies religiosa* and *P. hartwegii*, are those with the least suitable climatic habitat projected for the decade centered on 2060 (Fig. 7D, E). Moreover, for these two species, the upward shift would be the lowest, since the emergent habitat is limited along the flanks of the volcanoes.

The expected changes in the distribution of suitable habitat in the TMVB for the decades centered on the years 2030 and 2090, in addition to that of 2060, are available in Appendix S4 (Figs. S1–S5, one figure per species).

Dɪsᴄᴜssɪᴏɴ

Fit of bioclimatic model and relevant climatic variables

As measured by the overall classification error, the fit of our bioclimatic model, using from six predictors for *A. religiosa* to 10 for *P. hartwegii*, is similar to those for 74 western U.S. species for which the same methods were applied (Crookston et al. 2010). For conifers of Mexico, the error was 4.5% for *Picea* spp. (Ledig et al. 2010), 4.7% for *Pinus chiapensis*, (Sáenz-Romero et al. 2010) and 4.6% for *Pinus leiophylla* (Sáenz-Romero et al. 2015). The prediction of the 1961–1990 distribution is in general agreement with maps developed based on field observations by Perry (1991) and Farjon and Styles (1997). In our analyses, like those of many western U.S. species (see Crookston et al. 2010), errors of omission were exceptionally low (<0.029), a result directly linked to the sampling protocol that weights the observations in which the species of interest was present by a factor of two (see Rehfeldt et al. 2009).

As is normal in climate niche modeling, the area where the 1961–1990 climate is predicted to be suitable for each species is greater than the actual distribution. This result is to be expected when habitat suitability is predicted on the basis of climate alone. Many factors other than
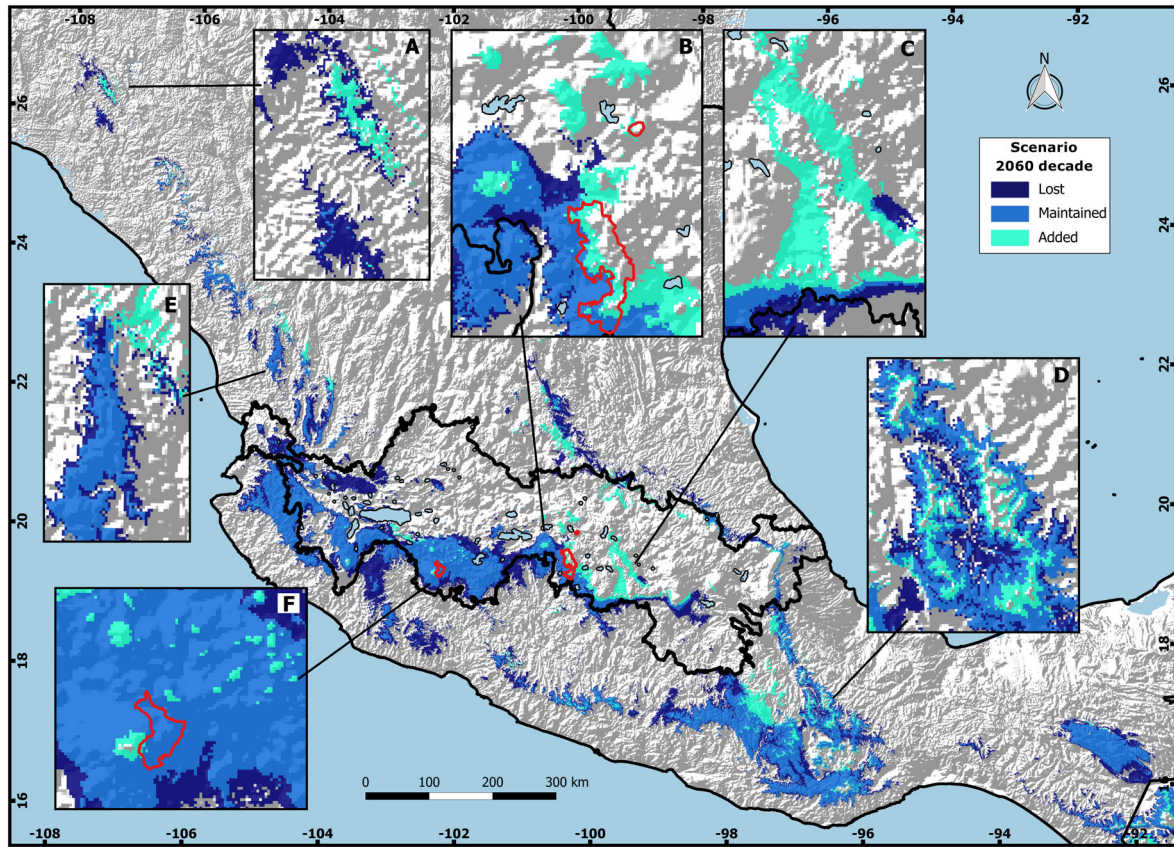
Fig. 3. Mapped prediction of the climatic habitat of *Pinus devoniana* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel B shows the Monarch Butterfly Biosphere Reserve (red contour). Panel F shows the forest of the Native Indigenous Community of Nuevo San Juan Parangaricutiro (red contour), Michoacán state.

climate may restrict where species actually occur (see Soberón and Peterson 2005, Pearson and Dawson 2003). In addition, using the majority of votes (>0.5) to predict presence or absence, prevents identification of locations where the climate may only approach suitability. Nevertheless, a portion of the classification error results from correctly predicting suitable niche space that is unoccupied as a result of other factors, such as limitations of species germplasm dispersion, competitive exclusion, human disturbances, soil conditions, among others (Rehfeldt et al. 2006).

Regarding the climatic variables of major importance used to generate the bioclimatic model of each species, the results suggest that those related to precipitation (summer, spring, and winter precipitation) are more relevant to those species that occur at low altitudes in the transition toward the dry tropical forest, such as *P. oocarpa*. For species that occur at higher altitudes (such as *P. hartwegii* and *A. religiosa*) the extreme temperatures of the warmest month (mean temperature of the warmest month, mean maximum temperature in the

warmest month) and/or the precipitation that occurs during the dry season (spring precipitation) or precipitation during the growing season (GSPMTCM, PRATIO) are the most important variables controlling species distribution (Table 2).

Shifting and loss of suitable climatic habitat

According to future projections, as the time slices considered become more distant in the future (decades centered on the years 2030, 2060, and 2090), the climatic habitat of each species should eventually reduce and move toward higher elevation sites, especially toward those located along the Trans-Mexican Volcanic Belt (TMVB; see Appendix S4). These results are in accordance with previous projections realized by Gómez-Mendoza and Arriaga (2007), Gómez-Díaz et al. (2011), Monterroso-Rivas et al. (2013), and Gutiérrez and Trejo (2014).

Of the five study species, those with the broadest climatic habitat, *P. oocarpa*, *P. devoniana*, and *P. pseudostrobus*, should lose less area since their suitable
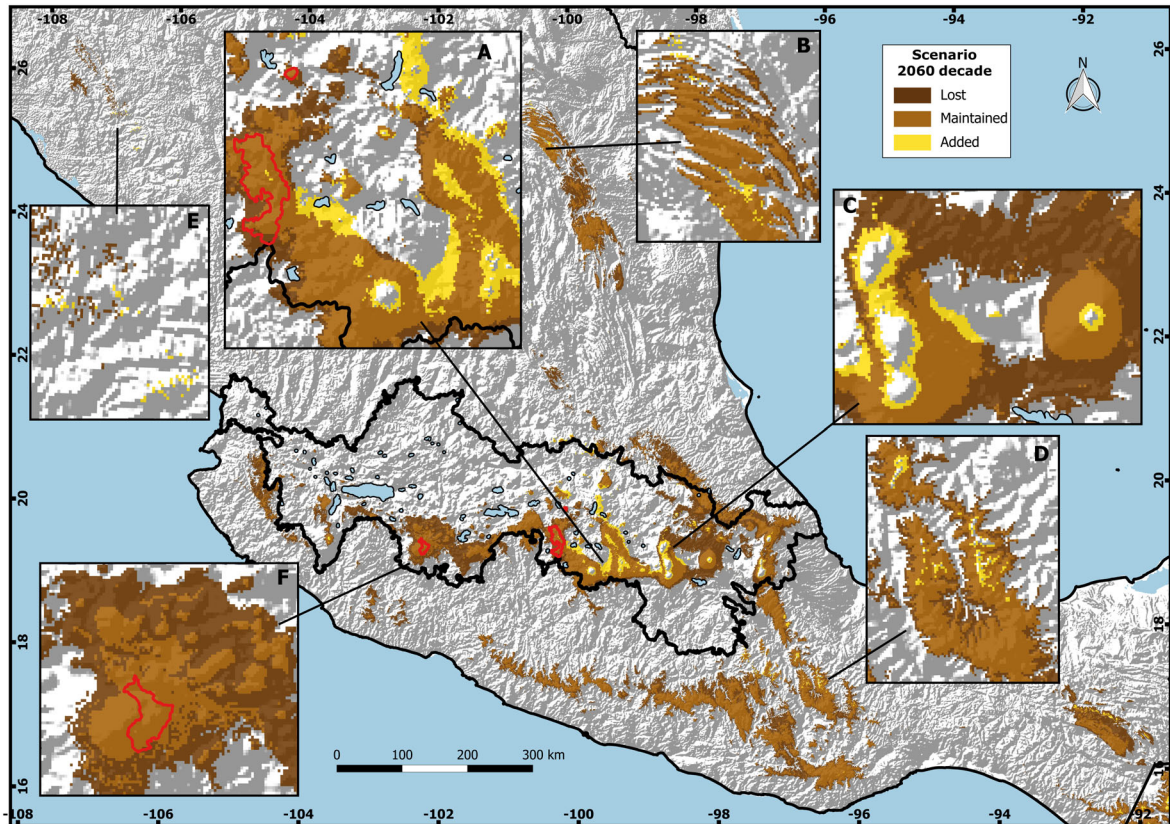
Fig. 4. Mapped prediction of the climatic habitat of *Pinus pseudostrobus* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel A shows the Monarch Butterfly Biosphere Reserve (red contour). Panel F shows the forest of the Native Indigenous Community of Nuevo San Juan Parangaricutiro (red contour), Michoacán state.

climate will shift to sites located at higher elevations (between 300 and 400 m higher compared to the present distribution), which would partially compensate for the current area lost. On the other hand, the species with the most restricted climatic habitat, *P. hartwegii* and *Abies religiosa* (the latter will shift 500 m higher), would have the highest proportion of range lost, since new suitable climatic habitat would be restricted to the highest parts of the mountains, which, due to the conicity of the mountain, will comprise an increasingly smaller area. This does not even consider the impoverished soils characteristic at altitudes above timberline, where the soils are mostly composed of volcanic ashes and stones (See Lauer 1978).

Due to altitudinal climate displacement, the contemporary climatic habitat most subject to loss is located at the lower limit of the present distribution of each species (see Fig. 7a–e), i.e., the xeric limit (sensu Mátyás 2010). At this interface, massive and sudden decline of forest populations has already been documented for several forest tree species (Rehfeldt et al. 2009, Allen 2010, Mátyás 2010, Mátyás et al. 2010) as

a result of temperature increases promoting increasingly frequent heat waves and droughts that exceed mechanisms of phenotypic plasticity and forest population recovery (Mátyás et al. 2010, Alfaro 2014, Allen et al. 2015). In Mexico, for example, within the forest area of the Native Indigenous Community of NSJP, populations of *P. pseudostrobus* that are located in the lower reaches of their altitudinal distribution frequently show poor health and low fecundity due to environmental stress and/or pest attacks derived from the higher temperatures of the dry season (López-Toledo et al. 2017). This is consistent with our models, which indicate that, by 2060, the climate of this area (NSJP, Michoacán) will be suitable for *P. oocarpa* (Fig. 2F) and *P. devoniana* (Fig. 3F), which are currently distributed at lower altitudes.

Indeed, the direct effects of moisture stress at the xeric limit seem especially critical at lower TMVB elevations where the pine-oak vegetation changes into the deciduous tropical dry forest, and consequently, the habitat at the xeric limits of *P. devoniana* and *P. oocarpa* seems particularly vulnerable to the increasingly arid climate.
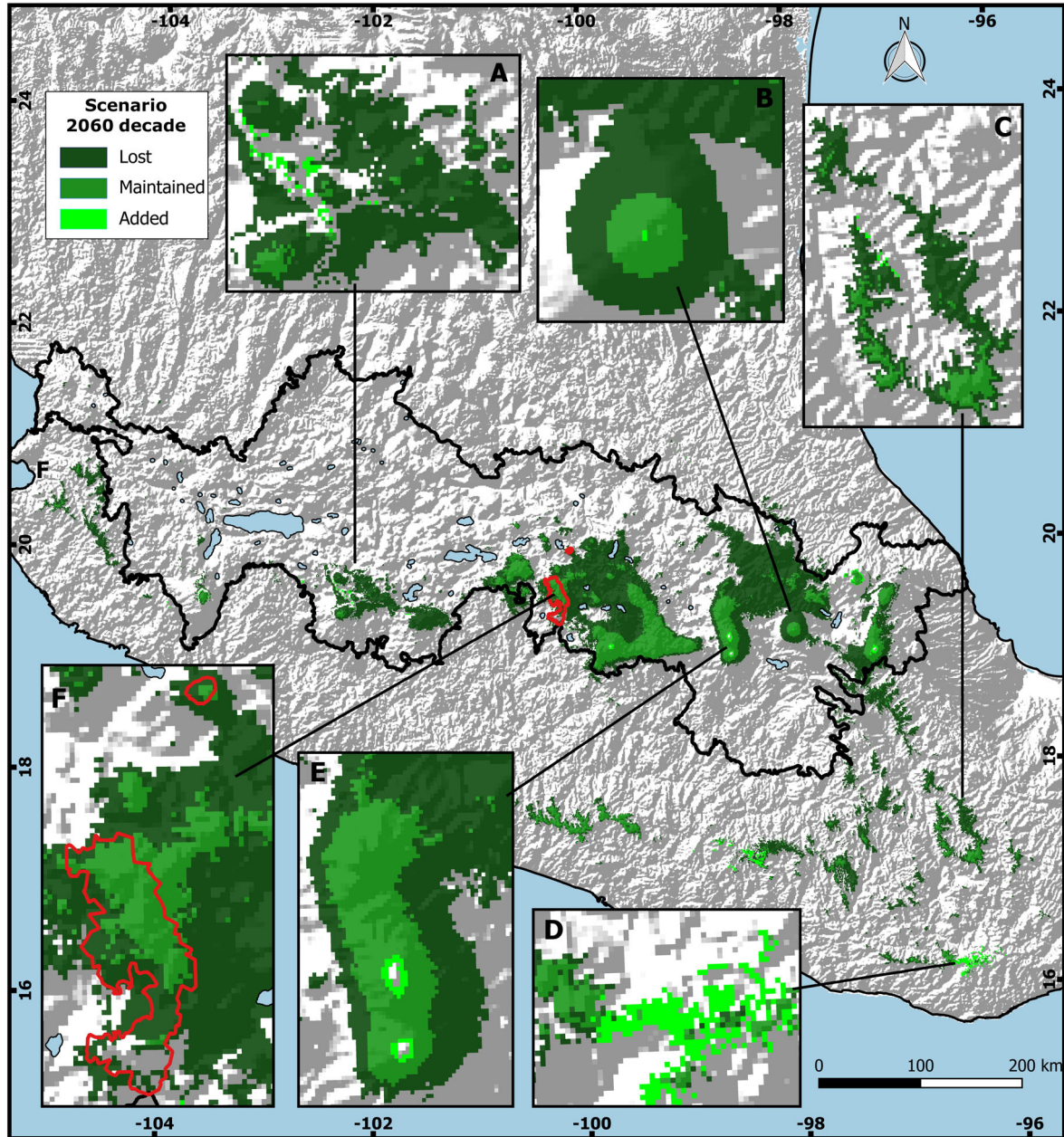
Fig. 5. Mapped prediction of the climatic habitat of *Abies religiosa* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel F shows the Monarch Butterfly Biosphere Reserve (red contour).

At higher elevations where conditions are less xeric, loss of habitat can be viewed as an interaction between competitive ability and environmental stresses. Loss of habitat of *A. religiosa* to *P. pseudostrobus*, for instance, may be determined more by competitive exclusion of *A. religiosa* by the faster growing *P. pseudostrobus* (C. Sáenz-Romero, *personal observation*). Accordingly, Avendaño et al. (2009) and Flores-Nieves et al. (2011) documented foliar biomass

reduction due to death of twigs and foliage in adult individuals from the lower part of the altitudinal distribution of *A. religiosa* on mount Tlaloc, where our model suggests that the species would lose climatic habitat (Fig. 5E) and which would eventually become suitable for *P. pseudostrobus* (Fig. 4C). Our projections for the Monarch Butterfly Biosphere Reserve (MBBR) are more optimistic than those of Sáenz-Romero et al. (2012a), likely because the
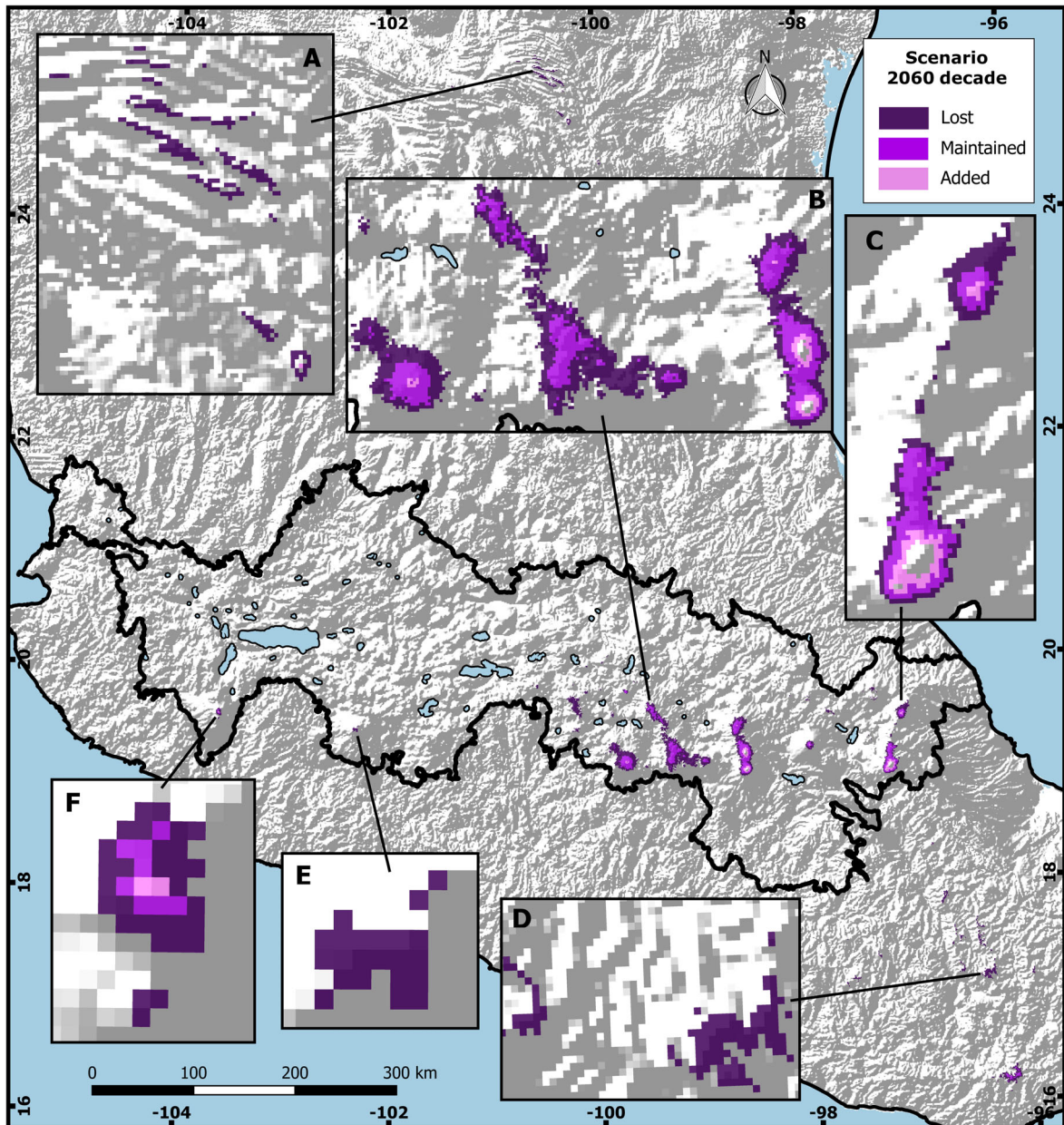
FIG. 6. Mapped prediction of the climatic habitat of *Pinus hartwegii* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt.

projections of precipitation of the model ensemble used is more optimistic that the consensus among the three general circulation models used on Sáenz-Romero et al. 2012a, but nonetheless suggest that the persistent *Abies religiosa* habitat (Fig. 5F) would also be suited for the co-occurrence with *P. pseudostrobus* (Fig. 4A) and that much of the area projected to be lost would then be suited to *P. devoniana* (Fig. 3B) and *P. oocarpa* (Fig. 3B), which are currently absent within the MBBR.

Limits to altitudinal upward migration

Highest elevations within the MBBR are about 3,500 m a.s.l. This elevation coincides with the highest occurrence of extant actual *A. religiosa* populations in Mexico. With its climate niche shifting upward toward 4,000 m a.s.l. (Fig. 7d), *A. religiosa* must migrate upward to higher mountains outside the Reserve. Similarly, *P. hartwegii* already occupies sites of up to 4,000 m
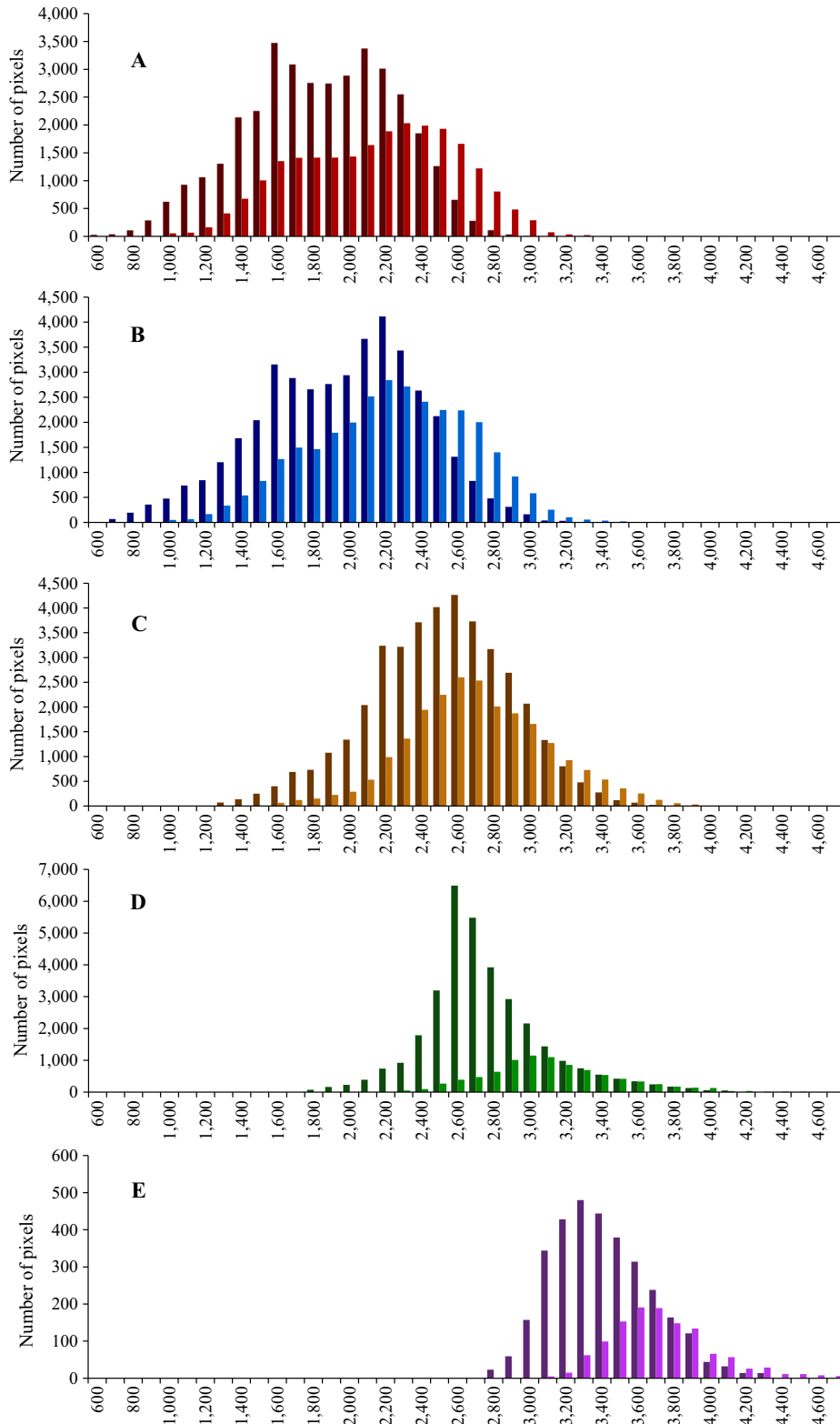
FIG. 7.   Number of pixels that occur at each altitude along the Trans-Mexican Volcanic Belt in the reference period (1961–1990) climate (dark tones) and 2060 climatic habitat (light tones): (A) *P. oocarpa*; (B) *P. devoniana*; (C) *P. pseudostrobus*; (D) *A. religiosa*, and (E) *P. hartwegii*. Bar colors are the same for each species as those used in Figs. 2–6, and as in Appendix S3: Figs. S1–S5. Note that the interval values for the *y*-axis differ among species, but the *x*-axis uses the same scale throughout.

of altitude, the highest timberlines in Mexico. Beyond that point, the soils become limiting (Lauer 1978). Consequently, migration of *P. hartwegii* to sites of between 4,000 and 4,700 m a.s.l. in elevation, as suggested in Fig. 7e, presents serious biological challenges.

Discrepancy between the required migration speed and actual migration

As an apparent response to ongoing climatic change, forest plant populations are migrating to and colonizing altitudes higher than those they currently inhabit (Lenoir et al. 2008), although this is occurring at a speed less than that required to keep them coupled with their suitable climatic habitat (Peñuelas et al. 2007). For example, in western Europe the upward shift in species optimum elevation averages 29 m in altitude per decade. That represents an upward shift of 65 m for the time periods compared (mean year of surveys 1975 vs. 1993) when, in fact, a shift of 150 m (or 68 m per decade) would be required to compensate the increase in average temperature of about 1°C that already has occurred (Lenoir et al. 2008). Thus, the speed at which migration takes place is much slower than that required to keep up with the changing climatic conditions, since it is estimated that the required migration rate would be much higher than that observed in the post-glacial period (McLachlan et al. 2005). For example, Siberian populations of *Pinus sylvestris* would have to migrate at a rate of 110 km per decade in order to cope with the warming that is projected in the area toward the end of the century (Rehfeldt et al. 2002, Tchebakova et al. 2005). In the case of the five conifer species distributed in the TMVB, an upward migration of 300–400 m would be required to compensate for the change in climate expected by the year 2030 (Sáenz-Romero et al. 2010). This represents a required altitudinal migration speed of 55–73 m per decade.

The lag between the speed of the natural migration of populations and the speed at which climate change occurs requires human assistance in order to realign forest populations to sites where the climates for which they are adapted will occur. This is possible through assisted migration, assisted colonization, assisted relocation, or facilitated migration (Rehfeldt et al. 2002, Tchebakova et al. 2005, Aitken et al. 2008, Pedlar et al. 2012).

Alternative forest management needed for the xeric limit

Our results clearly indicate that ecological restoration efforts through assisted migration would have to be implemented at the low altitudinal limit (the xeric limit in some cases) of each species. For example, in the NSJP forest area, populations of *P. pseudostrobus* that are at their xeric limit and showing signs of decline, should be replaced by the assisted migration of individuals located at the upper altitudinal distribution limit of *P. devoniana*. In the MBBR, *Abies religiosa* must be replaced at its

xeric limit by individuals from the upper limit of *P. pseudostrobus*, and in turn, populations at the xeric limit of *P. pseudostrobus* must be replaced by populations from the upper limit of *P. devoniana*.

In order to maintain pure stands of *Abies religiosa*, their populations must immigrate to the new locations where their climatic habitat is projected to appear (Fig. 5D) or to the xeric limit of *P. hartwegii*, where habitat loss and contraction of their populations are already underway, while at the same time recruitment of individuals is occurring at altitudes of over 4,000 m a.s.l. (Astudillo-Sánchez et al. 2017). Field evidence indicates that the habitat loss of *P. hartwegii* is offset by its recent colonization of alpine grassland (Ramírez-Amezcua et al. 2016).

Expected impacts on timber production

The previously described species replacement expected at the xeric limit presents silvicultural and conservation challenges. From the silvicultural perspective, for example, the replacement of the highly productive and fast-growing *P. pseudostrobus* species at its xeric limit by the slower growing, grass stage *P. devoniana*, at NSJP, Michoacán, is a justified measure based on our projections, but one that is difficult to accept from the perspective of commercial forestry in that region. The tradeoff that exists between drought resistance and growth rate is expressed clearly when comparing these two species. If a fast-growing species that is susceptible to drought stress is replaced with another more tolerant of drought, timber yield will have to be sacrificed (Sáenz-Romero et al. 2016). In other words, the decision will necessitate a strategy to deal with the economic losses due to the future impacts of climatic change: whether or not to accept future economic losses now in a climate projected to be warmer and dryer, in exchange for the possibility of having healthy future forests established through assisted migration (Millar et al. 2007).

In addition to considering shifting provenances and species upward in altitude as part of a commercial management strategy, other practices such as commercial thinning to higher intensities than is currently practiced might be recommended. By lowering stand densities, such practices would reduce competition for water and vulnerability to forest fires as the climate becomes warmer and drier (Millar et al. 2007).

Implications for conservation in Protected Natural Areas

A second management dilemma involves conservation. It is very difficult to accept that a relatively successful Mexican program for conserving Monarch butterfly overwintering sites might be insufficient alone to preserve the dense *Abies religiosa* stands that serve as winter hosts for this butterfly, especially when the current conservation efforts include local community organization, field surveillance against illegal logging, and ecotourism development. Replacement of the low altitudinal limit of

Abies religiosa with pine species not currently present within the MBBR, such as *P. devoniana* and even *P. oocarpa*, is in opposition to the accepted paradigm of in situ conservation: i.e., that ecological restoration should be conducted only with local endemic species.

Assisted migration has been proposed as a tool for recovery of ecosystem services and not necessarily involving reconstruction of the ecosystem composition (Lunt et al. 2013, Williams and Dumroese 2013). Ecosystem composition cannot be maintained if species replacement is the appropriate management alternative. However, our projections indicate that if forest decline continues at the *A. religiosa* lower altitudinal limit, the actual managerial alternative might be decimated *A. religiosa* stands or even treeless tracts on the one hand or having a planted stand of a different conifer species (such as *P. pseudostrobus*) on the other hand. On the sites where suitable climatic habitat for *P. pseudostrobus* (a species currently present within the MBBR) persists, the priority should be maintaining this species, perhaps by selecting drought-resistant genotypes from the local populations. However, decay of *A. religiosa* will act to reduce forest diversity toward stands dominated by *P. pseudostrobus*, a species that is not preferred by Monarch butterflies when overwintering in the MBBR.

Although alternatives such as the two examples described above that include assisted migration at the lower altitudinal limit (or xeric limit) might be unattractive, they must be considered in view of the inevitable outcome of continued inaction. With such inaction, a large body of worldwide evidence on forest decline (Allen 2010, Mátyás 2010, Mátyás et al. 2010, Allen et al. 2015) suggests that species will be lost as degradation of the Mexican pine and conifer forest takes place, beginning at the corresponding xeric limit of each species.

Opportunities for ex situ conservation

The new suitable climatic habitat, displayed as added habitat on Figs. 2–6 and the total area of which per species is presented in Table 3, also represents an opportunity for ex situ conservation, given that the species is not currently present there. Translocation of genotypes from their natural contemporary distribution to a place currently not occupied naturally, but one that is projected to have a suitable climatic habitat under a given climatic change scenario, can be viewed as "assisted colonization," sensu Ledig et al. (2010). However, most of the germplasm movement would be within the areas currently occupied by the species. In other words, most of the seed and seedling movement would be from the contemporary lower altitudinal limit to the mid-altitudinal range, and from the latter to the upper altitudinal limit, and only a small portion of transfers would exceed the contemporary upper altitudinal limit. This must be stressed, since a concern of some ecologists is the potential risk of species replacement (Ricciardi and Simberloff 2008, Hewitt et al. 2011, Seabrook et al. 2011).

Limitation of the study

The use of an ensemble of 17 global circulation models, aiming to represent an average of numerous models and thus to explore the range of possibilities, has the drawback of not individually exploring the projections yielded by each global circulation model, which sometimes present important differences, particularly due to differences in projections of precipitation patterns. Although this would be an interesting approach, it is beyond the stated aim of this work. A possible suggestion for follow-up work would therefore be to run the analysis for each individual global circulation model, and then to construct a map of the resulting consensus.

The present study focused on what we considered to be the most ecologically and economically important five conifer tree species along altitudinal gradients in the TMVB. However, in a megadiverse country such as Mexico, there are many more conifer and broadleaf species to be considered; for example, in terms of conservation, the very rare, fragmented and endangered *Pinus rzedowskii*; for commercial management and timber production, *Pinus montezumae*; for Christmas trees, *Pinus ayacahuite*, to mention only a few. There is therefore the need for further suitable climatic modeling addressing these other species.

Conclusions

The results suggest that, by 2060, the climate niche of each species will occur at elevations that are between 300 to 500 m higher than at present. By 2060, countrywide habitat loss could amount to 46% (*Pinus devoniana*) to 77% (*Abies religiosa*), mostly affecting the lower limits of distribution of each species. The two species at the highest elevation, *P. hartwegii* and *A. religiosa*, would suffer the greatest losses while, at the lower elevations, *P. oocarpa* would gain the most niche space (+25% of the contemporary distribution at the Trans-Mexican Volcanic Belt). Our results suggest that conifers will require human assistance to migrate altitudinally upward in order to recouple populations with the climates to which they are adapted. Traditional in situ conservation measures are likely to be equivalent to inaction and will therefore be incapable of maintaining current forest compositions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2041/full

DATA AVAILABILITY

Data are available on Figshare: https://doi.org/10.6084/m9.figshare.9827231.v3