



Abies religiosa habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico

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ABSTRACT

Abies religiosa (HBK) Schl. & Cham. (oyamel fir) is distributed in conifer-dominated mountain forests at high altitudes along the Trans-Mexican Volcanic Belt. This fir is the preferred host for overwintering monarch butterfly (*Danaus plexippus*) migratory populations which habitually congregate within a few stands now located inside a Monarch Butterfly Biosphere Reserve. Our objectives were to predict and map the climatic niche for *A. religiosa* for contemporary and future (2030, 2060 and 2090) climates, suggest management strategies to accommodate climate changes, and discuss implications for conservation of monarch butterfly overwintering sites in Mexico. A bioclimate model predicting the presence or absence of *A. religiosa* was developed by using the Random Forests classification tree on forest inventory data. The model used six predictor variables and was driven primarily by the mean temperature of the warmest month, an interaction between summer precipitation to and winter temperatures, and the ratio of summer to annual precipitation. Projecting the contemporary climate niche into future climates provided by three General Circulation Models and two scenarios suggested that the area occupied by the niche should diminish rapidly over the course of the century: a decrease of 69.2% by the decade surrounding 2030, 87.6% for that surrounding 2060, and 96.5% for 2090. We discuss assisted migration of *A. religiosa* upwards in altitude by 275 m so that populations of 2030 would occupy the same climates as today. The projections also show that by the end of the century, suitable habitat for the monarch butterfly may no longer occur inside the Biosphere Reserve. We therefore discuss management options and associated research programs necessary for assuring perpetuation of future butterfly habitat.

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1. Introduction

Abies religiosa (oyamel fir) is distributed in a high-altitude, coniferous-dominated mountain forest along the Trans-Mexican Volcanic Belt, mainly between 2400 and 3600 m of altitude and between 19° and 20° LN (Sánchez-Velásquez et al., 1991; Jaramillo-Correa et al., 2008). Its distribution is coincidental to the cloud belt that forms around the mountain peaks during the summer wet season (Brower et al., 2002). Populations occurring within the Monarch Butterfly Biosphere Reserve (MBBR, Fig. 1) at altitudes of 2900–3400 m serve as an almost exclusive host for overwintering monarch butterflies (*Danaus plexippus*) (Fig. 2) eastern migra-

tory populations (Anderson and Brower, 1996; Oberhauser and Peterson, 2003).

Vegetation models suggest, however, that by the end of the current century, suitable climates for the conifer forests in the Trans-Mexican Volcanic Belt could be reduced by 92%, a value obtained from the average impact of three General Circulation Models and two greenhouse gas emission scenarios (Rehfeldt et al., 2012). These changes result from temperatures that are projected to increase by 3.7 °C and precipitation to decrease by 18.2% by the end of the century in Mexico (Sáenz-Romero et al., 2010). If the climate to which *A. religiosa* populations are adapted shifts, it is likely that current forests are soon to exhibit decline. Such decline or die-off of large masses of forest with causes related to climatic change is underway in many parts of the world: e.g. *Pinus edulis* at low altitudinal limits in south-western USA (Breshears et al., 2005) *Populus tremuloides* in the Rocky Mountains, USA (Worrall et al., 2008) and Canada (Hogg et al., 2002), *Cedrus atlantica* in the Moyen Atlas mountain range, Morocco (Mátyás, 2010), and

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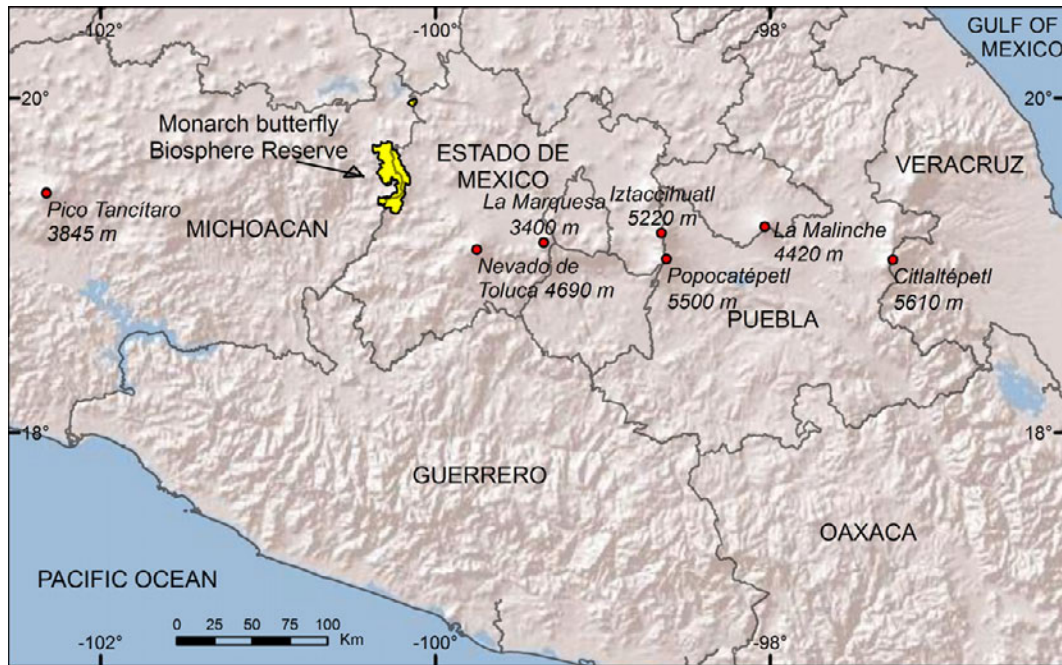


Fig. 1. Map of the Trans-Mexican Volcanic Belt locating the Monarch Butterfly Biosphere Reserve (yellow areas), major volcanoes (red dots) and their altitudes (masl).



Fig. 2. Overwintering colony of Monarch butterfly (*Danaus plexippus*) on *Abies religiosa* tree branches. Sanctuary El Rosario, Monarch Butterfly Biosphere Reserve, Michoacán, México.



Fig. 3. *Abies religiosa* tree with signs of decay on the upper part of a crown. Sanctuary El Rosario, Monarch Butterfly Biosphere Reserve, Michoacán, México.

Fagus sylvatica in South-west Hungary (Mátyás et al., 2010) and in NE Spain (Peñuelas et al., 2007).

Generation after generation of monarch butterflies have overwintered in the MBBR such that today, the overwintering population numbers between 100 and 500 million (Ramírez et al., 2003). The butterflies take advantage of the umbrella and blanket effect of *A. religiosa* forest canopy and branches, packing together in colonies where butterflies cluster side-by-side on the stems and branches (Fig. 2) to prevent mortality during cold and rainy winter nights (Anderson and Brower, 1996). The near exclusiveness of *A. religiosa* as host makes it difficult to envision survival of overwintering butterflies at this site as their host becomes increasingly poorly adapted to the MBBR climate. There are an increasing number of recent observations of *A. religiosa* trees inside the MBBR with signs of dieback apparently due to drought stress in the changing

climate (Fig. 3). In addition, deforestation inside the reserve due to illegal logging and changing use of land is a historical problem (Brower et al., 2002; Ramírez et al., 2003) that continues to present with heterogeneous site-to-site effects. Some areas of the reserve are relatively well conserved and others are under a severe process of degradation (Navarrete et al., 2011).

The objectives of this work were to: (1) define the contemporary realized climate niche for *A. religiosa*, (2) predict and map contemporary and future distribution of climatic suitable habitat for *A. religiosa*, (3) suggest management strategies for relocation of *A. religiosa* populations to accommodate climatic changes, and (4) discuss implications for conservation of Monarch butterfly overwinter sites in México. For simplicity, we call the 'contemporary realized climate niche' the 'climate profile'. We use the Random Forests classification tree (RFCT; Breiman, 2001) to predict the presence

or absence of *A. religiosa* from climate variables and to project contemporary climate niches into future climate space. This work builds on that of Oberhauser and Peterson (2003) who used an ecological niche model along with a genetic algorithm for rule-set prediction to assess the response of *A. religiosa* to climate at the MBBR.

2. Materials and methods

2.1. Presence–absence data input

Our data came largely from the permanent plots of the Mexican Forest Inventory.¹ The data we used consisted of 6674 plots that contained conifers and ca. 13,000 plots with species other than conifers. Of these plots, 128 were inhabited by *A. religiosa*. Mexican Inventory customarily establishes plots with four subplots which were combined for our analysis.

To assure that our sample was representative of the vegetation of Mexico, we also used a systematic sampling of point locations within the digitized map of the Biotic Communities of North America (Brown et al., 1998). Technical procedures, described in detail in Rehfeldt et al. (2006) and used also by Ledig et al. (2010) involved the use of ARCMAP software to procure 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). Absence data points from all communities within which *A. religiosa* can occur (Transvolcanic, Madrean, and Guatemalan Conifer Forests) were discarded. The procedure provided ca. 67,000 additional data points, all of which were assumed to lack *A. religiosa*.

In order to be sure that the highest and coldest sites in Mexico were represented among the data points that lack *A. religiosa*, the digitized elevations of GLOBE (1999) were used to obtain a geographic sample of points on the flanks of Mexico's seven tallest volcanic peaks. This procedure produced a data set of 30 observations that, for instance, contained seven data points for Iztaccíhuatl (tallest volcanoes or mountains indicated on Fig. 1) that ranged in elevation from 4291 to 5142 m.

These procedures produced a dataset of ca. 87,000 observations. The climate of each was estimated from the spline climate surfaces of Sáenz-Romero et al. (2010), available at URL: <http://forest.moscowfsl.wsu.edu/climate/>. These climate surfaces predict monthly values of temperature and precipitation from which 18 variables of demonstrated importance in plant geography are derived. Additional variables involving the interaction of the 18 derived variables are used herein to produce 34 variables available for developing bioclimate models. Of the possible interactions, we concentrated on those involving temperature and precipitation (see Rehfeldt et al., 2006, 2009).

2.2. Bioclimate model

We use the Random Forests classification tree (Breiman, 2001), available in R (R Development Core Team, 2004; Liaw and Wiener, 2002), to predict the presence–absence of *A. religiosa* from climate variables. Our model follows the pioneering framework of Iverson and Prasad (1998), Iverson et al. (2008), and closely parallels Rehfeldt et al. (2006).

To comply with Breiman's (2001) recommendation that the number of observations within classes be reasonably balanced, we used the sampling protocol of Rehfeldt et al. (2009) to draw from our database 25 datasets such that 40% of the observations in each dataset are those containing *A. religiosa*; 40% lack *A.*

religiosa but are from climates that would be difficult to separate from those containing *A. religiosa*; and 20% represent a broad range climates from beyond the climatic distribution of *A. religiosa*. Each dataset contained about 640 observations.

In the vernacular of the Random Forests software, our analyses built 25 'forests', each of which consisted of 100 'trees'. Each forest used one of our datasets. Variables were eliminated according to a stepwise procedure that culled the least important variable at each step, using a statistic called the 'mean decrease in accuracy' to judge variable importance (see Breiman and Cutler, 2004). The mean value of this statistic was calculated across the 25 forests to determine which variable should be eliminated at each iteration.

The assortment of climate variables to be included in our bioclimate model was chosen according to the classification errors calculated at each iteration. The final model was based on 25 'forests' and 500 'trees'.

2.3. Mapping realized contemporary climate niche

About ~4.6 million grid cells of ~1 km² (0.0083°) resolution comprises the terrestrial portion of our geographic window (33° LN, 13° 54' LN; 117° LW, 74° LW). By using the digitized elevations of GLOBE Task Team (1999), we estimated the climate of each cell from the spline surfaces of Sáenz-Romero et al. (2010). The climate of each grid cell was then run through the bioclimate model using R programs (modules randomForest and yalmpute), with each 'tree' of each 'forest' providing a vote as to whether a grid cell fell within the realized climate niche of *A. religiosa*; a grid cell was assumed to have a suitable climate when receiving a majority (>0.5) of favorable votes.

2.4. Prediction of future suitable habitats

We projected the contemporary climate niche into future climate space for decades surrounding 2030, 2060, and 2090), using climate grids (available URL: <http://forest.moscowfsl.wsu.edu/climate/>), for three General Circulation Models (GCM) and two scenarios: (1) Canadian Center for Climate Modeling and Analysis, using the CGCM3 (T63 resolution) model, SRES A2 and B1 scenarios; (2) Met Office, Hadley Centre, using the HadCM3 model, SRES A2 and B2 scenarios; and (3) Geophysical Fluid Dynamics Laboratory, using the CM2.1 model, SRES A2 and B1 scenarios. Data, their descriptions, and explanation of the scenarios are available from the Intergovernmental Panel on Climate Change Data Distribution Center (<http://www.ipcc-data.org/>). See Rehfeldt et al. (2006) for a description of downscaling techniques and grid development.

In mapping projections, we adopt the view that disagreement among the projections reflects uncertainty for the future (see also Hansen et al., 2001). Maps of suitable climate are presented according to the consensus among six projections for the decades centered on years 2030, 2060 and 2090. When only three or fewer projections agree, we assume that uncertainty is high. Using this threshold means that a confident prediction would require an agreement between the disparate A and B scenarios.

2.5. Estimation of altitudinal upward shift

To produce a guideline for land-use management, we estimate the upward shift required by contemporary populations in order to be inhabiting in 2030 the same climate they inhabit today. To do this, we use contemporary and future climate estimates (<http://forest.moscowfsl.wsu.edu/climate/>) for each of the 128 populations in the Mexican Inventory database to develop a linear regression (Proc REG of SAS, 2004) to predict population climate from altitude for both the contemporary climate and the future climate. As an estimate of the future climate, we use the mean of the six projections. The difference between the intercepts in the

¹ Personal communication with Miriam Vargas-Llamas and Rigoberto Palafox-Rivas, Databases Department, Mexican National Forestry Commission (CONAFOR), 23rd March 2010.

two regressions represents the altitudinal displacement required for there to be equilibrium between contemporary altitudinal distributions and future climates.

3. Results and discussion

3.1. Bioclimate model

The 34-variable model produced a classification error that averaged 2.11% across the 25 ‘forests’. As variables were eliminated in the stepwise procedure, this error fluctuated between 1.85% and 2.12% until two variables remained. Errors for the 2-variable model increased to 3.85% and to 11.67% for one-variable model. The lowest error was for the 6-variable model which, when run anew to produce the bioclimate model, had an error of 1.9%, with errors caused by predicting *A. religiosa* to be present when absent averaging 3.2% while those caused from predicting *A. religiosa* to be absent when present were null. The six climatic variables, listed in order of importance, were: MTWM, GSPMTCM, PRATIO, SDI, TDIFF and GSPTD (Table 1). The climate space of the two most relevant variables (MTWM and GSPMTCM) are illustrated for the 128 locations inhabited by *A. religiosa* in Fig. 4 against a background of four of the most abundant and ecologically important conifers in the Trans-Mexican Volcanic Belt. Of these four, *Pinus hartwegii* occurs at upper timberline and *Pinus oocarpa* occurs at lower pine-timberline. As measured by the overall classification error, the fit of our bioclimate model using six predictors is among the lowest of those for 74 western USA species for which the same methods have been used species (Crookston et al., 2010). For the latter group, classification errors ranged from 1.4% to 11.0%. For conifers of Mexico, errors were 4.5% for *Picea* spp. (Ledig et al., 2010) and 4.7% for *Pinus chiapensis* (Sáenz-Romero et al., 2010). This comparison of climate niche analyses of many disparate species combined with Fig. 4 illustrates the exceptionally small climatic niche of *A. religiosa*.

In bioclimate modeling, the most serious errors are in predicting the absence of a species when it was present, that is, the errors of omission. While many ecologically sound reasons may prevent a species from occurring in climates for which it is well suited, the most likely source of the errors of omission are in the model fitting process (see, for instance, Rehfeldt et al., 2009). In our analyses, like those of many western USA species (see Crookston et al., 2010), errors of omission were essentially nonexistent, a result directly linked to the sampling protocol which weights by a factor of two those observations in which the species of interest was present (see Rehfeldt et al., 2009).

3.2. Mapped contemporary climate profile

The precision of the bioclimate model is further apparent by superimposing the locations inhabited by *A. religiosa* on climate

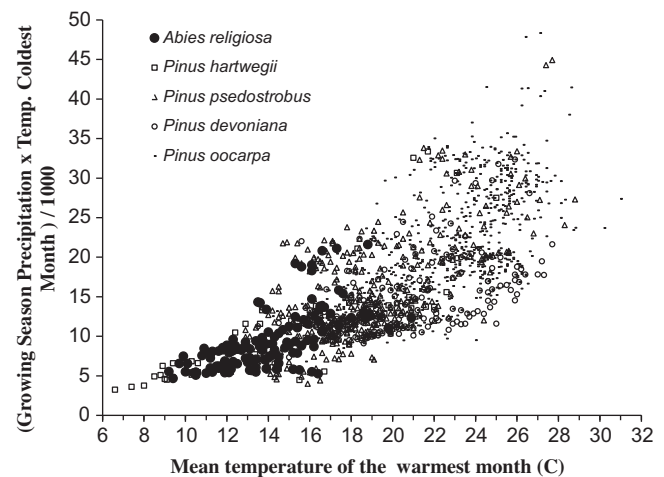


Fig. 4. Scatter of 128 *Abies religiosa* populations and four other conifers occurring the Trans-Mexican Volcanic Belt plotted in relation to the two most important climate variables in the bioclimate model (see Table 1 key to acronyms).

profile (Fig. 5). Nearly all data points occur in grid cells for which the likelihood was high that the climate would be suited for the species. No data points reside in grid cells receiving <50% of the votes. The model correctly predicts that the lower altitudinal limit of the climatic niche at about 2000 m and an upper limit at about 3600 m, both of which circumvent the volcanoes of the Trans-Mexican Volcanic Belt (Fig. 5; volcanoes names on Fig. 1). At present, *P. hartwegii* occurs between the upper limits of *A. religiosa* (Fig. 4) and upper tree line, which is about 4000 m (Lauer, 1973).

The area where the climate is predicted to be suitable for *A. religiosa* is greater than the actual distribution. This result is to be expected when habitat suitability is predicted on the basis of climate alone. Many other factors may restrict where a species actually occurs, e.g. substrate, interactions with other species, or restrictions on seed dispersal (see Pearson and Dawson, 2003; van Zonneveld et al., 2009). In addition, using the majority of votes (>0.5) to predict presence or absence prevents identification of locations where the climate may approach suitability (for example, with: 0.25 < votes < 0.50). Nonetheless, a portion of the classification error results from correctly predicting suitable niche space that is, by chance, not occupied.

3.3. Future suitable habitat for *A. religiosa*

Predicted suitable habitat for *A. religiosa* for the decades centered around 2030, 2060 and 2090 (Fig. 6) is based on the consensus of six projections. In this figure, current area is determined by >50% of the votes from the classification tree, but future

Table 1

Acronyms, derivation, and ranking of climatic variables of greatest relevance to the climate profile of *Abies religiosa*.

Acronym	Definition	Importance ranking
MAT	Mean annual temperature (°C)	–
MAP	Mean annual precipitation (mm)	–
DD5	Degree-days >5 °C	–
ADI	Annual dryness index: (DD5 ^{0.5})/MAP	–
GSP	April–September precipitation	–
GSDD5	Degree-days >5 °C summed between the last freeze of spring and the first freeze of autumn	–
MTCM	Mean temperature of the coldest month	–
MTWM	Mean temperature of the warmest month	1
GSPMTCM	(GSP × MTCM)/1000	2
PRATIO	GSP/MAP	3
SDI	Summer dryness index: (GSDD5 ^{0.5})/GSP	4
TDIFF	Summer–winter temperature differential (MTWM – MTCM)	5
GSPTD	(GSP × TDIFF)/100	6

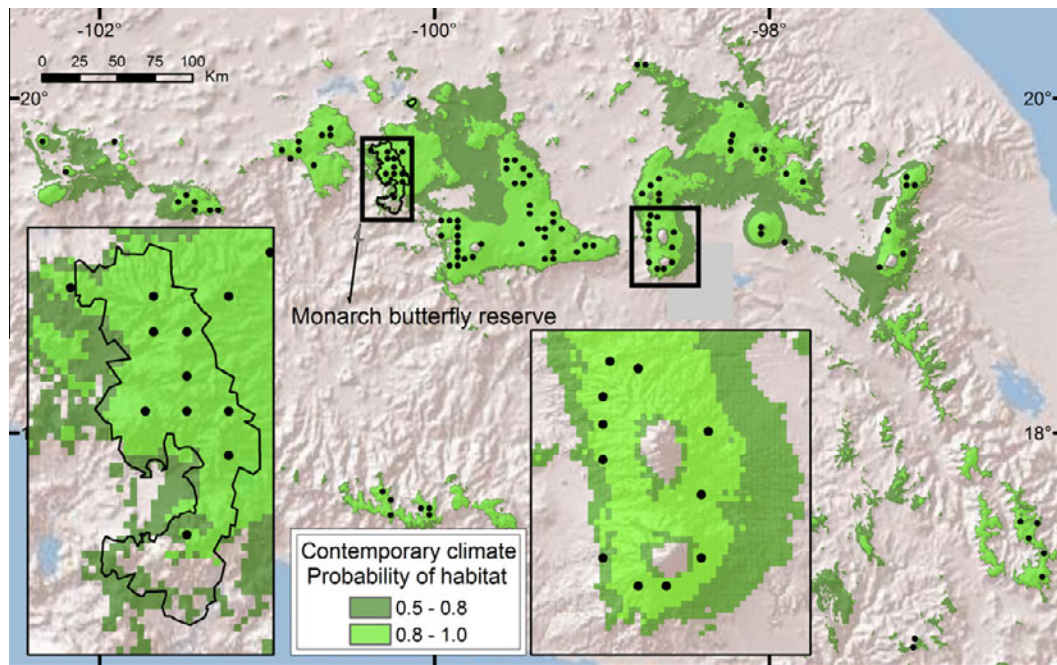


Fig. 5. Mapped locations of areas predicted by the bioclimate model to lie within the contemporary climate niche of *Abies religiosa*. Shades of green show the likelihood that the climate is suitable. Symbols locate existing populations as recorded by the Mexican forest inventory. Inserts zoom in on the Monarch Butterfly Biosphere Reserve (left) and the area surrounding the volcanos Iztaccíhuatl and Popocatepetl (right, see Fig. 1).

predictions require agreement of at least four of the six projections before being accepted as a likely prediction. The figure suggests a dramatic reduction of the climatically suitable habitat for *A. religiosa*, by 69.2% in relation to contemporary area by 2030, 87.6% by 2060, and by 96.5% by 2090 (Table 2).

In general, as the century advances, suitable habitat for *A. religiosa* is predicted to occur at higher and higher altitudes along the Trans-Mexican Volcanic Belt. Inside MBBR, however, projected

suitable habitat rises in elevation toward the mountain summits such that by 2090 there would no longer be a single square kilometer of suitable habitat remaining. For the region surrounding La Marquesa and for the La Malinche volcano (see Fig. 1), suitable habitat should reach the summits by 2090. For the tallest volcanoes, suitable habitat should shift from lower elevations towards the summits, and only elevations above 4500 m would remain unsuitable for *Abies*.

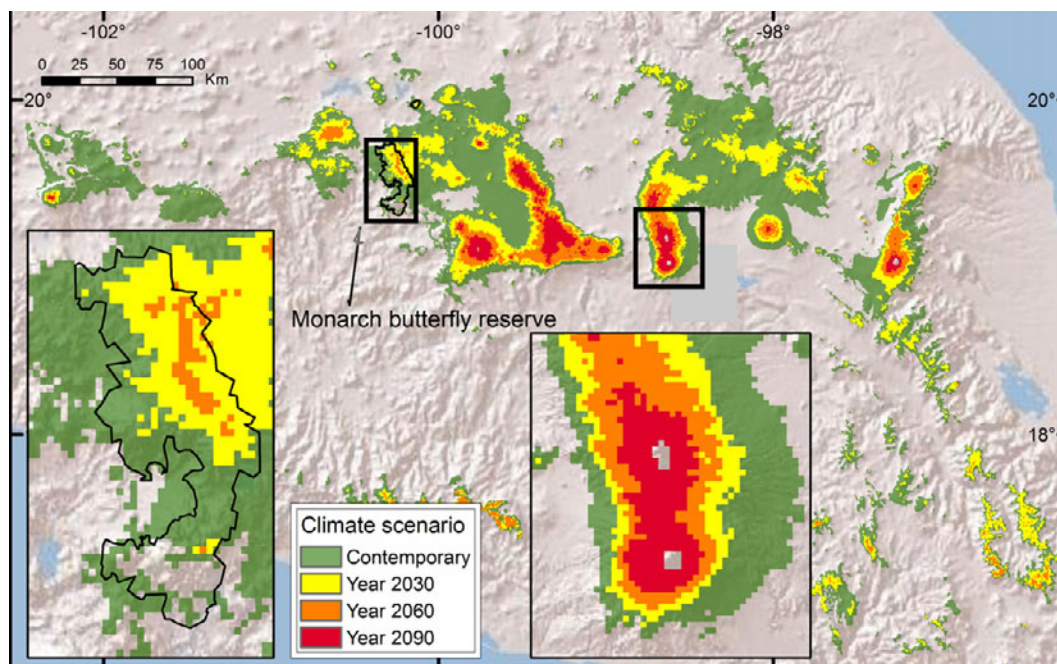


Fig. 6. Mapped locations of areas predicted by the bioclimate model to lie within the climate niche of *Abies religiosa* for four time frames (current and decades surrounding 2030, 2060, and 2090). For current climate, grid cells colored green indicate the likelihood that the climate is suitable (votes > 0.5, Fig. 5); for future climates, colors indicate the consensus of six projections that predicting suitable climate (at least four of six, each one with votes > 0.5). Volcanos are named in Fig. 1.

Table 2

Predicted nation-wide area of suitable climate for *Abies religiosa* for contemporary and for decades centered in years 2030, 2060 and 2090 (only when consensus of majority of model-scenarios – at least 4 of 6).

Contemporary suitable climate predicted area (km ²)	Future predicted area (km ² and % of present)					
	2030		2060		2090	
	km ²	%	km ²	%	km ²	%
47,356	14,562	30.8	5856	12.4	1642	3.5

Maps such as Fig. 6 showing projected climate profiles of the future do not necessarily predict that the tree populations will actually occupy the future locations of their climatic niches. Although there are well documented examples of populations that are migrating to and colonizing altitudes higher than those they occur in today as an apparent response to the ongoing climatic change (Lenoir et al., 2008), the speed at which migration is occurring is much slower than that needed for tracking the changing climatic. For example, an examination of the altitudinal distribution of 171 forest plant species (woody and non-woody) in West Europe, indicates that on average there has been an altitudinal upward shift of 65 m, when, in fact, a shift of 150 m would be required to compensate for the increase in average temperature that already has occurred (Lenoir et al., 2008). In the case of four pine species distributed in the Trans-Mexican Volcanic Belt, an upward migration of 300–400 m would be required to compensate for the change in climate expected for year 2030 as predicted, for instance, by the A2 scenario of the Canadian GCM (Sáenz-Romero et al., 2010).

3.4. Assisted migration as management option for *A. religiosa*

Because the speed of the changing climate is far faster than rates of migration of forest trees (McLachlan et al., 2005; Aitken et al., 2008), human-assisted movement of tree populations by massive plantation programs seems inescapable if future populations are to inhabit the climates to which they are physiologically attuned (see Rehfeldt et al., 2002; Tchebakova et al., 2005). This management option has been named ‘assisted migration’ (McLachlan et al., 2007), or ‘assisted colonization’ (Ledig et al., 2010).

Most forest tree species are composed of genetically different populations adapted to a range of climates that encompasses only a portion of the climatic niche of the species. Assisted migration programs, therefore, must select for the new climate not only the appropriate species but also the appropriate genotypes (Rehfeldt et al., 2002; Rehfeldt and Jaquish, 2010). Genetic variation among populations within species inhabiting mountainous environments is usually displayed as clines associated with temperatures that parallel altitudinal gradients (Rehfeldt, 1988, 1989; Sáenz-Romero and Tapia-Olivares, 2008). At present, no information is available concerning either the existence or steepness of clines that relate genetic variation among populations to climatic gradients associated with altitude in *A. religiosa*. Therefore, we assume that populations separated by about 300 m in altitude are probably genetically different for a suite of traits that convey adaptation to temperature regimes, whether the amount of winter cold or summer heat. This altitudinal interval, in fact, separates genetically different populations in five other Trans-Volcanic conifer species: *P. oocarpa* (Sáenz-Romero et al., 2006), *Pinus devoniana* (Sáenz-Romero and Tapia-Olivares, 2008), *P. hartwegii* (Viveros-Viveros et al., 2009), *P. patula* (Sáenz-Romero et al., 2011), and *Pinus pseudostrobus* (Sáenz-Romero et al., submitted for publication).

Without knowledge of genetic variances among *A. religiosa* populations and the clines it forms on forested landscapes, we assume that populations of today must inhabit in the 2030 the same climates as they inhabit today if they are to be adapted (e.g. physio-

logically attuned) in future climates. We use the correlation between the elevation of *A. religiosa* populations and values of the most important variable in the climate profile of the species, MTWM (Table 1). The correlation between these variables is very strong for both the contemporary ($r^2 = 0.8580$, $P < 0.0001$) and 2030 climates ($r^2 = 0.8596$, $P < 0.0001$) (Fig. 7). The MTWM used for the latter correlation is the average of six GCM projections. From the correlations presented in Fig. 7, we conclude that assisted migration of *A. religiosa* populations would require an upward shift of about 275–300 m for populations to inhabit the same climate in 2030 that they inhabit today.

Thus, until overridden by results of new studies of genetic variation, an interim management strategy might simply be to subdivide of the altitudinal distribution of *A. religiosa* into zones (or bands) of 300 m. To assist colonization, seed sources could be moved upward into the adjacent seed zone, that is, an average transfer of +300 m in altitude. This recommendation is easy to apply, and, more importantly, also is compatible with a predicted increase of mean temperature of 1.5 °C by year 2030 and the well-known temperature lapse rates of about 0.5 °C for each 100 m of altitude for mountainous regions of México (see Sáenz-Romero et al., 2010). The approach has the added advantage of establishing a founder population that eventually could serve as a seed source for natural migration.

3.5. Risks of moving altitudinally upwards

Moving altitudinally upwards at present would transfer populations from warmer climates to which they are reasonably well adapted to cooler climates, and, therefore, would impose additional risk of frost damage in seedlings. For example, for *P.*

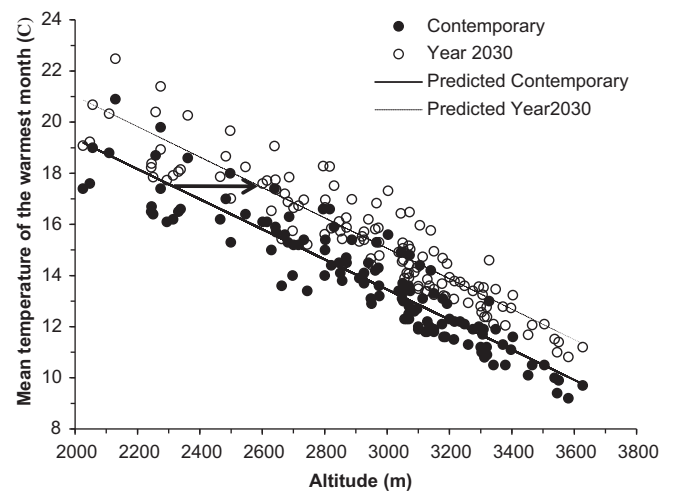


Fig. 7. Mean temperature of the warmest month of 128 *Abies religiosa* locations plotted against altitude for the current climate and for the decade surrounding 2030, as estimated from the mean of six emission scenario projections. The arrow indicates the altitudinal upward shift required for the regressions (lines) to superimpose.

devoniana populations in Michoacán, México, for every 100 m of altitudinal shift upwards, there is an increase in frost damage risk of 5.2% (Sáenz-Romero and Tapia-Olivares, 2008). A possible solution would be to plant, one year in advance of the *A. religiosa* seedlings, a nursing plant able to protect the young seedlings of *A. religiosa* from frost damage (see Blanco-García et al., 2011). Showing promise in this regard are the nitrogen-fixing perennial shrub, *Lupinus elegans*, or other local legumes (e.g. *Lupinus montanus*), most of which are suited to high altitudes (Lara-Cabrera et al., 2009).

An upward transfer of *A. religiosa* populations obviously would be constrained by the summits of the mountains they inhabit. This means that populations currently near or at the summits would need to be relocated to different mountain ranges to find 2030 climates similar to those inhabited today. This is particularly true for *A. religiosa* populations presently occupying the highest elevations at MBBR (Fig. 6). The most promising new areas for assisted migration seem to be on the flanks of the highest volcanoes (red areas in Fig. 6), such as Nevado de Toluca, Popocatepetl, Iztaccíhuatl, La Malinche and Citlaltépetl (Fig. 1). However, an important consideration is that many of these sites are likely to be above the present tree line (at approximately 4000 m). They frequently have poor soils that support at low density boreal grasses, such as *Festuca toluensis*, *Calamagrostis* sp. and *Mühlenbergia* sp. (Lauer, 1973); they may even be completely uninhabitable volcanic rock and ash. To be sure, establishing viable colonies of *A. religiosa* would be challenging under such conditions (see Blanco-García and Lindig-Cisneros, 2005; Lindig-Cisneros et al., 2007).

3.6. Implications for conservation of monarch butterfly overwinter sites

By year 2090, our models suggest that the climates currently inhabited by *A. religiosa* should disappear from within the current MBBR boundaries (Fig. 6). This result suggests a threat to the fir that applies also to overwintering colonies of the monarch butterfly. For both, suitable habitat would disappear. However, even if *A. religiosa* populations could survive elsewhere, it is not known whether the monarch butterfly would “accept” a transfer of their overwinter areas to different mountains, such as the Nevado de Toluca, the nearest volcano with suitable habitat projected for the end of the century. The mechanism used by the monarchs to guide their travels to overwintering areas is enigmatic: individuals en route to the overwintering sites were born in USA and have never before visited Mexico fir forests (Oberhauser and Peterson, 2003; Batalden et al., 2007). Nonetheless, monarch colonies return year after year to specific populations of *A. religiosa* in the MBBR.

A first step in acquiring an understanding of monarch overwintering behavior might be to replace *A. religiosa* inside MBBR with a species that should be suited to the future climate. From the human perspective, *P. pseudostrobus* is an obvious choice, as populations of this species occurring at their upper altitudinal limits presently co-occur with *A. religiosa* at MBBR. However, there are no observations known to us of monarch colonies overwintering fully on *P. pseudostrobus* trees.

A second step might be to replace *A. religiosa* with a species that phenotypically resembles the fir but does not occur presently in the reserve. Surprisingly, *Picea martinezii* seems like an ideal candidate. This species is an extremely rare and endangered relict conifer that occurs in only six populations, all located several hundred km north of the MBBR in Nuevo León. Projections for this species are for suitable habitat to arise within the MBBR after mid-century as suitable habitat in its current distribution is lost (Ledig et al., 2010). The possibilities are appealing: use assisted migration to avert the potential extinction of *P. martinezii* and thereby provide the monarch butterfly in MBBR a new overwintering host. Particu-

larly problematic would be whether the monarch would overwinter on the crowns of *P. martinezii* rather than *A. religiosa*. Another question concerns the ecological niche of *P. martinezii*. This species frequently occurs currently in microsites such as the bottom of barrancas or under the shade of a cliff (Ledig et al., 2010). If such microsites are obligatory, then site availability in MBBR may be quite limited. Obviously, considerable field experimentation is required.

A third step might be an experimental attempt to relocate monarch overwintering populations to mountain ranges expected to have suitable climate for *A. religiosa* by the end of the century. Objectives would include testing monarch survival at a new location and determining the ability of subsequent generations to return the following year. This trial would require the transfer *A. religiosa* populations from MBBR or other populations from their present provenances to mountains of higher altitudes, as discussed earlier. Fortunately, interest in the biology of monarch butterflies is so strong in Canada, USA and México that social support for conducting the necessary research seems favorable (Richardson et al., 2009).

Biologists specializing in the monarch butterfly acknowledge that it is not yet possible to predict the response of the butterflies to the demise of contemporary populations of *A. religiosa* at MBBR and subsequent re-establishment of the species at new locations. It is possible that *A. religiosa* trees themselves are not crucial for monarch overwintering, but that both organisms require the same microhabitat (Karen Oberhauser, personal communication²). Consequently, translocation of *A. religiosa* trees to new habitats would likely benefit monarchs only if: (a) the newly colonized habitat was also suitable to monarchs, and (b) the addition of the trees at the new habitat would provide roosting substrate that was not otherwise available. If so, our maps (Fig. 5) would also indicate the suitable microhabitat needed for future butterfly colonies.

4. Conclusions

The predicted suitable climate niche for *A. religiosa* will diminish rapidly over the course of the century: a decrease of 69.2% by the decade surrounding 2030, 87.6% for that surrounding 2060, and 96.5% for 2090.

To realign genotypes to the new locations of those climates for which they are adapted, the distribution of *A. religiosa* would need to shift upwards 300 m by 2030. The only feasible way for migration of this magnitude to be accomplished in such a short time is by the adoption of assisted management strategies.

By the end of the century, suitable habitat for the monarch butterfly may no longer occur inside the Monarch Butterfly Biosphere Reserve. Research is needed on appropriate techniques for successfully transferring contemporary populations of *A. religiosa* to higher altitudes and poorer site conditions than those at which they currently exist. Research is also needed on whether monarch butterfly migrating populations would overwinter on *A. religiosa* transferred to new sites or on other species transferred to sites currently inhabited by *A. religiosa*.

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