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# Projections of suitable habitat for rare species under global warming scenarios[1]

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- *Premise of the study:* Modeling the contemporary and future climate niche for rare plants is a major hurdle in conservation, yet such projections are necessary to prevent extinctions that may result from climate change.
- *Methods:* We used recently developed spline climatic models and modified Random Forests statistical procedures to predict suitable habitats of three rare, endangered spruces of Mexico and a spruce of the southwestern USA. We used three general circulation models and two sets of carbon emission scenarios (optimistic and pessimistic) for future climates.
- *Key results:* Our procedures predicted present occurrence perfectly. For the decades 2030, 2060, and 2090, the ranges of all taxa progressively decreased, to the point of transient disappearance for one species in the decade 2060 but reappearance in 2090. Contrary to intuition, habitat did not develop to the north for any of the Mexican taxa; rather, climate niches for two taxa re-materialized several hundred kilometers southward in the Trans-Mexican Volcanic Belt. The climate niche for a third Mexican taxon shrank drastically, and its two mitotypes responded differently, one of the first demonstrations of the importance of intraspecific genetic variation in climate niches. The climate niche of the U.S. species shrank northward and upward in elevation.
- *Conclusion:* The results are important for conservation of these species and are of general significance for conservation by assisted colonization. We conclude that our procedures for producing models and projecting the climate niches of Mexican spruces provide a way for handling other rare plants, which constitute the great bulk of the world's endangered and most vulnerable flora.

**Key words:** assisted colonization; climatic models; conservation; *Picea engelmannii*; *Picea martinezii*; *Picea mexicana*; Random Forests algorithm; Trans-Mexican Volcanic Belt.

Climate change may threaten a great number of species with extinction. Some may be saved if the conditions to which they are adapted reappear elsewhere within a reasonable time frame. Conservation by transfer and establishment into newly suitable habitat will require extensive planning. Therefore, it is crucial to project if, where, and when suitable climatic conditions will reoccur. We undertook projections of the future climate niche for several rare species with fragmented distributions. Such species pose an especially difficult challenge for modeling and conservation.

Organisms respond to climate change by adaptation, a shift in their geographic distribution, or extinction. For many species, adaptation will not be swift enough to cope with rapidly changing conditions, and shifts in geographic distribution may be the only alternative to extinction. Shifts in geographic distribution have been modeled for many tree species, mostly those of the eastern United States (e.g., Iverson et al., 2005). Approaches to modeling originally used climate envelopes, multivariate limits of the climate conditions in which a species now finds itself (see Box et al., 1993, 1999) and projected the distribution of those conditions into the future using general circulation models (GCMs). Envelope analyses evolved into empirically based bioclimatic models with the incorporation of statistical procedures (Iverson and Prasad, 1998; Elith et al., 2006), of which Random Forests (Breiman, 2001) has proven to be robust for predicting the realized climate niche (Iverson et al., 2005; Rehfeldt et al., 2006).

Dispersal and change in distribution of arboreal species occurred rapidly during the warming period that followed the last glacial maximum (see Davis and Zabinski, 1992), but not as rapidly as climate changes projected for this century. It is likely that many species will be unable to disperse and establish rapidly enough to colonize newly suitable habitat. In fact, analogues to the present climate may not exist for 4–48% of the earth's land area by the year 2100, and even when analogues exist, they may well be far removed; i.e., over 500 km distant 14–85% of the time (Williams et al., 2007).

Management strategies to accommodate the expected adaptational and dispersal lags created by rapid global warming may include an active program of relocating genotypes as the

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environments to which they are adapted move in time and space. This will mean planting with seed or seedlings of nonlocal sources, often assumed to originate from populations to the south or from lower elevation (Ledig and Kitzmiller, 1992; Rehfeldt et al., 2002; Tchebakova et al., 2006). Such management is known as assisted colonization or assisted migration (Rehfeldt et al., 2002; Tchebakova et al., 2006; McLachlan et al., 2007). We will use the phrase assisted colonization to avoid confusion with the use of the term migration, which refers to intragenerational movements in animals, and also because more than dispersal of propagules will be needed to assure survival of translocated species. Because the environment to which species are adapted is, and will continue to be, a moving target, more than one generation of assisted colonization may be necessary.

Delay or inaction is not an option (McLachlan et al., 2007; Aitken et al., 2008) because the gradual increase in stress will eventually exceed the limits of adaptability afforded by phenotypic plasticity (Rehfeldt et al., 2001; del Castillo et al., 2009). A point would be reached where seed production was at such a low level that establishing ex situ populations would be impossible. Therefore, early action is needed, and the first step is to project where threatened species might find suitable habitat in future decades.

If global warming poses a challenge for species in general, it is even more of a problem for narrowly distributed species fragmented into small, widely separated populations. For example, the subalpine zone in northern Mexico, the sole habitat of Mexican spruce (*Picea mexicana* Martínez), is expected to totally disappear, and the cool, temperate forest in Mexico is also projected to disappear under three different climate change scenarios (Villers-Ruiz and Trejo-Vázquez, 1997). To help conserve rare species like Mexican spruce and prevent their extinction, conservation biologists would like to know where habitats offering a high potential for survival will exist in the future.

The distribution of suitable habitats, either contemporaneous or under global warming scenarios, can be predicted for forest tree species based on detailed climatic models, such as spline climatic models (Rehfeldt, 2006; Rehfeldt et al., 2006, 2008) and climate envelope modeling (van Zonneveld et al., 2009). The recent development of a spline climatic model for contemporaneous and future climates of Mexico (Sáenz-Romero et al., in press) created an opportunity to predict the distribution of suitable habitats for endangered Mexican forest tree species. Considering the great biodiversity of tree species in Mexico (Nixon, 1993; Styles, 1993), projections are urgently needed. There are approximately 3600 woody species in Mexico, and an estimated 42% may be endemic (Villaseñor and Ibarra-Manríquez, 1998). Narrowly distributed species, however, have been especially difficult to model statistically because of the paucity of present climatic points at which they occur (e.g., Stockwell and Peterson, 2002; Schwartz et al., 2006).

Endemic species, like Mexican spruce and two other congeners in Mexico, are especially susceptible to climate change (Ledig et al., 2000b). We modeled present and future suitable habitats for the three species of spruce endemic to Mexico—Mexican spruce, Chihuahua spruce (*Picea chihuahuana* Martínez), and Martínez spruce (*Picea martinezii* Patterson). Chihuahua spruce is the most widely distributed of these three species, but even it is known from only 39 locations sparsely distributed across 687 km southeast to northwest in the Sierra Madre Occidental. Chihuahua spruce, moreover, is separated latitudinally into two distinct mitotypes on the basis of mitochondrial DNA, with 23 of the populations within the northern mitotype and 16 in the southern mitotype (Jaramillo-Correa et al., 2006). Mexican spruce is found only on the two tallest peaks of the Sierra Madre Oriental in the states of Coahuila and Nuevo León and on the tallest peak of the Sierra Madre Occidental in the state of Chihuahua, 676 km distant. Martínez spruce is known from only six stands, all within 147 km of each other north to south in the Sierra Madre Oriental. All three species are considered endangered, are relicts of the last glaciation, and the only representatives of the largely boreal genus *Picea* to reach such southern latitudes in North America—Chihuahua spruce extends just south of the Tropic of Cancer (Ledig et al., 2000b).

Chihuahua spruce and Martínez spruce grow in cool, temperate, montane forests. Chihuahua spruce, in particular, occurs mostly on sites exposed to direct sun for only brief periods of the day, usually in the bottom of arroyos or at the foot of barrancas at elevations between about 2100 m and 3000 m a.s.l. Martínez spruce is found between about 1800 m and 2500 m a.s.l. Mexican spruce is found in the subalpine zone on the tops of the highest peaks and ridges of northern Mexico, above 3100 m a.s.l. (see Fig. 1 and detailed description in Ledig et al., 2000b).

The spruces of Mexico have been profoundly affected during climate change in the past. Spruce pollen of undetermined species occurs in the sediments of Lake Texcoco and the Chalco Basin in the Valley of Mexico, indicating that the genus grew around Mexico City as recently as 7000 to 8000 yr BP (Clisby and Sears, 1955; Lozano-García et al., 1993). The distance from Mexico City to the southernmost occurrence of spruce is now about 700 km. We conclude that the scattered stands of spruces in the Sierra Madre Occidental and Sierra Madre Oriental are relicts of the last glacial period and that Holocene warming resulted in the extinction of spruce in the Valley of Mexico and contraction of the range northward. In addition, the lower elevational range of Chihuahua spruce in the Sierra Madre Occidental contracted upward at least 510 m in elevation between 13 000 yr BP and the present (Ortega-Rosas et al., 2008).

We believe that the three species of Mexican spruce are emblematic of the challenges that Mexico will face in implementing management to prevent extinctions due to global warming. Our goal was to develop ways to use the Random Forests classification tree of Breiman (2001) to predict the realized climate niche for the spruces of Mexico and to project where such conditions will exist in 2030, 2060, and 2090 under three GCMs and two scenarios for each. We predicted and then mapped the climate niche on a grid of about 1 $km^2$ (0.0083°) and then evaluated the predictions in light of information about the genetic and demographic structure of each species. We included populations of Engelmann spruce (*P. engelmannii* Parry ex Engelm.) studied by Rehfeldt (1994) in the southwestern United States south of 37°N latitude in our analyses as a comparison to the spruces of Mexico. Our models, therefore, include five spruce taxa: Mexican spruce and Martínez spruce, two mitotypes of Chihuahua spruce, and the southernmost populations of Engelmann spruce. By separating the mitotypes of Chihuahua spruce, we make one of the first attempts to take intraspecific genetic variation into consideration when projecting future distribution of climate niches.

The projections reveal a transient disappearance of contemporaneous climate for one of the species and a counterintuitive

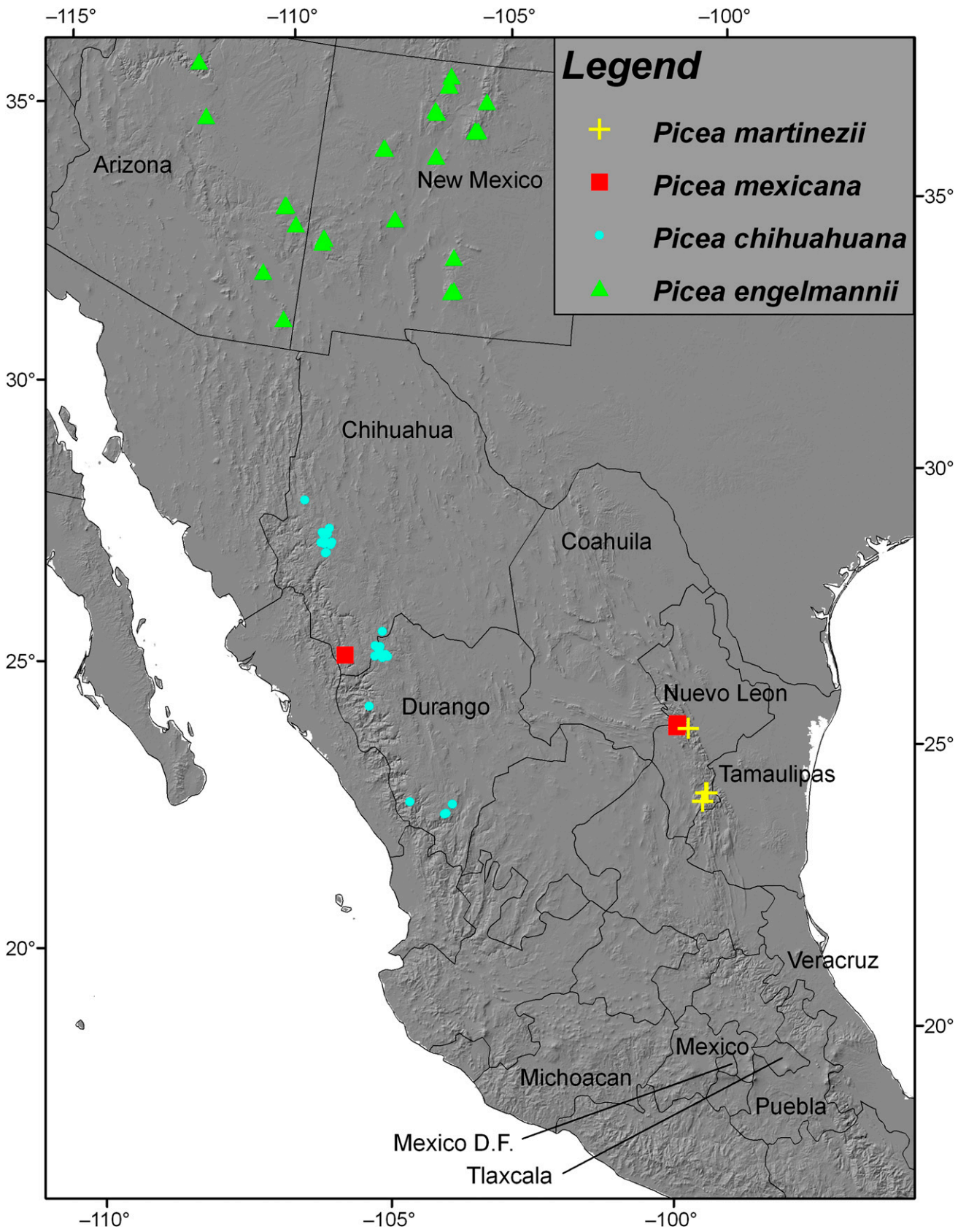



Fig. 1. Location of spruce species and their populations considered in the bioclimate analyses along with state names referenced in the text. Symbol size greatly exaggerates population size.

southward displacement of the climate niche by hundreds of kilometers for two of the species and one mitotype. The results suggest that directed colonization will be needed to prevent extinction of the spruces of Mexico and the southernmost populations of Engelmann spruce. This outcome is likely to be similar for many species of limited distribution.

## MATERIALS AND METHODS

***Presence–absence data***—Our analyses deal with 76 locations where spruce is present (Table 1). Of these, 48 are in Mexico (see Ledig et al., 2000b). The additional 28 locations included all populations of Engelmann spruce occurring south of 35°N latitude, where it is rare, and an ecologically diverse sample of those between 35° and 37°N, where it is more common (see Rehfeldt, 1994). To obtain a sample of ecologically diverse locations lacking spruce, we 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), involved the use of ARCMAP software to procure a systematic sample of point locations from each polygon on the file, and the digitized elevation model of GLOBE (1999) to associate each point sample with an elevation. Because spruce locations in Mexico were from a census, we could assume that all other locations within the 48 biotic communities of Mexico would be without spruce. Of the 25 biotic communities that occur in the southwestern USA, Engelmann spruce occurs in only one, the Rocky Mountain subalpine community, and, therefore, all sample locations from this community were discarded. In total, ca. 51 000 data points without spruce were available for Mexico while ca. 22 000 were available for the southwestern USA.

To assure that the highest and coldest sites in Mexico were represented among the data points that now lack spruce, 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 Iztaccíhuatl (ca. 19.18°N, 98.64°W) for instance, contained as many as seven data points that range in elevation from 4291 m to 5142 m a.s.l. In total, our procedures produced a data set of ca. 73 000 locations where spruce does not occur.

***Climate estimates***—Normalized (1961–1990) monthly means of total precipitation and of the average, maximum, and minimum temperatures for each observation in the presence–absence data set were estimated from the thin plate spline surfaces of Sáenz-Romero et al. (in press) for locations in Mexico and of Rehfeldt (2006) for locations in the USA. These surfaces, constructed with Hutchinson's (1991, 2004) software, provide point predictions of climate from geographic input (latitude, longitude, and elevation). Our analyses employed 18 variables derived from monthly estimates (see Rehfeldt, 2006). The derived variables include simple expressions of average temperature and precipitation (e.g., mean annual temperature, mean annual precipitation), temperature sums (e.g., degree-days > 5°C, degree-days < 0°C), freezing dates (e.g., date of the last freeze of spring), and expressions of the balance between temperature and precipitation (e.g., the ratio of degree-days > 5°C to mean annual precipitation). Additional variables were constructed from interactions of these 18, giving a total of 34 climate variables suited for developing bioclimate models. Of these variables, the 15 relevant to the discussion that follows are defined in Table 2.

***Bioclimate model***—Our statistical models are built on the framework of Iverson and Prasad (1998) and parallel those of Rehfeldt et al. (2006). We used the Random Forests classification tree (Breiman, 2001) to predict from climate variables the presence–absence of five taxa: two mitotypes of Chihuahua spruce, Mexican spruce, Martínez spruce, and Engelmann spruce. The model thus predicts the realized niche for the contemporary climate. The Random Forests algorithm, available in the program R (R Development Core Team, 2004; Liaw and Wiener, 2002), constructs a set of trees from an input data set. The trees in their aggregate are called a forest. The process draws a bootstrap sample consisting of about 64% of the total number of observations. This sample is used to build a tree, while the points omitted, collectively termed the out-of-bag sample, are used to compute classification errors. At each node of a tree, a random sample of the predictor variables is selected, ordinarily equaling the square root of the number of predictors. Of these, the variable that minimizes the classification error is selected. Nodes are further split until no more improvement can be achieved.

TABLE 1. Number of observations by species, their proportion to the total number of spruce (*Picea* spp.) observations, the contributions by species to the pool of observations without spruce that exist within a multivariate climatic hypervolume that surrounds the climatic niche of each spruce species, and the expansion factor used on climatic limits of distribution to achieve the allocation.

| Species | Number of observations | Percentage of total spruce observations | Hypervolume allocation | Expansion factor (±SD) |
|---|---|---|---|---|
| *P. chihuahuana* | 39 | 51 | 1560 | 2.8 |
| *P. mexicana* | 3 | 4 | 120 | 21.0 |
| *P. martinezii* | 6 | 8 | 240 | 2.9 |
| *P. engelmannii* | 28 | 36 | 1120 | 2.3 |

Out-of-bag errors are composed of errors of omission (a prediction of false when true) or errors of commission (a prediction of true when false) and are calculated as the proportion of the total number of errors to the total number of observations in the forest. In making predictions, each tree of each forest provides a "vote" concerning the classification of an observation. Because the error converges to a limit as the number of trees in the forest becomes large, overfitting is inconsequential. That is, adding independent variables to a model does not necessarily reduce the residual variance. Our analyses consist of 500 trees in each of 20 forests.

For classification trees, Breiman (2001) recommended that the number of observations within classes be approximately equal, otherwise errors of estimate will accrue in the classes with the fewest observations. This recommendation, however, creates an impasse for using the algorithm with species of limited distribution because the sample of absence becomes greatly restricted. Our approach is to combine the five spruce taxa into a single classification analysis, using the sampling protocol of Rehfeldt et al. (2006) to satisfy Breiman's (2001) recommendation. Accordingly, for each forest, we drew a sample from the available observations that included the 76 observations with spruce, weighted by a factor of 2. These observations were fixed at 40% of the total number to be included in the sample. Weighting allowed twice as many observations with no spruce to be included in the sample while maintaining presence at 40% and absence at 60% of the total. Each of the 20 samples, therefore, would contain ca. 380 observations, 152 with spruce and 228 without.

For selecting the observations without spruce from the 73 000 available observations, we developed a procedure that would allocate most of the observations to those climates for which separating presence from absence would be the most difficult. To do this, we produced a pool of observations consisting of

TABLE 2. Acronyms and definitions of climate variables of relevance to the bioclimatic model. Boldfaced acronyms are predictors of greatest relevance in the model.

| Acronym | Definition |
|---|---|
| DD5 | Degree-days >5°C |
| MAP | Mean annual precipitation (mm) |
| GSP | April–September precipitation (mm) |
| **MTWM** | Mean temperature in warmest month (°C) |
| MTCM | Mean temperature in coldest month (°C) |
| **MMAX** | Mean maximum temperature in warmest month (°C) |
| MINDD0 | Degree-days <0°C based on the minimum temperature |
| GSDD5 | Degree-days <5°C summed between the last spring freeze and first autumn freeze |
| ADI | Annual dryness index: $(DD5)^{0.5}$/MAP |
| **SDI** | Summer dryness index: $(GSDD5)^{0.5}$/MAP |
| **ADIMINDD0** | ADI × MINDD0 |
| **SDIMINDD0** | SDI × MINDD0 |
| **TDIFF** | Summer–winter temperature differential (MTWM-MTCM) |
| **PRATIO** | GSP/MAP |
| **TDGSP** | TDIFF/GSP |

those lying within an 18-variable climatic hypervolume (sensu Hutchinson, 1958) surrounding the climatic limits of each spruce species. The 18 variables comprising the hypervolume were those derived directly from the climate model and did not include interactions of variables. The proportion of observations to be drawn from the pool was fixed arbitrarily at 40% of the total observations in the sample, ca. 152 observations. To have a reasonably good probability that each observation in the pool was used in at least one of the 20 forests, the pool consisted of ca. 3040 observations. The hypervolume surrounding each species contributed proportionally to the pool (Table 1). To achieve proportional allocation, we expanded the dimensions of the hypervolume according to the standard deviation of the 18 climate variables (Table 1), and an observation had to be within the expanded limits for all of the 18 variables to be included in the pool. A random sample of ca 152 observations was drawn from the pool for each of the 20 samples.

The remaining 20% of a sample (i.e., 76 observations) was drawn randomly from the ca. 70 000 observations outside the hypervolume pool. To do this, we calculated the first and second principal components from all observations and randomly drew ca. four observations from each of 10 uniform classes within each component. To complete the sample, two observations were randomly drawn from the 36 observations located on the flanks of Mexico's high volcanic peaks.

This sampling procedure used all observations with spruce, concentrated the remainder of the sample in those climates for which separating presence from absence would be the most difficult, and still produced a data set that represented the full range of variation among the observations. Weighting permitted a higher proportion of the total observations to be used in each forest than would otherwise be the case and, thereby, minimized errors of omission (Rehfeldt et al., 2006, 2009).

For each observation in a sample, the Random Forests algorithm calculates a local importance value for all predictor variables. Local importance relies on an iterative process of randomly permuting (noising up) a predictor variable to assess the effect of the variable on the classification error. We used these local importance statistics as an aid in selecting predictors for the bioclimate model and to assess the climate variables most critical to predicting the realized climate niche of each taxon.

To develop the bioclimate model, we used a stepwise procedure to iteratively eliminate variables one variable at a time. We began the process by using a full complement of the 34 climate variables, and we eliminated variables according to the average of their importance values for the 500 trees in all forests. This analysis not only identified superfluous variables but also established the relationship between the out-of-bag error and the number of predictors in the model. A concern in using the stepwise procedure to select a parsimonious model is that the algorithm might eliminate variables important to the occurrence of the rarest taxa because they would have the least effect on the overall variance. Therefore, from the stepwise analysis, we accepted as candidate variables those that appeared in the 12-variable model.

To obtain the final model, values of local importance for each variable in the 12-variable model were averaged for each taxon across the 20 forests. The two most important variables for predicting the occurrence of a taxon were identified, and of the remaining variables, the one having the least influence across taxa was discarded. An 11-variable model was then computed. We repeated the process until a model was produced that satisfied two criteria: (1) predictors included the two most important variables for each taxon, and (2) the out-of-bag error was consistent with the relationship between the errors and the number of variables in the model as previously established by the stepwise procedure; e.g., elimination of a variable from a six-variable model would result in a five-variable model with an error similar to that established by the stepwise procedure for the same number of variables, that is 4.5–4.6% in this case (see below).

After the variables to appear in the bioclimate model were selected, the Random Forests program was run anew with 1000 trees in each of the 20 forests.

***Mapping realized climate niches***—About 4 million pixels of ~1 km (0.0083°) resolution comprise the terrestrial portion of our geographic window. By using the digitized elevations of GLOBE (1999), we estimated the climate of each pixel from the surfaces of Rehfeldt (2006) and of Sáenz-Romero et al. (in press). The climate of each pixel was then run through the bioclimate model, with each tree of each forest providing a vote as to whether a pixel fell within the realized climate niche of one of the spruce taxa; a pixel was assumed to have a suitable climate when receiving a majority of favorable votes.

***Prediction of future suitable habitats***—We projected the contemporary climate niche into future climate space for three General Circulation Models (GCM) and two scenarios: (1) Canadian Center for Climate Modeling and Analysis (CCCMA), using the CGCM3 (T63 resolution) model, SRES A2 and B1 scenarios; (2) Met Office, Hadley Centre (UKMO), using the HadCM3 model, SRES A2 and B2 scenarios; and (3) Geophysical Fluid Dynamics Laboratory (GFDL), 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/). In general, the SRES A2 scenario reflects unrestrained carbon emissions, while the B1 and B2 scenarios incorporate social and economic restraints; the scenarios we use should begin diverging by 2030.

We used GCM output to calculate the monthly change in climate between the normalization period and the decades surrounding 2030, 2060, and 2090 for each weather station used to develop the climate surfaces (for details, see Rehfeldt et al., 2006, for the western USA and Sáenz-Romero et al., in press, for Mexico). For calculation of monthly changes in average, minimum, and maximum temperature, we used actual values; for precipitation, we used proportions. To downscale from the relatively coarse grids of the GCMs to the point locations of the weather stations, we used a weighted average of the monthly change in climate calculated for the GCM cell centers lying within 400 km of a station. The inverse of the square of the distance from the station to the cell center was used for weighting. Monthly climate surfaces for average, minimum, and maximum temperature, and precipitation were then fit anew for each GCM and each scenario. By updating weather from existing weather stations, we circumvented downscaling issues that would result from adjusting the two-dimensional GCM grids of coarse resolution to the complex three-dimensional topographic surfaces of Mexico and the southwestern USA.

## RESULTS

***Bioclimate model***—Out-of-bag errors for the 34-variable model averaged 4.3% across the 20 forests. This error remained relatively constant, fluctuating between 4.2 and 4.4% throughout the stepwise elimination of variables until 20 variables remained and between 4.5 and 4.6% until only five remained. Thereafter, the errors increased slowly as variables were removed, reaching 4.8% with four variables, 5.5% with three, 6.8% with two, and culminating with 23.5% error with a one-variable model. We chose the eight-variable model that contained the two most important variables for each taxon yet had an average out-of-bag error (4.5%) consistent with overall error rates.

Out-of-bag errors for the eight-variable model were comprised entirely of errors of commission, i.e., the error that arose from predicting the presence of one of the spruce taxa when it was, in fact, absent. Nearly all of these errors resulted from predicting the presence of either Engelmann spruce or Chihuahua spruce when they were absent. Errors of prediction were nil for Mexican and Martínez spruces.

Values of local importance summarized from output of the 20 forests showed that the most important variables (Table 2) for separating the occurrence of taxa from each other and from areas without spruce were, in order of importance: (1) MMAX and PRATIO for Engelmann spruce; (2) MTWM and SDI for Mexican spruce; (3) ADIMINDD0 and TDIFF for Martínez spruce; (4) TDIFF and TDGSP for the northern mitotype of Chihuahua spruce; and (5) TDIFF and MMAX for the southern mitotype. Thus, predicting the occurrence of these taxa relied primarily on variables expressing the heat in the warmest part of summer and potentials for summer moisture stress. Notice that PRATIO reflects the periodicity of precipitation, while TDIFF ordinarily reflects the degree by which the climate is controlled by continental or maritime climates, but for Mexico both variables may be related to the balance between dry

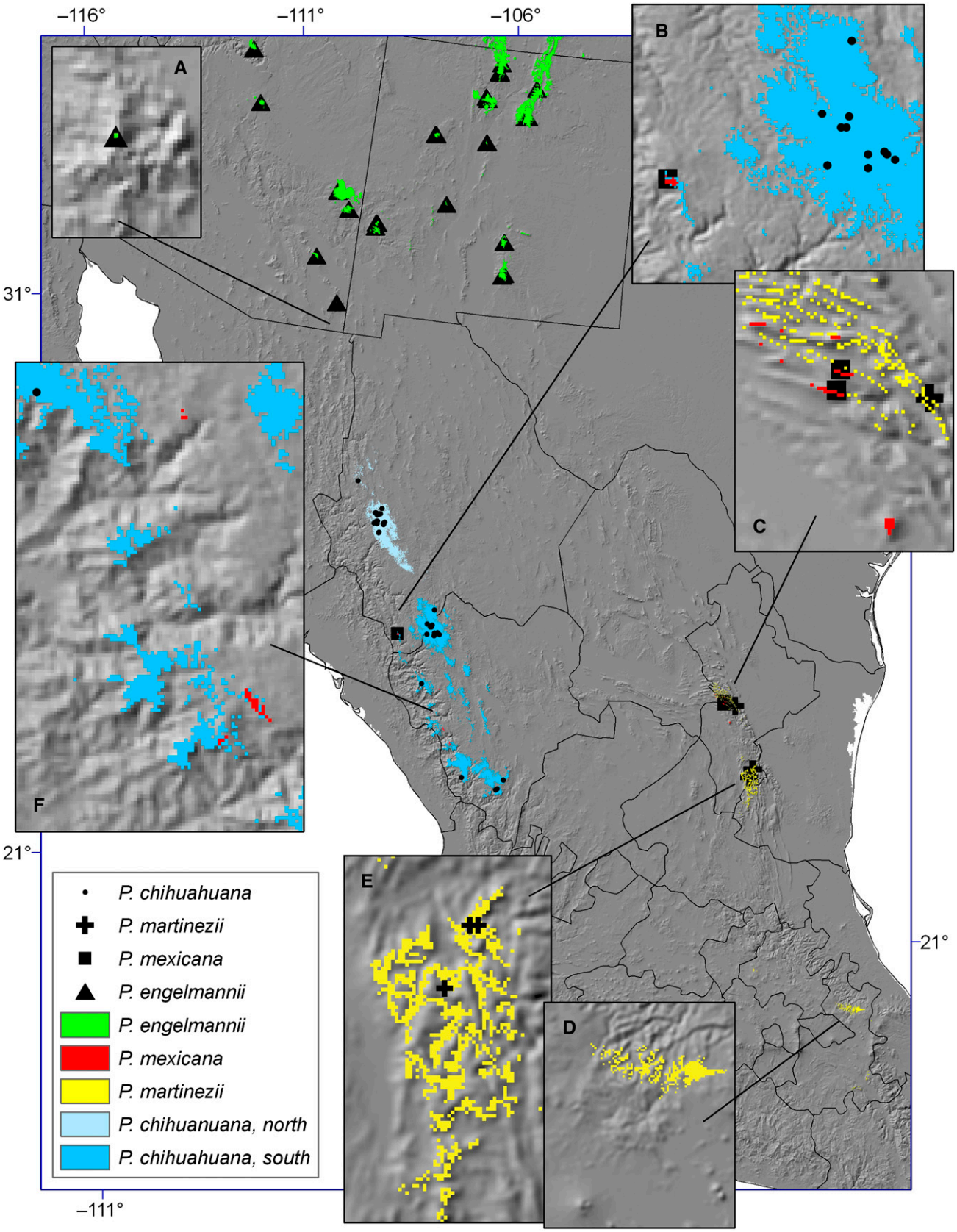



Fig. 2. Mapped locations of areas predicted (colored pixels) by the bioclimate model to lie within the contemporary climate niches of four spruce species, of which the northern and southern mitotypes are separated for *Picea chihuahuana*. Symbols locate existing populations.

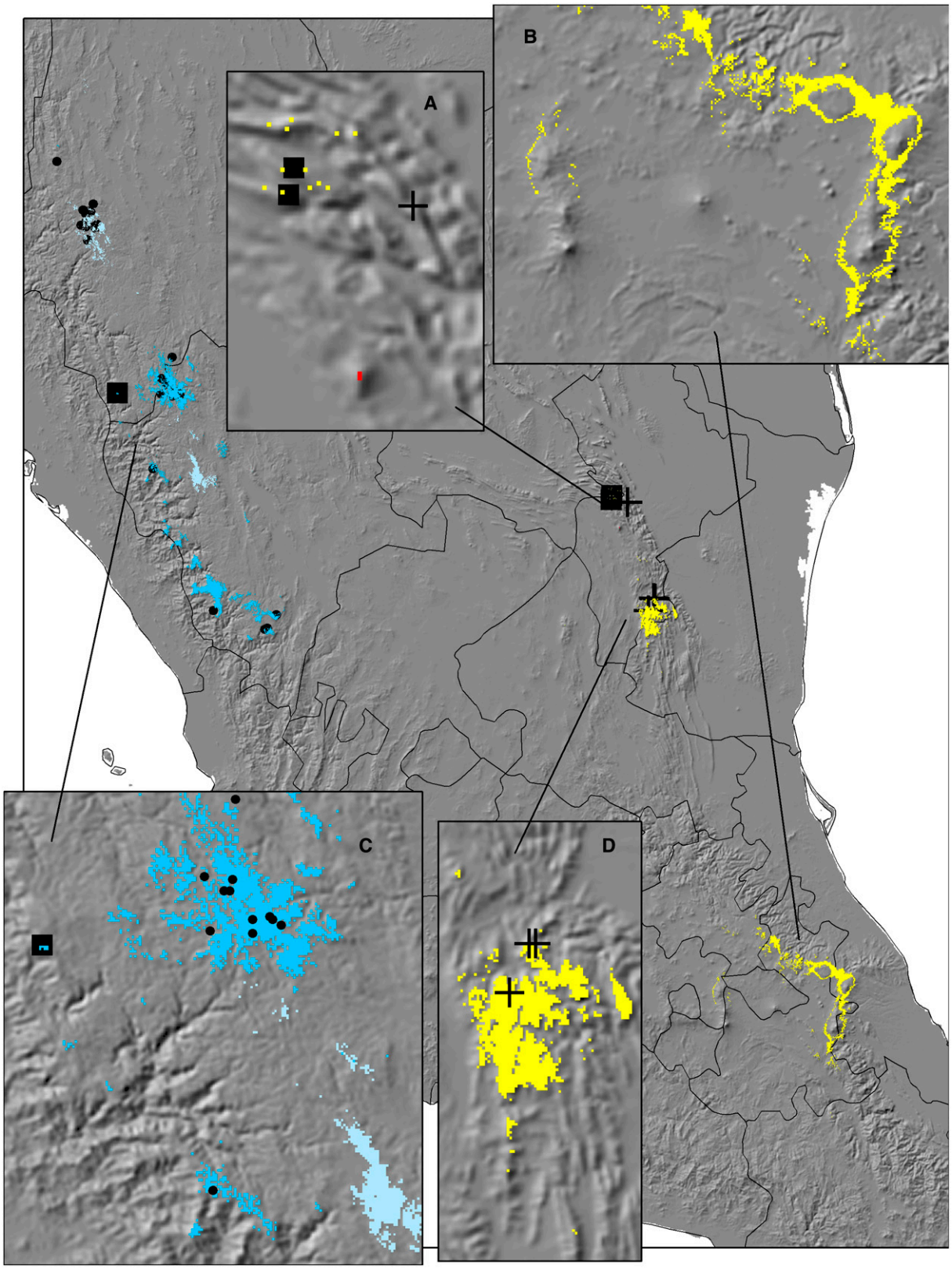



Fig. 3. Composite mapping of six projections made from output of three general circulation models (GCMs) and two scenarios for the decade surrounding 2030 using the majority of votes cast by the Random Forests classification tree to determine presence or absence of four of Mexico's spruce taxa. Red, *Picea mexicana*; yellow, *P. martinezii*; light blue and sky blue, northern and southern mitotypes of *P. chihuahuana*, respectively. Symbols locating existing populations are keyed to Fig. 2.

Pacific westerlies vs. monsoonal Atlantic influences. TDGSP is summer precipitation weighted by the summer–winter temperature differential.

***Realized climate niches***—The predicted distribution of suitable habitats for contemporaneous climate are inclusive of all known populations of the three spruces of Mexico (Fig. 2), including the isolated population of Mexican spruce at Cerro Mohinora in the state of Chihuahua, the only population of Mexican spruce in the Sierra Madre Occidental (Fig. 2B). Predicted suitable habitat also coincides with the occurrence of the isolated populations of Mexican spruce at Sierra la Marta and Sierra el Coahuilon, near the border between the states of Coahuila and Nuevo León (Fig. 2C). Our analysis also suggests a limited occurrence of locations (Fig. 2C and F) with suitable climates that are not currently occupied by Mexican spruce, including Cerro Potosí (bottom of Fig. 2C) and Sierra de Arteaga and Sierra Potrero de Ábrego (top right of Fig. 2C) in the Sierra Madre Oriental, and in three locations in the Sierra Madre Occidental in the State of Durango (lower right of Fig. 2F), which are near Cerro Santa Efigenia, Cerro el Táscate, and Cerro de la Virgen.

The present distribution of Martínez spruce is completely within the area where the climate is predicted to be suitable (Fig. 2C and E). Additional areas of suitable climate for Martínez spruce are predicted in northern and southeastern Puebla and western Hidalgo where no Martínez spruce now occurs (Fig. 2D).

For Chihuahua spruce, all known populations lie within the area predicted to have a suitable climate, and the classification tree was capable of separating the northern and southern mitotypes perfectly. However, the distribution portrayed in Fig. 2 tends to be broad and continuous, whereas the actual distribution is fragmented. The natural occurrence of Chihuahua spruce seems to be determined by effects of local topography (Ledig et al., 2000b) superimposed on the regional climate.

Engelmann spruce reaches its southern limits of distribution on isolated mountains of Arizona and New Mexico, which for our analysis were thoroughly represented. The analysis correctly predicted the occurrence of suitable climate in all of these sky islands, including the small southernmost population in the Chiricahua Mountains of southern Arizona (Fig. 2A). The map also realistically describes the situation in northern New Mexico, which is part of Engelmann spruce's more nearly continuous distribution.

***Future climate niches***—In mapping future distributions of the realized climate niche of today, we overlaid six projections, two from each of three GCMs and presented them as a composite. This composite exaggerates the agreement among the projections because the visual impression is dominated by the most optimistic of the predictions (i.e., the one that predicts the least change, or least loss of the realized climate niche), which for the spruce populations of Mexico is the A2 scenario of GDFL. For Engelmann spruce, however, the B2 scenario of UKMO is the most optimistic.

***Mexican spruce***—In projections for 2030, suitable climates essentially disappear for Mexican spruce except on Cerro Potosí, where it is not found today (Fig. 3). Predictions for the decade centered in the year 2060 (Fig. 4), suggest a continuation of the previous (2000 to 2030) trend. By 2060, the suitable climate niche for Mexican spruce would disappear entirely. For none of the GCMs did a pixel garner enough votes to be declared suitable for Mexican spruce in 2060.

The projections for Mexican spruce in 2090 are most intriguing (Fig. 5). Potential habitat for this species appears for the first time on the peaks of the Trans-Mexican Volcanic Belt, such as Tláloc and La Malinche and along the flanks of Popocatépetl (summit at ~5454 m a.s.l.) and Iztaccíhuatl (~5230 m a.s.l.). According to the digitized elevations of GLOBE (1999), the altitude on La Malinche suited for Mexican spruce would be ~3900 to 4200 m a.s.l., an increase in elevation of about 600 to 700 m above its present elevational range.

***Martínez spruce***—In 2030, suitable climates for Martínez spruce near the border of the States of Coahuila and Nuevo León (Fig. 3A) almost disappear. Conversely, the climate niche for the southern populations of Martínez spruce at the border between the States of Nuevo León and Tamaulipas actually increases, as does area predicted in the States of Puebla, Veracruz, Mexico, Tlaxcala, and Hidalgo, much to the south of its present range (Fig. 3D). Suitable habitat expands in northern Puebla, an area known as Sierra Norte del Puebla, and to the east in the State of Veracruz around Citlaltépetl (~5610 m a.s.l., the highest mountain of Mexico), also known as Pico de Orizaba, and around Cofre de Perote (~4200 m a.s.l.), also known as Naucampatépetl (Fig. 3B). New predicted habitat also occurs around Tláloc (~4158 m a.s.l.), the northernmost volcanic peak in the Iztaccíhuatl-Popocatépetl chain; in the states of Mexico, Puebla, and Tlaxcala; small spots in the southeast of Puebla, northeast of the Reserva de la Biosfera Tehuacán-Cucatlán; and in eastern Hidalgo.

In 2060, the climate niche for Martínez spruce near the Coahuila–Nuevo León border would be reduced farther, almost to the point of disappearing (Fig. 4), but nonetheless would replace that for Mexican spruce on Cerro Potosí (summit ~3713 m a.s.l.). However, the maps also show a farther expansion of the climate niche in areas where it does not now occur in the eastern portion of the Trans-Mexican Volcanic Belt: in the State of Puebla, around Tláloc on the border of the States of Mexico and Tlaxcala, and, for the first time, around La Malinche (~4420 m a.s.l.), also known as Matlacuéyetl, in the State of Tlaxcala. Suitable climate niche appears for the first time in the year 2060 on the highest peaks near the border of the States of Mexico and Michoacán. In Michoacán, the new habitat is in and near the Reserva de la Biosfera de la Mariposa Monarca (Monarch Butterfly Biosphere Reserve). In the State of Mexico, the new habitat includes the slopes of Nevado de Toluca (~4680 m a.s.l.), also known as Xinantécatl, in a national park; Cerro la Guadalupana (3360 m a.s.l.), Cerro Veguachi (3080 m), Cerro Pelón (3325 m), and Cerro las Palmas (3200 m). Small areas appear in the state of Querétaro on Cerro el Gallo (2900 m) and in the state of Guanajuato on Cerros los Rosillos (3180 m) and Siete Cruces (3100 m).

By 2090, projections for the northwest of the Sierra Madre Oriental indicate a near complete disappearance of Martínez spruce at the borders between the States of Coahuila and Nuevo León (Fig. 5A). Furthermore, only a few patches, much reduced in area, remain suitable near the border of Nuevo León and Tamaulipas (Fig. 5D). However, our model predicts that suitable climate niche will still exist in the States of Puebla, Mexico, and Michoacán, but may move up in elevation. While there are losses in suitable area around Tláloc, for example, the predicted climate niche for Martínez spruce enlarges around La Malinche, Nevado de Toluca, and on peaks of the Trans-Mexican

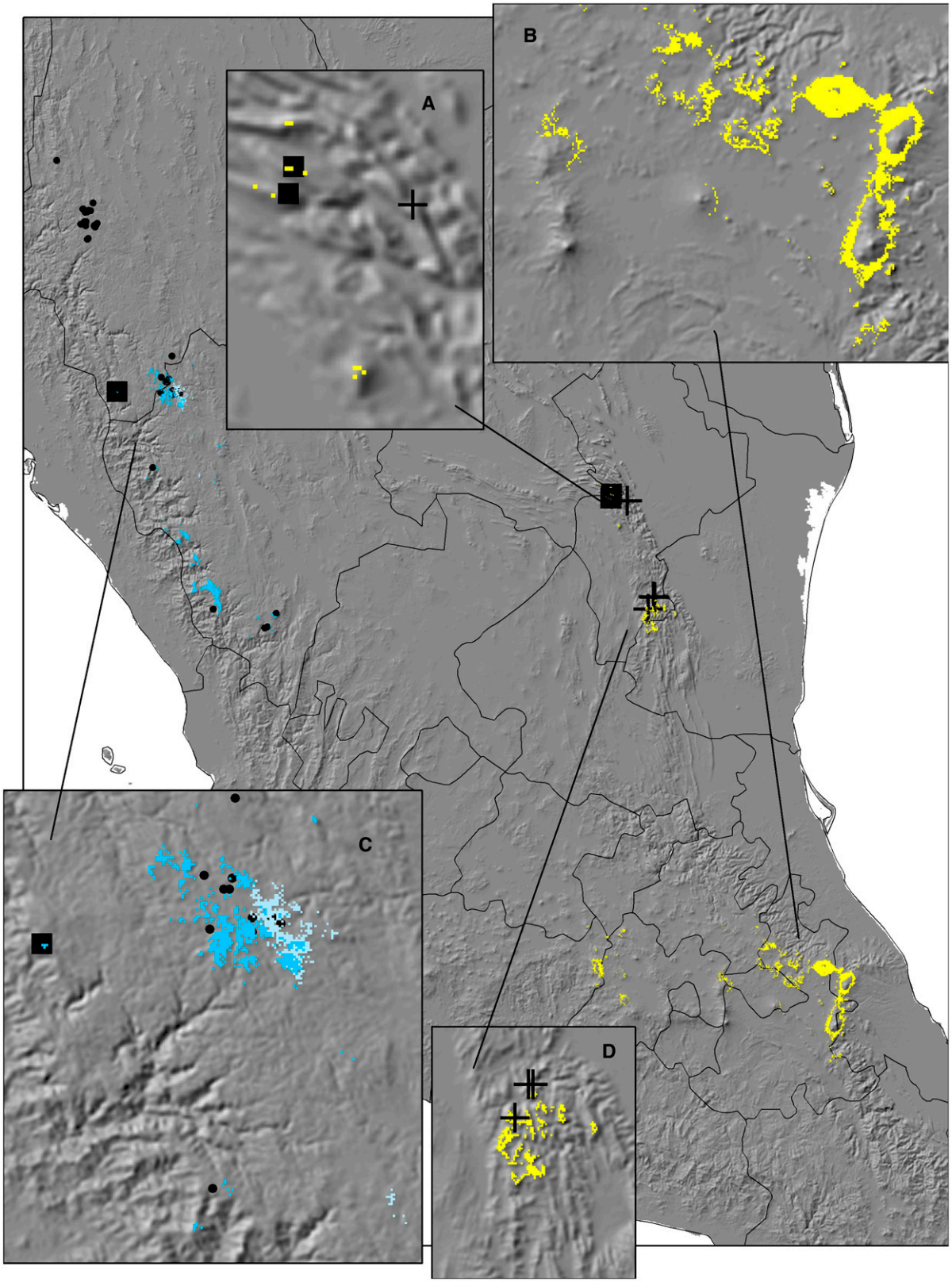



Fig. 4. Composite mapping of six projections made from output of three general circulation models (GCMs) and two scenarios for the decade surrounding 2060 using the majority of votes cast by the Random Forests classification tree to determine presence or absence of four of Mexico's spruce taxa. Red, *Picea mexicana*; yellow, *P. martinezii*; light blue and sky blue, northern and southern mitotypes of *P. chihuahuana*, respectively. Symbols locating existing populations are keyed to Fig. 2.

Volcanic Belt near the border between the Distrito Federal and the state of Morelos. The projections for La Malinche show a belt of suitable climate for Martínez spruce immediately below the climate niche for Mexican spruce (Fig. 5B). The altitude on La Malinche suited for Martínez spruce would be ~2700 to 3200, representing an increase in elevation of about 600 to 700 m above what it occupies today.

***Chihuahua spruce***—Predictions for the decade centered in year 2030 (Fig. 3), indicate a reduction of the suitable climate niche for Chihuahua spruce relative to its present distribution. In particular, the area suited to the northern mitotype of Chihuahua spruce would almost disappear from the northern Sierra Madre Occidental. Also projected is a large reduction and extensive fragmentation of the suitable climate niche for the central and southern population clusters of the southern mitotype of Chihuahua spruce (Fig. 3C). Interestingly, the results suggest that Cerro Mohinora in the Sierra Madre Occidental, now inhabited by Mexican spruce, should take on a climate more suited to Chihuahua spruce (Fig. 3C).

Predictions for the decade centered in the year 2060 (Fig. 4), suggest an acute reduction in the climate niche for Chihuahua spruce. It essentially disappears in central Chihuahua. The climate niches of the southern and northern mitotypes would overlap near the border between the states of Durango and Chihuahua (Fig. 4C); the climate niche of the northern mitotype would lie on the east slope and the southern mitotype on the west slope of the Sierra Madre Occidental. The climate niche of the southern mitotype would also shrink farther south in the State of Durango, but still would include the areas presently occupied, such as Arroyo del Infierno and Arroyo de la Pista

Predictions for Chihuahua spruce in the decade 2090 (Fig. 5), continue the previous trend: a drastic reduction and fragmentation of habitat. Climate now favorable to both mitotypes coalesces along the border between the States of Chihuahua and Durango. The model also predicts some suitable climate for the southern mitotype toward the south in Durango, but not in the areas the southernmost populations currently occupy.

***Engelmann spruce***—Projections for Engelmann spruce suggest that the climates currently inhabited by this species will systematically migrate northward and upward with time (Fig. 6). By the end of the century, habitat would be largely lost in Arizona and be confined to the northern mountains of New Mexico. The elevations suitable for this spruce should be about 800 m higher than today. However, an increase of the lower altitudinal limits of Engelmann spruce from the ca. 2700 m of today to ca. 3500 m by the end of the century seems problematic because it is questionable whether the rocky substrates at those elevations can support forest.

***Concurrence of projections***—Variation is obscured when GCM projections are presented as a composite. While variation among the three GCMs for temperature variables was relatively slight, that for precipitation was large (Sáenz-Romero et al., in press), and of the eight climate variables used as predictors, five were interactions involving precipitation. This suggests the possibility of large variations among predictions from our bioclimate models for the GCMs and their scenarios.

However, for Martínez spruce that was certainly not the case. Each of the six projections tended to concur with the general trends illustrated in Figs. 3–5: the climate inhabited today moved southward and upward, eventually coalescing in the Trans-Mexican Volcanic Belt. Likewise, the 2090 distribution of suitable climates for Engelmann spruce were in general accord for the A2 scenario of the three GCMs, although CCCMA suggested that the distribution of favorable climates would be only 25% of that shown in Fig. 6. Projections for the B scenarios implied a slower northward and upward migration of the climate niche, with the 2090 distribution of the B scenarios at the approximate limits of the 2060 projections for the A2 scenario.

For Chihuahua spruce and Mexican spruce, however, variation among the six projections was indeed large. Nonetheless, nearly all projections agreed that the climate niche of the northern mitotype of Chihuahua spruce would appear in 2030 in west central Durango (Fig. 3). However, most of the area shown as having a suitable climate for Chihuahua spruce in Figs. 3–5 was derived from a favorable vote from only half or fewer of the projections; indeed, concurrence among projections was rare.

For Mexican spruce, the climate now inhabited recurred at only one locality in 2030 (Fig. 3A). This prediction, however, was from only one of the projections, the A2 of GFDL. Likewise, the 2090 reappearance of suitable habitat in the Trans-Mexican Volcanic Belt was a product of only the A2 and B1 scenarios of GFDL

To assess the impact of using majority rule on the results, we altered the rules for choosing suitable climates and mapped anew the current and projected climate niche of Mexican spruce. The results produced a different perspective for interpretation. Figure 7 is a composite of six projections for which pixels receiving at least 20% of the votes were deemed within the climate niche of Mexican spruce.

Figure 7 shows that the area suitable for Mexican spruce could be considerably larger than shown in Figs. 3–5, yet that predicted for the current climate is reasonably confined to the areas and their periphery where the species actually occurs. The maps show that marginally suitable climates indeed appear where majority rule resulted in complete disappearance of Mexican spruce by 2060. By 2090, considerable habitat could become available along the volcanic peaks in the Trans-Mexican Volcanic Belt (Fig. 7, lower right insert): peaks from west to east are Nevado de Toluca—lower left corner of insert; Popocatépetl, Iztaccíhuatl, and Tláloc—aligned south-north at center of insert; La Malinche—center right of insert; and Citlaltépetl and Cofre de Perote—aligned south to northeast at right side of insert. Note that in Fig. 7, a few pixels even occur on Volcán de Colima (summit ~3820 m), also called Tzapotépetl, near the west coast of Mexico.

Although Fig. 7 is a composite dominated by the projection with the least detrimental impact on Mexican spruce (A2 scenario of GFDL), there is nonetheless a remarkable general concurrence among projections. All six projections contribute to the colored pixels in Fig. 7. For 2090 (for example, Fig. 7, lower right panel), two projections contribute colored pixels not encompassed by the least pessimistic projection, and five of the six projections pinpoint locations on Citlaltépetl that should have a suitable future climate for Mexican spruce. All six projections predict suitable climates for the 2030 panel and five for both the 2060 and 2090 panels. The GCMs and scenarios, therefore, tend to agree where suitable climate should occur but disagree on the degree of suitability.

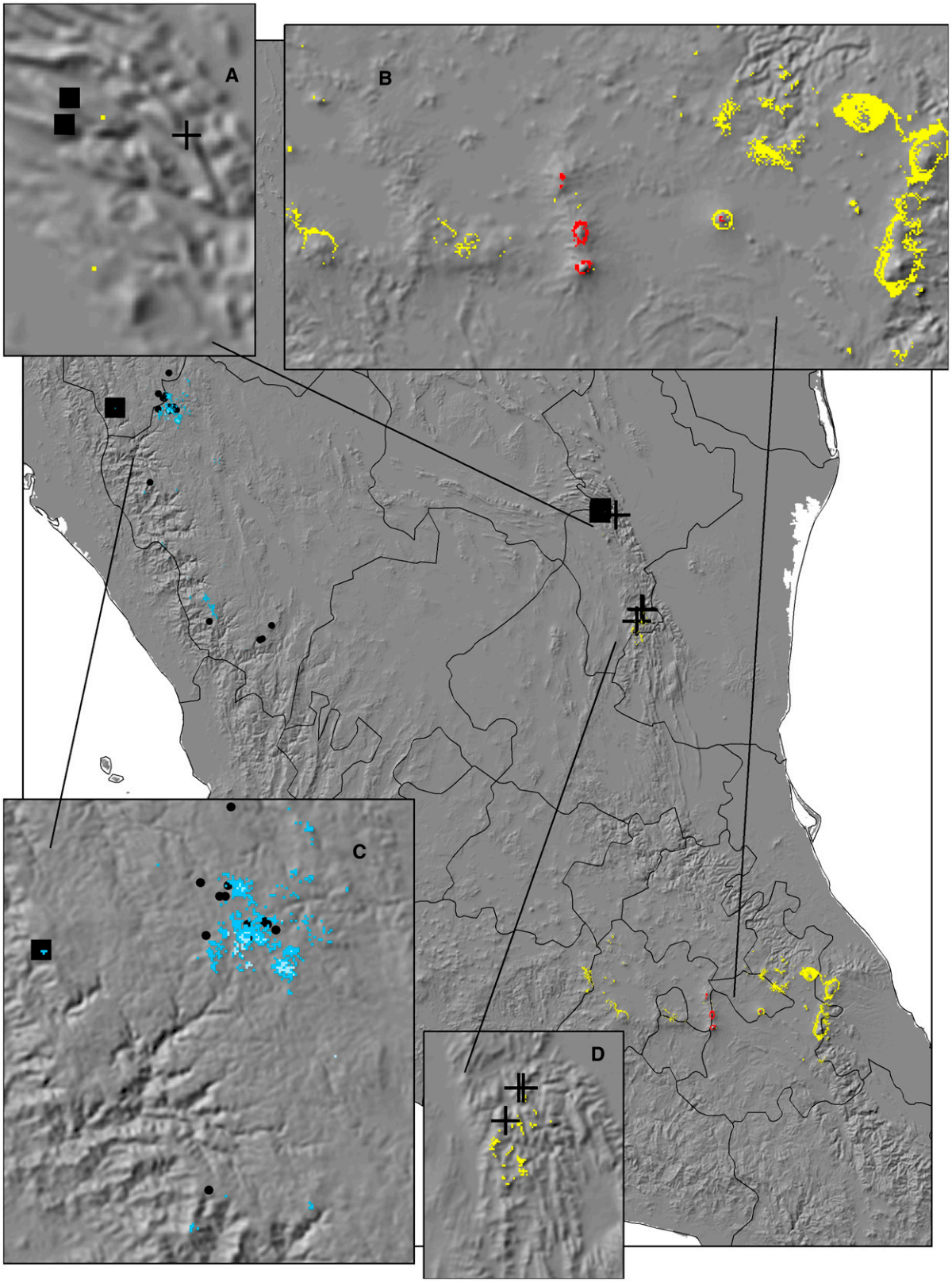



Fig. 5. Composite mapping of six projections made from output of three general circulation models (GCMs) and two scenarios for the decade surrounding 2090 using the majority of votes cast by the Random Forests classification tree to determine presence or absence of four of Mexico's spruce taxa. Red, *Picea mexicana*; yellow, *P. martinezii*; light blue and sky blue, northern and southern mitotypes of *P. chihuahuana*, respectively. Symbols locating existing populations are keyed to Fig. 2.

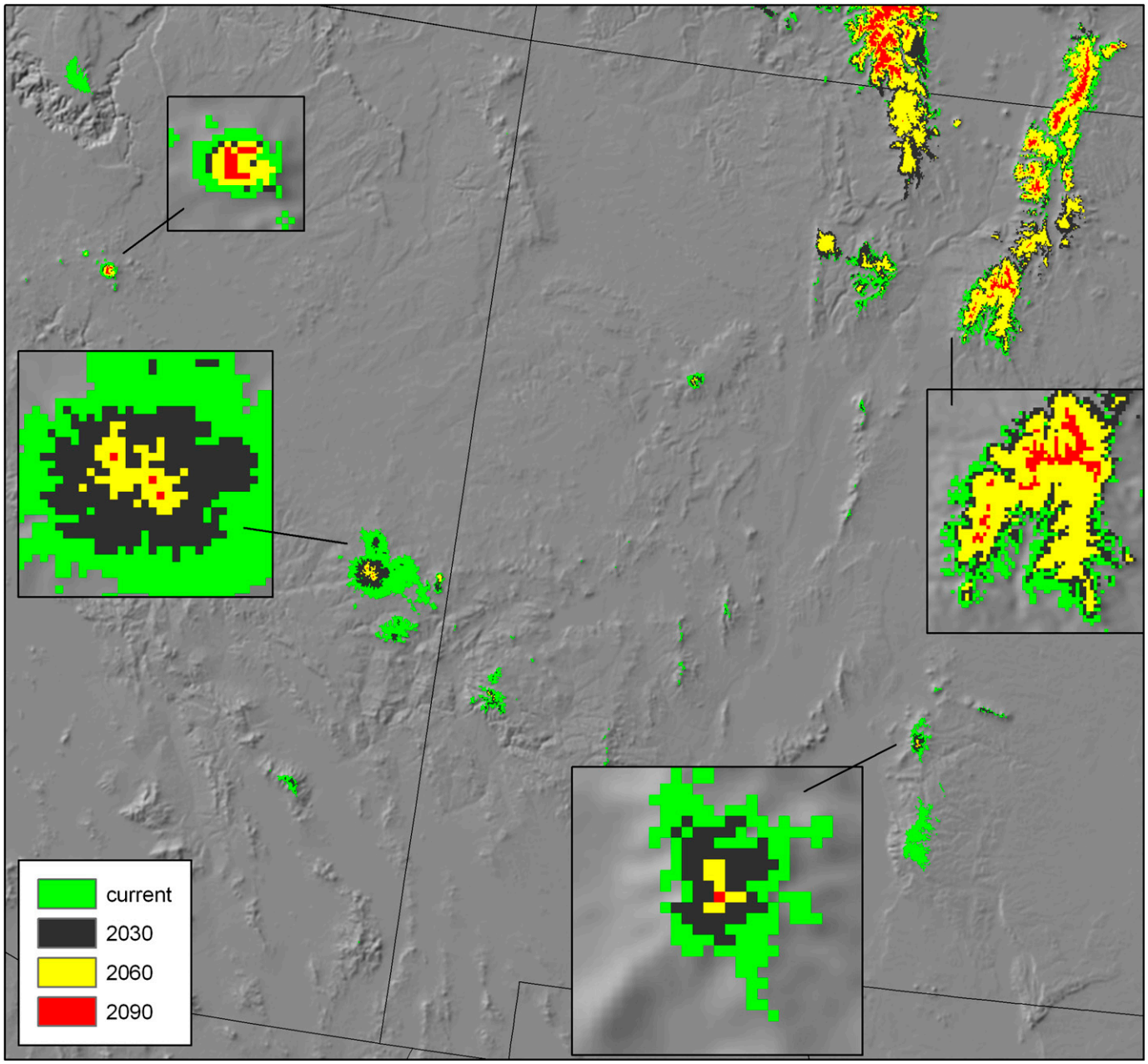
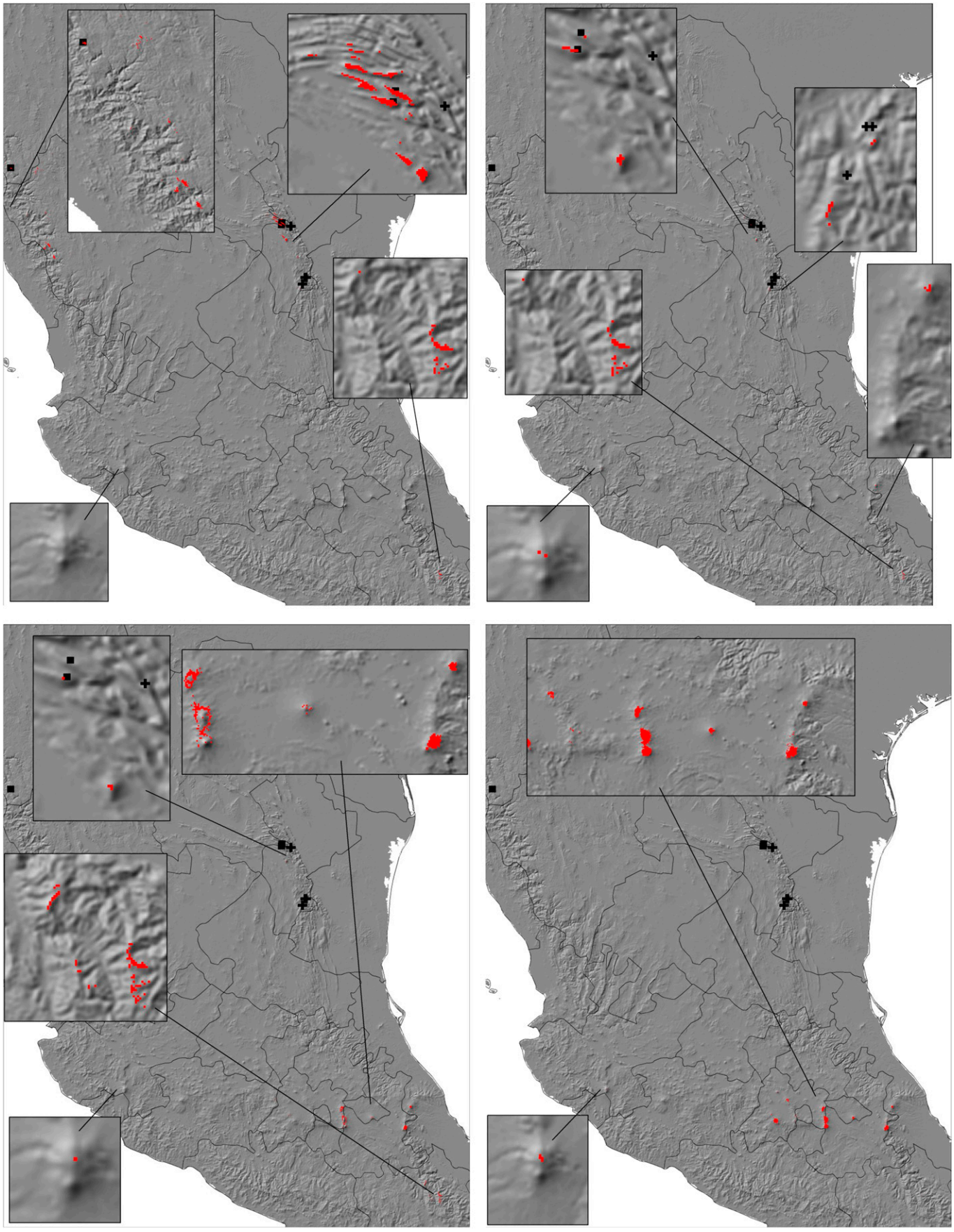



Fig. 6. Composite mapping of projected distributions of the climate niche of *Picea engelmannii* of southwest USA according to six projections made from output of three general circulation models (GCMs) and two scenarios. Projections for the decades surrounding 2030, 2060, and 2090 are superimposed sequentially on the contemporary climate niche (Fig. 1). Presence or absence was determined by the majority of votes cast by the Random Forests classification tree.

## DISCUSSION

***Contributions to bioclimate modeling***—The Random Forests algorithm of Breiman (2001) is of demonstrated robustness for predicting the contemporary realized climate niche from climatic variables (Iverson et al., 2005; Rehfeldt et al., 2006). Our contribution to statistical modeling with this algorithm has been to extend the approach to rare species by: (1) assuring that data recording the absence of a taxon in the training data set represent the full climatic range of locations where the species does not occur, (2) using a single model for multiple taxa, thereby increasing the amount of absence data incorporated into the training data for a single forest, and (3) using values of local importance to assure that critical variables were not inadvertently lost during stepwise elimination procedures.

The result was a model of extraordinary fit. Errors of prediction averaged 4.6% across 20 forests, but nearly all of the error was caused by predictions of suitable climate where the taxa do not presently occur. From the ecological perspective, this



result is satisfying: errors of omission result only from procedural errors, while those of commission can also reflect the fact that species do not always occur where the environment is suitable.

Critics of niche-based bioclimate models invariably focus on the inability of these empirical models to consider the fundamental niche (see Morin and Lechowicz, 2008; Jackson et al., 2009; Morin and Thuiller, 2009). Others (e.g., Rehfeldt et al., 2006), however, may argue that where competition is keen, the realized niche becomes more informative than the limits of the fundamental niche. In the application of our bioclimate model, we stress that projections of suitable climate represent the future distribution of climates bounding the contemporary realized climate niche. Although additional niche space may become available in future climates, one can conclude with little uncertainty that future analogs to the realized niche of today indeed will be suitable for populations of the future.

The argument becomes esoteric when dealing with rare or threatened species because mechanistic models of the fundamental niche require extensive data that are available for only a few common species (Morin and Thuiller, 2009). Practical programs, therefore, must rely on empirically based bioclimate models. Progress with process-based models (see Chuine and Beaubien, 2001; Morin and Chuine, 2005) suggests that in the future, practical programs can be devised using models of both the fundamental and realized niches as tools.

***Realized and predicted habitat***—The complete overlap of the predicted suitable contemporaneous climate with the presently known populations for each of the three spruces of Mexico indicates that the climate model is an excellent fit to the data. The overlap of predicted with realized occurrence is not automatic because in developing bioclimatic models for species with small distributions, one is forced to tacitly assume that existing distributions represent the range of suitable climates. This assumption is undoubtedly false; much of the Sierra Madre Occidental and the Sierra Madre Oriental are remote, and populations may have gone undiscovered, particularly populations of Chihuahua spruce. Likewise, areas capable of supporting spruce might not, simply because of lack of a seed source to colonize them. In addition, using the majority of votes to predict the presence or absence of spruce taxa prevents identification of locations where the climate may approach suitability. The use of voting majorities may also cover similarities among the GCMs and emphasize their differences—a result of the variability among them in their precipitation estimates.

The predicted suitable areas include more than the actual present distributions. This is common in models where suitable habitats are predicted based on climate alone. Many other factors may restrict where a species actually occurs, e.g., substrate, interactions with other species, or restrictions on seed dispersal (e.g., Pearson and Dawson, 2003; van Zonneveld et al., 2009). We believe that microsites, such as the bottom of shaded barrancas and arroyos for Chihuahua spruce and high elevation, summer fog, and winter snow for Mexican spruce, are necessary within the climatically suitable areas. Such microsites are much narrower than the habitat predicted in Figs. 2–5, because, in the case of Chihuahua spruce, the climate model is not yet capable of microtopographic projections, and in the case of Mexican spruce, three data points cannot possibly depict the extent of the suitable habitat. Yet, it is also true that species do not occur in all places ideally suited to them. In other words, a portion of the errors of commission are due to correctly predicting niche space that is, by chance, not occupied.

*Predicted trends*—For Mexican spruce, a disappearance of habitat in northern Mexico would also be predicted from the analysis of Villers-Ruiz and Trejo-Vázquez (1997) and from Hopkins' Law (Hopkins, 1938). Hopkins' Law predicts that an increase in elevation of 1000 m results in a decrease in temperature of 4.6°C. The elevational range of Mexican spruce is from 3185 m to 3500 m a.s.l. If global warming resulted in an increase in temperature of only 2.5°C, a reasonable expectation (e.g., Christensen et al., 2007), then we would expect Mexican spruce to migrate upward in elevation to ~3730–4045 m. This agrees relatively well with model results for the decade 2090 of 3900 m to 4200 m on La Malinche in the Trans-Mexican Volcanic Belt. However, no peaks in the Sierra Madres Oriental or Occidental are higher than ~3700 m. The disappearance of the climate niche for Mexican spruce in projections for 2030 and 2060 is very troubling from a conservation viewpoint (Figs. 3 and 4).

Predictions of the disappearance of Mexican spruce contrast somewhat with predictions for the rare Potosí, or dwarf, pinyon (*Pinus culminicola* Andresen et Beaman), a high-elevation associate of Mexican spruce (Gómez-Mendoza and Arriaga, 2007). Gómez-Mendoza and Arriaga's (2007) model of the effect of climate change predicted only an 18–41% reduction in the potential distribution of Potosí pinyon.

The model predicts that the climate niche for Chihuahua spruce also will move up in elevation, but not northward. From fossil pollen assemblages, Ortega-Rosas et al. (2008) found that Chihuahua spruce moved up in elevation at least 255 m in the northern Sierra Madre Occidental between 13 000 and 6500 yr BP. Based on its present occurrence (Ledig et al., 2000b), its lower elevational limit moved up another 255 m between 6500 yr BP and the present. Using Hopkins' Law (Hopkins, 1938), that a 1000 m increase in elevation is associated with a 4.6°C decrease in temperature, this upward displacement suggests at least a 2.3°C increase in temperature in the northern Sierra Madre Occidental since the last glacial maximum. An increase of 2.3°C is reasonable but less than the 4°C cooler temperatures estimated on Iztaccíhuatl in the Trans-Mexican Volcanic Belt at about 12 000 to 10 000 yr BP (Lozano-García and Vázquez-Selem, 2005). Of course, it is probable that changes in precipitation may have had more to do with changes in the distribution of spruce than changes in temperature. However, it is not clear where the boundary between westerly and monsoonal precipitation belts was in the late Pleistocene–early Holocene (Metcalfe et al., 2000).

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Fig. 7. Composite mapping of projected distribution of the climate niche of *Picea mexicana* (red pixels) projected by the bioclimate classification tree for three general circulation models (GCMs) and two scenarios for the contemporary climate (upper left) and for that of the decade surrounding 2030 (upper right), 2060 (lower left), and 2090 (lower right) using a threshold vote of 80% or greater for climate not suitable for spruce and 20% or greater for suitable climates.

Contrary to the common notion that suitable habitat will open in northern latitudes, predicted suitable climate niches for two of the spruces of Mexico in the years 2060 and 2090 would open in the south, on the highest mountains of the Trans-Mexican Volcanic Belt in central México. For Martínez spruce, climatically suitable areas are predicted in the mountainous north of the state of Puebla, on the volcanic peaks of Citlaltépetl, Popocatépetl, Iztaccíhuatl, La Malinche, and Tláloc, and on some high mountains near the border between the states of Mexico and Michoacán. Included in the latter is an especially interesting area for conservation—the Reserva de la Biosfera Mariposa Monarca where the monarch butterfly (*Danaus plexippus* L.), overwinters. The reserve is also home to another conifer with a fragmented distribution, sacred fir [*Abies religiosa* (Kunth) Schltdl et Cham.].

For Mexican spruce, new climatically suitable areas are predicted on the slopes of some of the highest peaks of Mexico by 2090: the volcanoes of Nevado de Toluca, Popocatépetl, Iztaccíhuatl, Tláloc, La Malinche, Cofre de Perote, and Citlaltépetl. Meanwhile, as the climates now occupied by Mexican spruce and Martínez spruce move up in elevation and southward, into the Trans-Mexican Volcanic Belt, that for Engelmann spruce of southwestern United States moves upward and northward toward the high mountains of northern New Mexico. Projected absence of this species in the mountains of southern and central Arizona and New Mexico illustrates that during periods of climate warming, separation of Madrean species from those of the Rocky Mountains increases rather than decreases.

***Spruce conservation***—*Adaptation*—The predictions of range loss do not take into account the potential for genetic adaptation (e.g., Skelly et al., 2007). However, the history of spruce in Mexico seems to make the possibility of adaptation unlikely. Some spruce occurred around Mexico City (about 700 km further south than the present distribution of the genus), but disappeared during the Holocene ca. 7500 yr BP (Lozano-García et al., 1993). If spruce failed to adapt to the early Holocene warming that occurred over a few millennia, it seems unlikely to respond to current climate change which is occurring at an accelerated tempo.

In addition, adaptation requires suitable genetic variants (Kellermann et al., 2009), and genetic diversity is low in Chihuahua spruce and Martínez spruce (Ledig et al., 1997, 2000a). Genetic diversity in Mexican spruce is only moderate (Ledig et al., 2002) and less than half that found in the closely related Engelmann spruce (Ledig et al., 2006). In general, genetic diversity decreases with range occupied, as in California conifers (Ledig, 1987) and, perhaps, in plant species in general (Hamrick and Godt, 1996). The raw material for evolution appears lacking in many narrowly distributed species. In her review, Parmesan (2006) documented local evolutionary responses to climate change but found no evidence for change in absolute climate tolerances of a species. Population extinctions, conversely, have been well documented at the southern and low-elevation edges of species' ranges (e.g., Worrall et al., 2008). In addition, the time frame for projected global warming militates against adaptation in many tree species. For example, in Scots pine (*Pinus sylvestris* L.), it might take 13 generations to adapt to climate change (Rehfeldt et al., 2002), but 13 generations in a tree species is on the order of millennia, whereas pronounced warming will occur on the scale of decades.

*Dispersal and colonization*—Species also respond to climate change by dispersal to, and colonization of, newly suitable habitat. For simplicity, we will use the term colonization to refer to the process of dispersal and colonization that results in changes in species' distribution and use the phrase gene flow to refer to exchange of genes among populations via pollen or seed movement. For most species, lack of information makes it difficult to predict colonization responses (Neilson et al., 2005). However, the future rate of climate change is likely to exceed the colonization rates of most plant species (Davis and Zabinski, 1992). Predicted suitable climates in 2030, 2060, or 2090 based on current realized climate niches for the spruces of Mexico seem too distant from their present distribution and lacking in connectivity to allow any reasonable expectation of natural colonization.

The topography between the present distribution of spruce in the Sierra Madre Oriental and the Trans-Mexican Volcanic Belt is less conducive to dispersal and colonization than it is between the Sierra Madre Occidental and the Trans-Mexican Volcanic Belt because of a greater elevational discontinuity (McDonald, 1993). Furthermore, the high endemism of the subalpine habitats in the Sierra Madre Oriental suggests that the vegetation there was not linked with the Trans-Mexican Volcanic Belt during the Pleistocene (McDonald, 1993).

However, even short distances between populations of spruce in Mexico seem to preclude gene flow via either pollen or seed, especially for Chihuahua spruce. On average, the number of migrants per generation among populations of Chihuahua spruce was estimated as only 0.43 to 0.76, depending on the method of calculation (Ledig et al., 1997). These are low rates, but even they are overestimates of the actual rate of gene exchange because they reflect past contact between populations, not current gene flow. Therefore, there seems little likelihood of seed dispersal even among relatively close, contemporary populations of Chihuahua spruce. The estimated number of migrants per generation is higher in Martínez spruce, but lower than expected for conifers, which suggests that dispersal between contemporary populations of Martínez spruce probably does not occur either.

The high level of ovule abortion in all three spruces of Mexico and, therefore, low seed yields, is also a handicap to colonization. Inbreeding leads to aborted ovules in conifers (Franklin, 1970). Aborted ovules ranged from 36 to 47% in the three populations of Mexican spruce, which suggests very high inbreeding coefficients of 0.73 to 0.84 of a possible maximum of 1.00 (Flores-Lopéz et al., 2005). The problem of inbreeding is even worse in Chihuahua spruce and Martínez spruce than in Mexican spruce. The relatively small size of populations and their isolation apparently have contributed to unusually high levels of selfing for a conifer. Based on genetic structure rather than ovule abortion, selfing is 41–60% for Martínez spruce (Ledig et al., 2000a), 85–100% for two small populations of Chihuahua spruce (Ledig et al., 1997), and 19–41% for Mexican spruce (Ledig et al., 2002).

***Conclusions***—Suitable contemporary and future climate niches were predicted for Chihuahua spruce, Mexican spruce, and Martínez spruce, species with very narrow and discontinuous population structures, by modeling the relationship between presence–absence of species and key climatic variables. A combination of spline climatic models and the Random Forests classification tree technique could be applied to project climate

niches for other rare species. Our projections for 2030, 2060, and 2090 indicate a progressive and severe reduction of climatically suitable habitats in the present ranges of all three endemic spruces of Mexico, with complete disappearance of the northern cluster of Chihuahua spruce populations and for all known populations of Mexican spruce by the year 2060. However, for Martínez and Mexican spruces, newly suitable habitats emerge far south of their present distributions, not to the north, in regions where they are presently absent. For Martínez spruce, these areas are mainly in the states of Veracruz, Puebla, Tlaxcala, Mexico, and Michoacán, with smaller areas in the states of Guanajuato, Hidalgo, Morelos, and Querétaro. Several high elevation volcanic peaks in the Trans-Mexican Volcanic Belt are predicted to have suitable climate niches for Mexican spruce by 2090. Under a relaxed criterion, suitable climate may even exist for Mexican spruce as far west as Volcán de Colima. The main area of refuge for Chihuahua spruce by 2090 seems to be in the northwest corner of the state of Durango near its border with the State of Chihuahua.

The results illustrate some important considerations for conservation in general. One is that transient disappearance of habitat, as in Mexican spruce, may complicate conservation efforts. Although models may project suitable climate at some future time, in the shorter term, suitable habitat may be lacking. This implies that some species will need interim preservation in seed banks or botanic gardens to bridge the gap between contemporary and future habitat.

Second, suitable habitat under a global warming scenario may not move northward. Although counterintuitive, suitable climate may appear southward, as in our projections for Martínez and Mexican spruces and the northern mitotype of Chihuahua spruce.

Third, a species is not a uniform monolith, and it may be necessary to consider intraspecific genetic differences. Not all populations of a species will necessarily respond the same. Our example shows that the two mitotypes of Chihuahua spruce respond to climate change in contrasting ways; the range contracts southward for the northern mitotype and northward for the southern mitotype.

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