Forest Ecology and Management 324 (2014) 126–137

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Realized climate niches

Gerald E. Rehfeldt [a,*], Barry C. Jaquish [b], Javier López-Upton [c], Cuauhtémoc Sáenz-Romero [d], J. Bradley St Clair [e], Laura P. Leites [f], Dennis G. Joyce [g]

[a] USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, 1221 S. Main, Moscow, ID 83843, USA
[b] Research Branch, B.C. Ministry of Forests, Lands and Natural Resource Operations, Kalamalka Forestry Centre, 3401 Reservoir Rd., Vernon, BC V1B 2C7, Canada
[c] Colegio de Postgraduados, Km 35.5 Carretera México-Texcoco, Montecillo, México, CP 56230, Mexico
[d] Instituto de Investigaciones Agropecuarias y Forestales, Universidad Michoacana de San Nicolás de Hidalgo (IIAF-UMSNH), Km 9.5 Carretera Morelia-Zinapécuaro, Tarímbaro, Michoacán 58880, Mexico
[e] USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331-4401, USA
[f] Department of Ecosystem Science and Management, Pennsylvania State University, University Park, PA 16802, USA
[g] 449 Walls Road, Sault Ste. Marie, Ontario P6A 6K4, Canada

ARTICLE INFO

Article history:
Received 6 November 2013
Received in revised form 17 February 2014
Accepted 25 February 2014
Available online 29 March 2014

Keywords:
Niche modeling
Climate change impacts
Douglas-fir
Ponderosa pine
Biogeography
Genecology

ABSTRACT

The Random Forests classification algorithm was used to predict the occurrence of the realized climate niche for two sub-specific varieties of *Pinus ponderosa* and three varieties of *Pseudotsuga menziesii* from presence-absence data in forest inventory ground plots. Analyses were based on ca. 271,000 observations for *P. ponderosa* and ca. 426,000 observations for *P. menziesii*, with ca. 6% of the observations in each dataset recording the presence of one of the varieties. Classification errors to the respective databases attributable to fitting the models were ca. 5%, most of which were from falsely predicting varietal occurrence. Confusion in classifying varieties was nil. The primary drivers of the niche model were summer precipitation, winter precipitation and summer degree-days >5 C for the varieties of *P. ponderosa* and the summer-winter temperature differential, summer maximum temperatures and summer precipitation for the varieties of *P. menziesii*. Projected impacts of global warming using output from an ensemble of 17 general circulation models were greater for *P. ponderosa* than for *P. menziesii* and for varieties of both species from inland climates than from coastal. Projected impacts imply dire consequences for the varieties of *P. menziesii* occurring in Mexico.

Published by Elsevier B.V.

1. Introduction

Ingrained in the foundations of biogeography is the concept that plant distributions are limited by climate, with species flourishing within a relatively narrow range of climatic conditions (see Dansereau, 1957). Entrenched in evolutionary biology is the concept that genetic variation within wide-ranging plant species has been molded by climate to produce clines that parallel climate gradients (see Morgenstern, 1996). The climate, however, is warming and will continue to warm at unprecedented rates (Hansen et al., 2012). As climate-change progresses, disruption of species distributions is inevitable (see Thomas, 2010), but the impact will vary among species largely because of intraspecific clines of different steepness (Rehfeldt, 1994; Sorensen and Weber, 1994). Impacts to forests are occurring presently (e.g., Breshears et al., 2005; Allen et al., 2010; Worrall et al., 2013) and are projected to continue (e.g. Iverson et al., 2008; Rehfeldt et al., 2006). Strategies, options and guidelines are needed by forest managers for accommodating the changing climate such that forest health, growth and productivity are maintained (e.g., Ledig and Kitzmiller, 1992; Mátyás, 1994; Rehfeldt et al., 1999; Pedlar et al., 2012).

The conclusion of many researchers is that climate change impacts on North American tree species involve contraction of ranges at trailing edges, the southern and low-altitudinal limits of distribution, with expansion at leading edges in the north and at higher elevations (e.g., Lavergne et al., 2010; Worrall et al., 2013). Yet, even where projected species are expected to persist, genotypes appropriate for the new climates invariably occur elsewhere today (St Clair and Howe, 2007; Rehfeldt and Jaquish,

---

* Corresponding author. Tel.: +1 208 882 3557; fax: +1 208 8832318.
E-mail addresses: jrehfeldt@gmail.com (G.E. Rehfeldt), barry.jaquish@gov.bc.ca (B.C. Jaquish), jlopezupton@gmail.com (J. López-Upton), csaenzromero@gmail.com (C. Sáenz-Romero), bstclair@fs.fed.us (J.B. St Clair), lpl3@psu.edu (L.P. Leites), dennis.joyce@vianet.ca (D.G. Joyce).

http://dx.doi.org/10.1016/j.foreco.2014.02.035
0378-1127/Published by Elsevier B.V.

2010; Joyce and Rehfeldt, 2013). To mitigate the adaptation and dispersal lags that accompany plant migrations, proactive management must be a component of the challenge facing forest managers (see Rehfeldt et al., 1999, 2001, 2002; Ledig et al., 2010; Sáenz-Romero et al., 2012b).

Our focus is on the potential impacts of the changing climate on the sub-specific varieties of *Pseudotsuga menziesii* and *Pinus ponderosa*, two of western North America's most widely distributed and economically important forest trees. Both species are comprised of varieties long-recognized by taxonomists: *P. p.* vars. *ponderosa* and *scopulorum*, and *P. m.* vars. *menziesii* and *glauca*. Varieties *ponderosa* and *menziesii* tend to occupy coastal regions while vars. *scopulorum* and *glauca* tend to be interior (Fig. 1). In *P. menziesii,* an unnamed third variety occurs in central and southern Mexico (Reyes-Hernández et al., 2006). The disparate evolutionary histories of the varieties of these species (e.g., Latta and Mitton, 1999; Gugger et al., 2010; Wei et al., 2011) portend disparate responses to historical climates and, therefore, deserve recognition when impacts from climate change are considered.

Our analytical approach first defines statistically the realized climate niche, that is, the climate profile (*sensu* Rehfeldt et al., 2006), such that climatically suitable habitat can be mapped. The second step defines the climatic clines that link intraspecific genetic variation to climate gradients occurring within the climate profile. Completion of these steps allows the climate profile and intraspecific genetic variation to be projected into future climate space provided by emissions scenarios of General Circulation Models (GCM). The results then can be used to develop seed transfer protocols suited to reforestation in a changing climate. This approach parallels those used for *Larix occidentalis* (Rehfeldt and Jaquish, 2010) and *Pinus strobus* (Joyce and Rehfeldt, 2013).

Analyses and discussion of this work are presented in three tandem papers in this issue of Forest Ecology and Management. The objectives of the present paper, PART 1 of the series, are (a) to develop from a comprehensive database techniques for predicting the occurrence of the contemporary realized climate niche of the sub-specific varieties of *P. menziesii* and *P. ponderosa*, and (b) to project the niche into mid-century climates representative of GCMs such that potential impacts can be quantified at both the trailing and leading edges.

The results of PART 1 provide a statistical framework for the second paper of this series (PART 2, Rehfeldt et al., 2014a), the objectives of which are (a) to synthesize disparate provenance test data so that the clines in genetic variability that occur within varieties can be described and mapped within the climate niche, and (b) to project genetic variation into mid-century climate space. PART 3 of the series (Rehfeldt et al., 2014b) integrates the results of PARTS 1 and 2, synthesizes potential impacts to natural ecosystems, and considers management options for promoting long-term persistence and health consistent with ecosystem resilience.

2. Methods

2.1. Climate data

Throughout this series, all point and gridded climate estimates were obtained from the thin plate spline surfaces of Crookston and Rehfeldt (2008) for North America >13.9° latitude. These climate surfaces produce monthly estimates of temperature and precipitation normals for 1961–1990. From the monthlies, twenty variables are derived directly, but additional variables can be constructed from temperature-precipitation interactions (see Rehfeldt et al.,

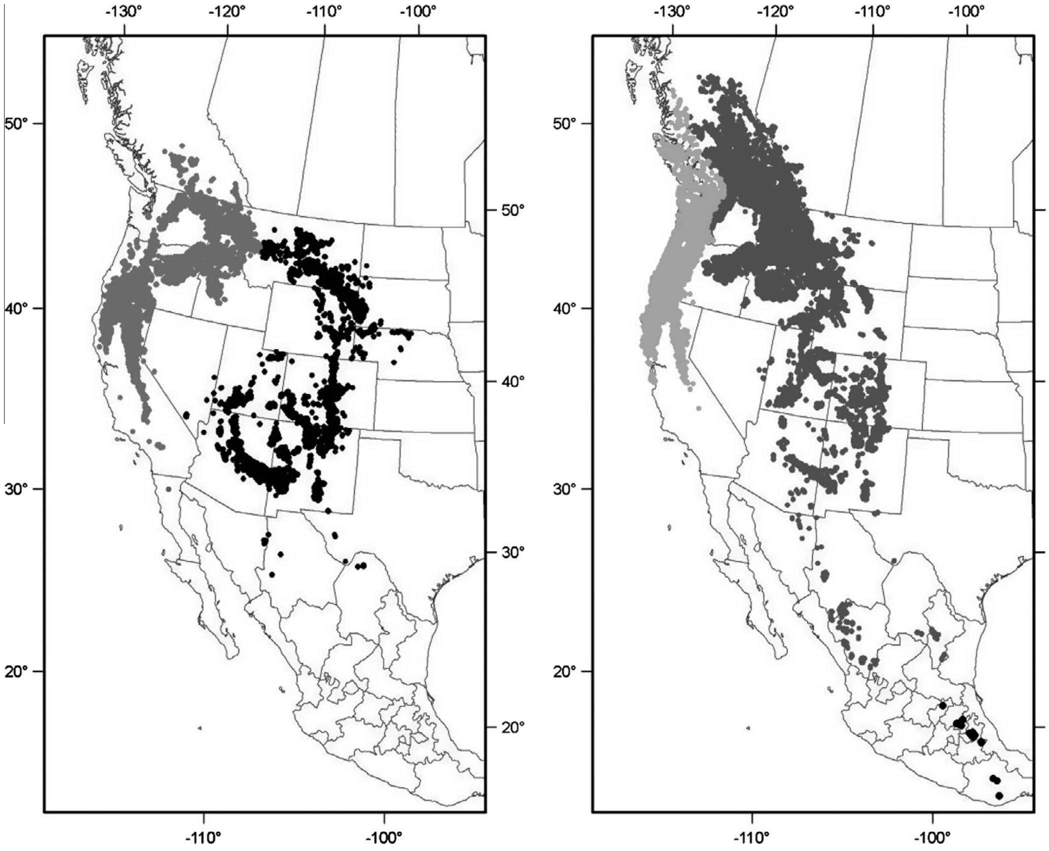

Fig. 1. Presence of ground plots (dots) of the varieties of *Pinus ponderosa* (left) and *Pseudotsuga menziesii* (right). Left panel: *P. p.* var. *ponderosa* (gray), var. *scopulorum* (black). Right panel: *P. m.* var. *menziesii* (light gray), var. *glauca* (dark gray), and unnamed Mexican variety (black).

2006). We use an additional 14 interactions and thereby have 34 climate variables at our disposal. Table 1 lists the climate variables and their acronyms referenced in this series.

2.2. Delineation of varieties

The varieties of *P. ponderosa* are separated according to well-documented morphological features (see Conkle and Critchfield, 1988) that tend to separate the varieties at the Continental Divide in Montana (see Little, 1971). Because gene flow is primarily west to east (Latta and Mitton, 1999), transitional populations would be classified as var. *scopulorum*. For *P. menziesii*, the crest of the Coastal Mountains of British Columbia tends to separate var. *menziesii* on the west from transitional and var. *glauca* populations to the east (see Krakowski and Stoehr, 2009, 2011). Extension of this demarcation line to the south along the crest of the Cascade Range with an exit from the Cascades along the divide between the Yakima and Klickitat Drainages in southern Washington would then account for recent genecological evidence (St Clair et al., 2005) of varietal distributions. Recognition and delimitation of the unnamed *P. menziesii* variety in sub-tropical climates of central and southern Mexico from var. *glauca* in the arid montane climates of northern Mexico follows the morphologic work of Reyes-Hernández et al. (2006).

2.3. Climate profile models

Our approach to model development was to apply well-established procedures (see Rehfeldt et al., 2006; Rehfeldt and Jaquish, 2010; Joyce and Rehfeldt, 2013; Ledig et al., 2010; Worrall et al., 2013), use as much of the available information as possible to develop the model, and carefully examine the errors of prediction to elucidate shortcomings. We use the Random Forests classification algorithm (Breiman, 2001; R Development Core Team, 2006) to produce range-wide models predicting from climate variables the presence or absence of the varieties of both species. In evaluating the models, the mechanics of fitting the Random Forests algorithm is such that the errors of estimate are obtained from samples not used in the model building process and therefore are essentially a cross-validated accuracy estimate (Cutler et al., 2007).

Table 1
Definition of acronyms used herein to reference climate variables.

Acronym	Definition
MTCM	Mean temperature in coldest month
MTWM	Mean temperature in warmest month
MMIN	Mean minimum temperature in coldest month
DD0	Negative degree-days using mean daily temperature for calculation[a]
MINDD0	Negative degree-days using minimum daily temperature for calculation[a]
MAP	Mean annual precipitation
GSP	April–September precipitation
SDAY	Date of last freezing temperature in spring
FDAY	Date of first freezing temperature in autumn
D100	Date the sum of degree-days above 5 °C reaches 100
DD5	Annual mean degree-days above 5 °C[a]
GSDD5	Mean degree-days >5 °C between SDAY and FDAY[a]
MMAX	Mean temperature in warmest month
SUMP	July–August precipitation
SPRP	April–May precipitation
WINP	November–February precipitation
PRATIO	Growing season precipitation balance[b]: GSP/MAP
SDI	Summer dryness index[b]: $(\mathrm{GSDD5})^{0.5}$/GSP
TDIFF	Summer–winter temperature differential: MTWM-MTCM
MAPDD5	(MAP × DD5)/1000[a]
SDIMINDD0	SDI × MINDD0[a]

Note: temperature is °C (one decimal), precipitation in mm (whole units). Bold face type, variables in the *Pinus ponderosa* profile; italics, variables in the *Pseudotsuga menziesii* profile.

[a] Rounded to whole units.

[b] Rounded to two decimals.

Presence-absence data from throughout the geographic distribution of these two species were assembled primarily from forest inventory and ecological research ground plots of organizations in USA, Canada and Mexico (see Acknowledgments). As mandated by federal law, data points from USA's Forest Inventory and Analysis are located systematically but presented with 'fuzzy' coordinates that approximate actual locations, but the degree of geographic imprecision is proprietary. To locate and remove the most flagrant errors, we calculated the difference between Euclidean distances in eight climate variables for actual coordinates not available to the public and 'fuzzy' coordinates. The differences were used to identify and cull about 1 % of the observations which were outliers from a general distribution. To assure the representation of non-forested data points in the analysis, we randomly sampled 50 % of the data points from non-forested biomes used in North American vegetation analyses (Rehfeldt et al., 2012).

The resulting database used for the *P. ponderosa* analysis contained ca. 271,000 observations of which ca. 14,000 recorded the presence of one of the varieties; that for *P. menziesii* contained ca. 426,000 observations of which ca. 26,000 recorded the presence of *P. menziesii*. The difference in database size was related to the smaller proportion of observations from Mexico that were necessary for *P. ponderosa* than for *P. menziesii*. Observations for both species were assorted into varieties according to geographical location. Because of the extensiveness of the sample, Fig. 1 becomes the best available approximation of a range map for these species as a whole, but especially for their varieties. While existing range maps for these species (e.g., Little, 1971) have served forestry well, accuracy is lacking particularly for Mexico but also for Canada.

To prepare training data within which observations are reasonably balanced between the presence and absence classes (see Breiman, 2001), we followed the procedures of Worrall et al. (2013) which are of demonstrated robustness (e.g., Rehfeldt et al., 2006; Ledig et al., 2010; Rehfeldt and Jaquish, 2010; Joyce and Rehfeldt, 2013) particularly for limiting errors of omission, that is, predictions of absence when present. Ten datasets were extracted from the database for each species, each containing a sample of observations not exceeding 100,000, a number suitable for our computing resources. Each dataset was used to construct a 'forest' in the Random Forests algorithm. The sample was drawn such that ca. 40% were locations where the species occurred (presence observations) with the remainder from where the species was absent (absence observations). Each data set destined for developing the climate profile of *P. menziesii* contained a sample of ca. 17,500 presence observations while those for *P. ponderosa* included all presence observations. Presence observations were then weighted by a factor of two (doubled) which set a limit of ca. 88,000 total observations for each dataset to be used in the *P. menziesii* analyses and ca. 70,000 total observations for those to be used for *P. ponderosa* analyses. For all data sets, absence observations were structured such that two-thirds of the observations would be difficult for separating presence from absence, while one-third sampled climatically distant observations.

To develop the climate profiles, the Random Forests algorithm was used to produce an ensemble of classification trees containing 10 'forests' each with 100 'trees'. Using multiple classes of presence observations (see Ledig et al., 2010) in the models provided for estimating the climate profiles of each variety, that is, the model incorporated three classes for the *P. ponderosa* analysis and four classes for the *P. menziesii* analysis. A stepwise procedure was used to determine which of 34 climate variables should be included as descriptors of the climate profile. Climate variables included 20 variables derived from the 1961–1990 normals and 14 precipitation-temperature interactions. Variables were eliminated during the stepwise procedure according to importance values averaged across the 10 forests, using the mean decrease in accuracy as the measure of importance. Out-of-bag errors were used to determine the number of predictor variables to be included in the final model. Because classification errors approach a limit as the number of trees in the forest increase, collinearity and over-parameterization are inconsequential (Breiman, 2001).

In judging the relative importance of variables, we view the variable remaining in the 1-variable model as being the most important. The second most important would be the additional variable in the 2-variable model. In developing the final model, values of 'local importance' were calculated. These statistics are the variable importance scores for each observation in the training data. Local importance was used in an attempt to determine which climate variables were most important in separating varieties.

In making predictions, observations were run down all trees in all forests, with each tree casting one of a total of 1000 votes (100 trees by 10 forests) as to climate suitability for each variety. We assumed that the climate of any data point would not be suitable to any variety of these species when the varieties in their aggregate received less than 50% of the votes, that is, the absence class received >50%. Otherwise, the prediction was the variety receiving the most votes.

Mapped predictions use elevations (GLOBE Task Team, 1999) and climate grids (Crookston and Rehfeldt, 2008) at 0.0083° resolution. Projections for the decade surrounding 2060 used means of 17 GCMs for the RCP60 scenario, a medium–high emissions scenario (see van Vuuren et al., 2011).

3. Results

3.1. Climate profile

The *P. ponderosa* climate profile included nine climate variables and had an overall out-of-bag error averaging 3.7% for the 10 forests, using nine climate variables; that for *P. menziesii* had an average out-of-bag error of 3.3% and was driven by six climate variables. For both, out-of-bag errors were concentrated in the errors of commission, predicting presence when the species were absent. In developing models with multiple forests, averaging out-of-bag errors across forests would underestimate actual error if the disparate samples of training data were not representative of the database. For this reason, we present confusion matrices (Tables 2 and 3) obtained by predicting climate suitability for each observation in the databases.

Table 2
Confusion matrix showing the class error and number of observations classified by the Random Forests algorithm for each variety of *Pinus ponderosa* in the database.

Observed occurrence	Predicted occurrence			Class error (%)
	Absent	*Ponderosa*	*Scopulorum*	
Absent	257,235	5,494	2,373	3.0
Ponderosa	11	10,280	0	0.1
Scopulorum	0	0	3,933	0.0

The statistics in Tables 2 and 3 closely parallel the out-of-bag errors, both of which illustrate a superb fit of the models. For both models, errors of prediction were concentrated in predicting the presence of a species when absent, that is, false positives. Errors of omission, the false negatives, varied between miniscule and none, but were detected for the inland varieties of both species. The models, moreover, showed no confusion in separating varieties on the basis of climate. While many ecologically valid reasons exist for species not occurring where the climate is suitable, the most damaging errors tend to be errors of omission. The most obvious reason for predictions of absent when present are from model fitting. Having errors primarily as false positives is, therefore, the most desirable outcome. The low error rates of these models attest to their high fit, a result typical of other work using these or similar methods (e.g., Rehfeldt et al., 2006; Ledig et al., 2010; Joyce and Rehfeldt, 2013; Worrall et al., 2013).

The three most important climate variables driving the *P. ponderosa* model were SUMP (see Table 1), WINP, and DD5; those driving the *P. menziesii* model were TDIFF, MMAX, and SUMP. 'Local importance' did not lead to a ready interpretation of which climate variables were responsible for separating the varieties.

Mapped climate profiles for the varieties of *P. ponderosa* (Fig. 2) capture the abruptness of the transition between varieties along the Continental Divide in Montana. Panel A shows the only area where the model purports confusion among the varieties, predicting suitable climate west of the Rocky Mountains for var. *scopulorum* in a region currently north of the species' distribution. Panels B and C illustrate the success of the model in correctly predicting the occurrence at isolated locations.

The mapped climate profiles for the varieties of *P. menziesii* (Fig. 3) depict the abrupt transition between varieties in the Coastal Mountains of British Columbia (upper panel A) along with intervarietal confusion along the crest of the Cascade Range toward the south (panels A and B) and especially along the transition following the relatively low divide between the Yakima and Klickitat River drainages where separation is equivocal (lower B). Other panels illustrate the occurrence of var. *glauca* at low elevation valley sites in the northern and eastern limits of distribution (panel C) but on high ridges in southern portions, especially in the isolated ranges of Texas (panel E) and the Sierra Madre Occidental and Oriental (panels F and G). Panel D shows that at the middle latitudes, this variety occupies middle elevations.

The Mexican variety of *P. menziesii* (Fig. 4) is shown to be distributed primarily along the Transvolcanic Axis of central Mexico where suitable climate typically rings the highest volcanoes (panels A and B) but also occurs in isolated locations to the north (panel C) and in the mountains of Oaxaca (panels D and E).

3.2. Projections

Losses of niche space by 2060 are projected for the lowest elevations in both varieties of *P. ponderosa* throughout the contemporary range, but gains in area would accrue at the higher elevations (Fig. 5, panels A, B, D and E). Panel C indicates that the separation of varieties along the Continental Divide would become

Table 3
Confusion matrix showing the number of observations classified by the Random Forests algorithm for each variety of *Pseudotsuga menziesii* in the database.

Observed occurrence	Predicted occurrence				Class error (%)
	Absent	*Menziesii*	*Glauca*	Mexican	
Absent	377,527	4876	16,458	52	5.4
Menziesii	0	8784	0	0	0.0
Glauca	249	0	18,139	0	1.4
Mexican	0	0	37	0	0.0

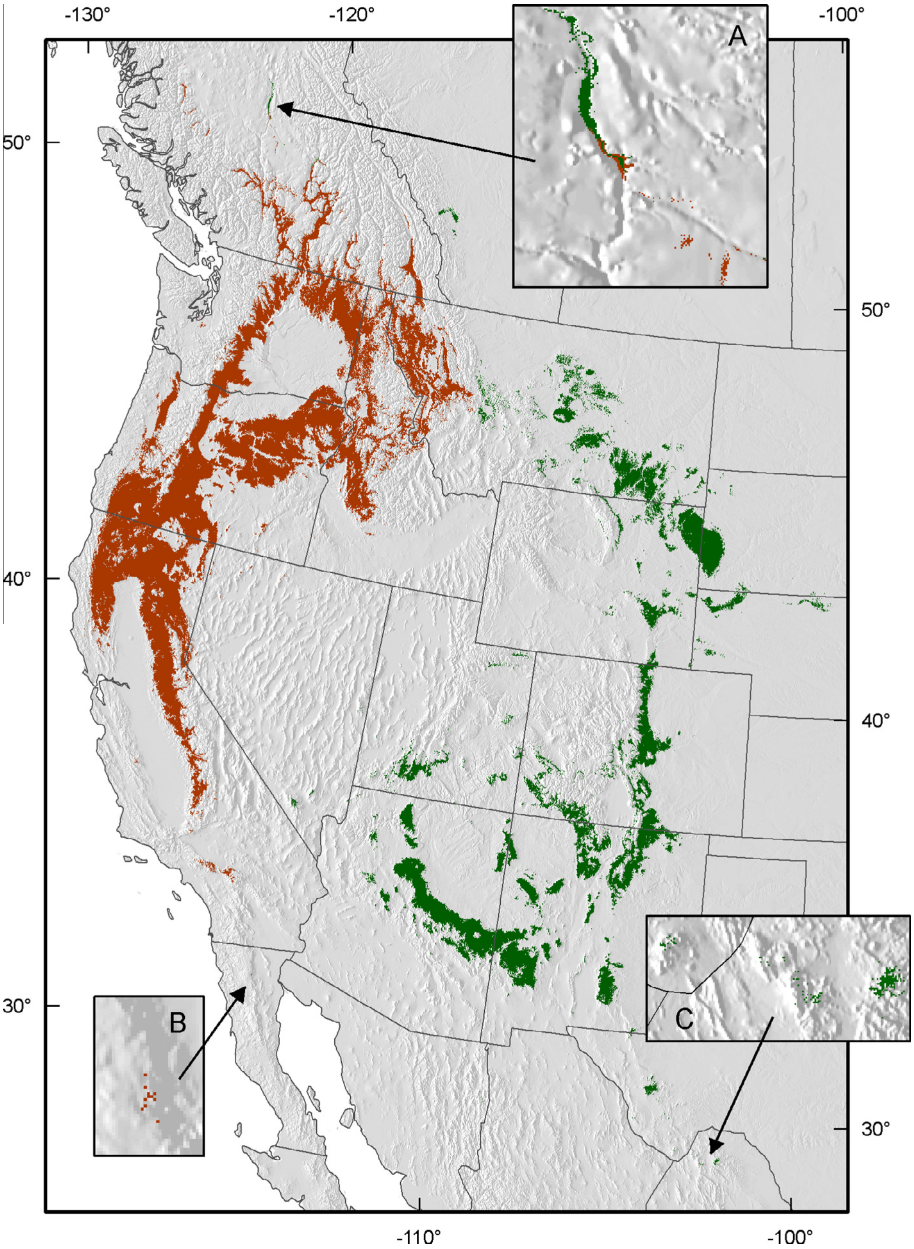

Fig. 2. Mapped prediction of the climate niche of *Pinus ponderosa* var. *ponderosa* (red) and var. *scopulorum* (green). Panels zoom in on areas discussed in the text.

more pronounced, as the niche of var. *ponderosa* recedes west while that of var. *scopulorum* would move east. For var. *ponderosa*, gains in niche space would tend to balance the losses: substantial gains in habitat are projected to the north, but large tracts are projected to be lost in eastern Oregon (location 2) and northern Idaho (location 1) but for different reasons. The habitat lost in Oregon apparently would result from infringement of grass-shrub communities but that in Idaho from a climate becoming more suited to mesic cedar-hemlock forests (see Rehfeldt et al., 2012). Isolated populations toward the south seem particularly precarious (panel B).

For *P. p.* var. *scopulorum*, the loss of climate niche would greatly exceed the gains, with niche space being reduced by about one-half by 2060 (Fig. 5). Niche space is projected to disappear in areas where the variety already occupies the highest elevations: eastern Montana (location 4), southern New Mexico (location 7), and in the Sierra Madre Oriental at the southern limits of the current distribution (panel F). Niche space, in fact, would disappear in isolated locations everywhere, but especially noteworthy is the loss of habitat in the Nebraska Sandhills (location 6), the easternmost outlier of this variety. Much of the habitat expected to remain suitable throughout the period is currently occupied by today's high altitude populations (panel D, location 5). Gains in habitat are limited to those few locations where suitable habitat may be available at higher altitudes (Panels D and E) or to the north (location 3) where in 2060 the largest single tract of suitable climate space may occur.

For *P. menziesii*, the projections show that the transition between vars. *menziesii* and *glauca* would remain relatively stable (Fig. 6 panels A and B). Note that in Fig. 6 itself, the transition between varieties is mapped to show loss of niche space of var. *glauca*, but in panels A and B, it is mapped to show gains in niche space of var. *menziesii.* Either presentation illustrates little encroachment of var. *menziesii* on the distribution of var. *glauca*. Nowhere in the interior, moreover,

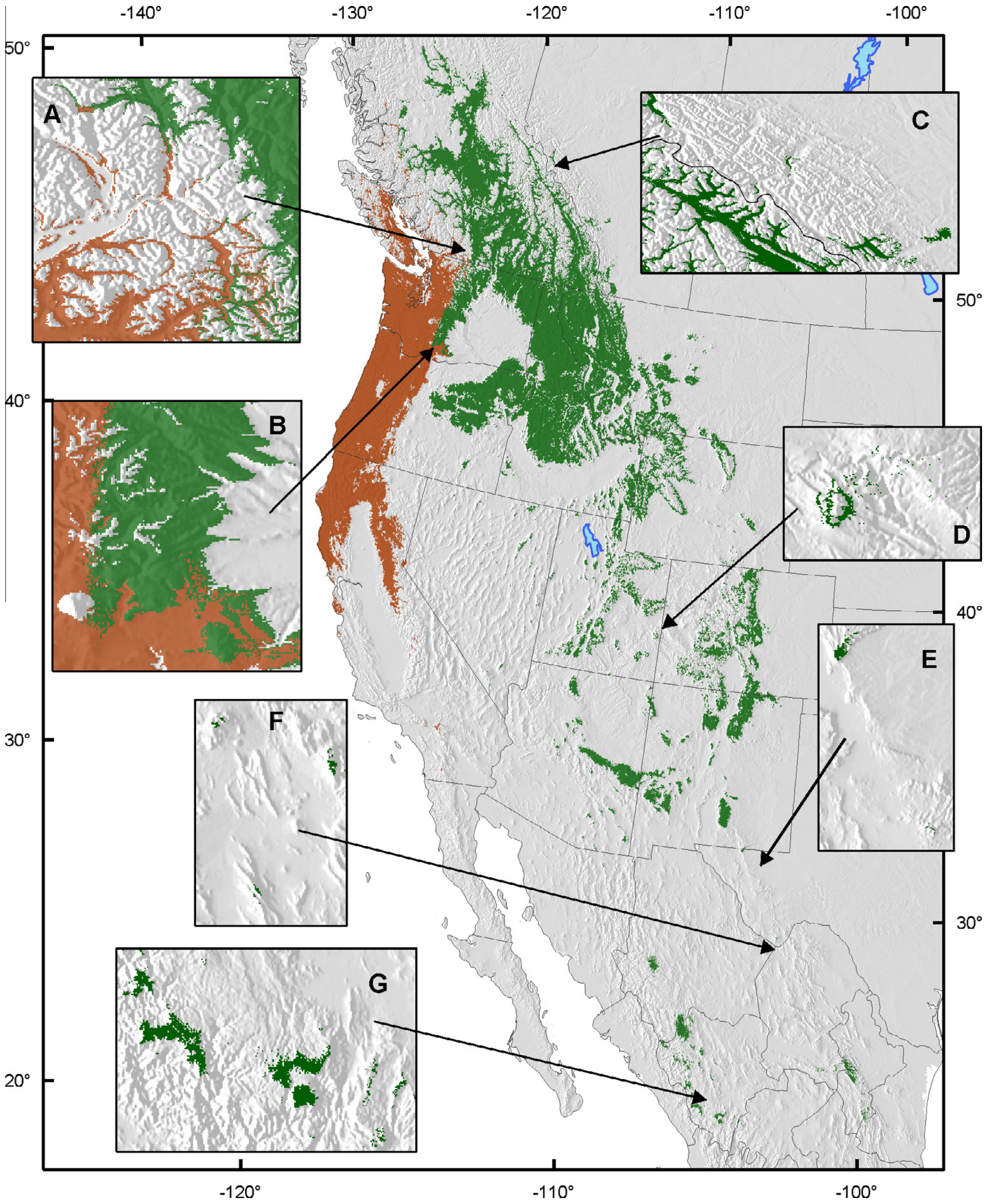

Fig. 3. Mapped prediction of the climate niche of *Pseudotsuga menziesii* var. *menziesii* (brown) and var. *glauca* (green). Panels zoom in on areas discussed in the text.

is the coastal variety's climatic niche projected to supplant that of the inland variety.

Impacts of climate change on the climate niche of *P. m.* var. *menziesii* are projected to be small (Fig. 6). Some losses are projected for the lowest elevations and gains at higher elevations (panel D) and in the north, but in general, the climate niche would persist in most of the locations where it occurs today. The projected loss of niche space in and around Puget Sound (Fig. 6, panel C) is counter-intuitive, however. Analyses of biome distributions (Rehfeldt et al., 2012) suggested that this area would have no contemporary analogs for the 2060 climate. In predicting that var. *menziesii* would not be suited for the future Puget Sound climate, our model is conveying the fact that the variety does not exist in those climates today. Yet, because there is no contemporary analog, there is no way judge the suitability of these climates in the future.

Projected impacts to *P. m.* var. *glauca* are much more complex than those for var. *menziesii*. In the interior northwest, var. *glauca* is projected to thrive. Gains in habitat should be substantial in the north while losses in habitat should be small, confined to the low elevation fringe in the interior USA and to the valleys of southeastern British Columbia (Fig. 6), where the climate is projected to become more suited to vegetation of ecosystems more mesic than inhabited by this variety (see Rehfeldt et al., 2012). In the remainder of the interior, however, the climate niche should shift upwards in elevation (panel E), causing extirpation where the variety already occupies the high elevations, particularly in the ranges of southwestern USA (panels F and G) and in northern Mexico (Fig. 7). By 2060, little suitable habitat is projected for the Sierra Madre Occidental (Fig. 7, panels A and B) and Sierra Madre Oriental (panels C and D) of Mexico.

Fig. 7 also illustrates a potentially dire impact of the changing climate on the Mexican variety on which crown dieback is already occurring (personal observations, CSR and JLU). Extirpation is projected for much of the contemporary distribution, with the southernmost populations of Oaxaca appearing particularly precarious (panel F). Emergence of new climate niche, moreover,

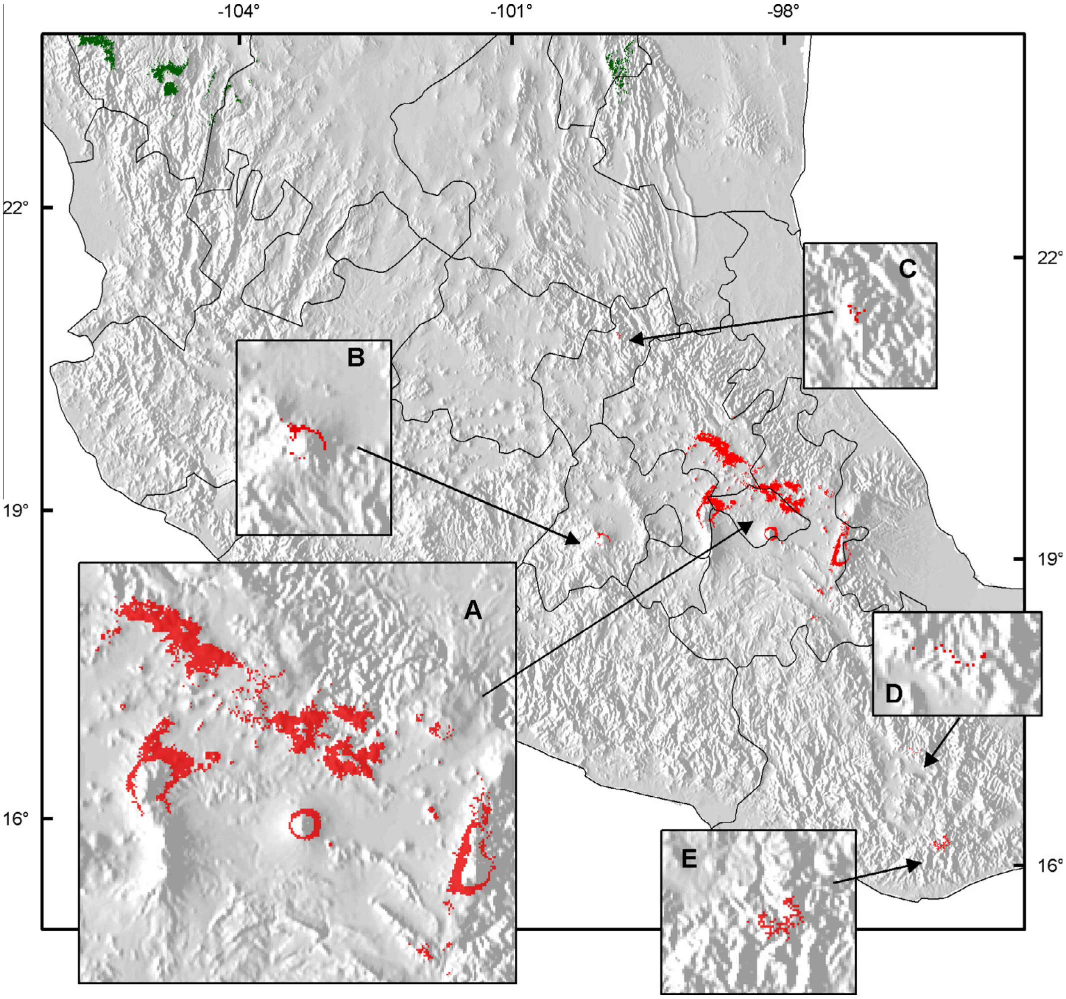

Fig. 4. Mapped prediction of the climate niche of the Mexican variety of *Pseudotsuga menziesii* (red) and the southernmost populations of *P. p.* var. *glauca* (green). Panels zoom in on areas discussed in the text.

should be limited, appearing only on the flanks of the volcanoes in the Transvolcanic belt (panel E). The projected impact is so great that few locations are projected to have suitable climate niche continuously until 2060.

4. Discussion

Our results affirm regional studies showing that the occurrence of two broadly distributed species of western North America can be predicted from a combination of precipitation and temperature variables (Rehfeldt et al., 2006; Hamann and Wang, 2006; Gray and Hamann, 2013). These results expand on the analyses of Rehfeldt et al. (2006) by including the Canadian and Mexican portions of the geographic distribution as well as that of western United States. Our approach also considers the taxonomic varieties of these species which have not been considered previously. We predict presence of *P. ponderosa* varieties from summer and winter precipitation and summer temperatures, and those of *P. menziesii* from climate continentality (summer winter temperature differential), summer heat, and summer precipitation. These combinations of variables are consistent with lower limits of distribution of species in the inland northwest (USA) being a function of summer moisture stress with upper limits determined by winter cold (Rehfeldt et al., 2008). Errors of prediction for the broad and comprehensive databases we use are extremely low, particularly in predicting the presence of these taxa.

Our model is a climate niche model, not to be confused with a species distribution model (e.g. Elith and Leathwick, 2009). The latter models attempt to predict actual occurrence of species from environmental factors that include but are not limited to climate. Obviously, whether or not species occur at a climatically suitable location is affected by many site-specific, biotic and abiotic factors such as substrate, topography (particularly effects related to aspect), successional status and other competitive relationships, insects and disease, and reproductive capacities. While species distribution models attempt to integrate this complex assortment of effects to predict distributions, climate niche models rely on the expertise of land managers to integrate local factors for determining which sites within the climate niche are unsuitable. In our presentation, we are careful to note that predictions and projections by our models pertain only to the distribution of suitable climates.

Impacts of climate change on the climate niche generally support the intuitive view that climate change will force an upwards and northwards shift in the niche distributions (Figs. 5–7). Because such projections pertain solely to the climate niche, they do not address the contingencies associated with extirpation on the trailing edge and migration on the leading edge that influence rates of response in natural ecosystems. Rates of demise are dependent on increasingly poor adaptation of plant populations to their environment, a subject dealt with in PART 2, with mortality

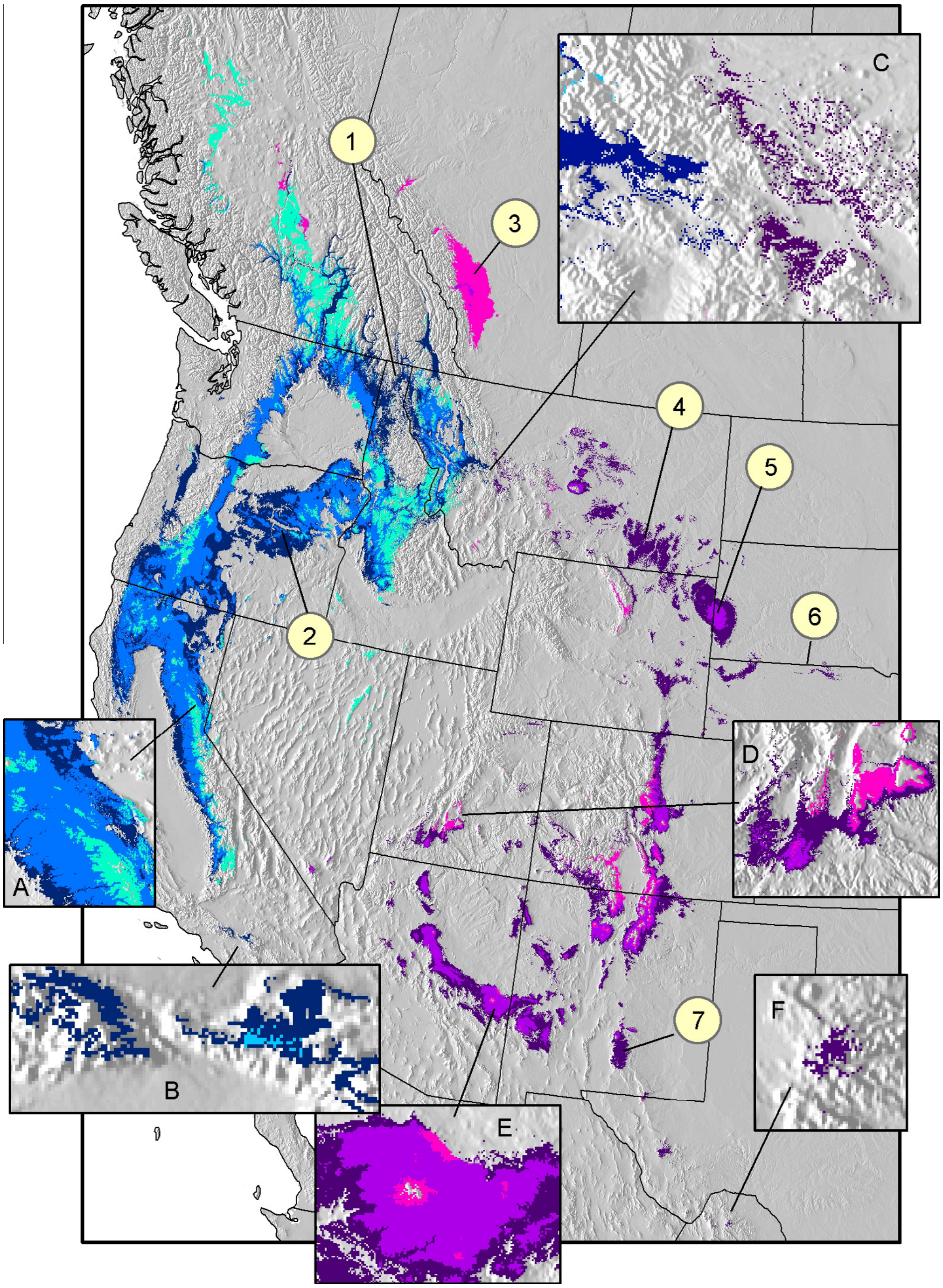

Fig. 5. Impact of climate change projected for *Pinus ponderosa* var. *ponderosa* (blue colorpath) and var. *scopulorum* (purple colorpath). Darkest tones color grid cells present in the contemporary climate niche but lost in 2060 niche space; middle tones color grid cells expected to be within the climate niche at both time periods; and brightest tones color grid cells expected to be added to the niche in 2060. Panels zoom in on locations discussed in detail; numbered locations are referred to in the text.

accruing as plants become poorly attuned physiologically to the environment in which they are rooted. Rates of immigration, moreover, are subject to the migration (Davis and Botkin, 1985; Davis, 1989) and adaptational (Mátýas and Yeatman, 1992) lags associated with immigration. Both topics have been discussed thoroughly in reference to climate change (e.g., Rehfeldt et al., 1999, 2001, 2002, 2006); the former encompassing all those seed source and dispersal contingencies that may delay for generations the colonization of new niche space. Adaptation lags refer to the generations required before evolutionary processes produced colonies physiologically attuned in the new habitat. Because of these contingencies, natural ecosystems will be subject to rates of immigration on the leading edge that are slower than rates of demise on the trailing edge, even when the amount of suitable niche space remains constant. Until a semblance of equilibrium is restored, the appearance in the short term will be a net loss of habitat. In managed forests, however, land managers have opportunity to reduce the lag times, the subject of PART 3.

Because of these uncertainties, controversy surrounds topics dealing with the future distribution of species, fate of contemporary populations, and effects of migration and adaptation lags. Yet, results of niche and species modeling tend to unanimously

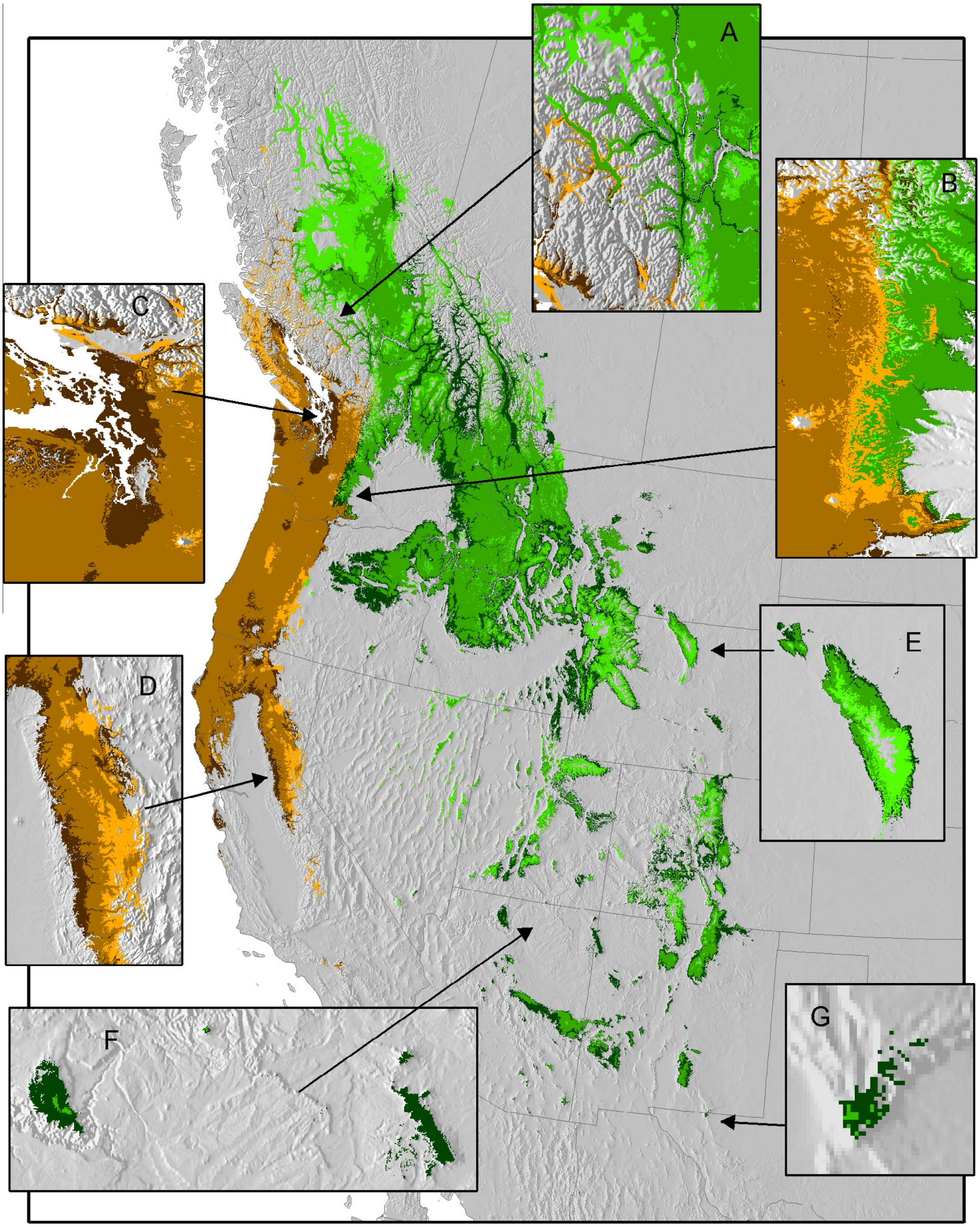

Fig. 6. Impact of climate change projected for *Pseudotsugs menziesii* var. *menziesil* (brown colorpath) and var. *glauca* (green colorpath) north of Mexico. Darkest tones color grid cells present in the contemporary climate niche but lost in 2060 niche space; middle tones color grid cells expected to be within the climate niche at both time periods; and brightest tones color grid cells expected to be added to the niche in 2060. Panels zoom in on locations discussed in detail.

agree that by mid-century, the climate of a portion of the current distribution of many taxa will change to climates in which the taxa do not occur today. Toward the end of the century, this portion may become substantial. The implication is that eventually, the taxa will no longer occur at these sites.

While our maps for 2060 (Figs. 5–7) show loss of niche space along trailing edges and new niche space at leading edges for all taxa, nuances abound. Most obvious are the greater negative impacts on *P. ponderosa* than on *P. menziesii*, and the greater negative impacts on inland varieties of both species inhabiting continental climates than on coastal varieties inhabiting climates with maritime influences. New niche space at the leading edge would be considerably greater for *P. menziesii* (Fig. 6) than *P. ponderosa* (Fig. 5), while losses in suitable habitat at the trailing edge would be much more severe in *P. ponderosa* than *P. menziesii*. For all varieties of both species, however, suitable habitat should move upwards in elevation.

Projected effects of climate change on the climate niche of both varieties of *P. menziesii* of Mexico suggest dire consequences. Suitable habitat for var. *glauca* would be confined to only the

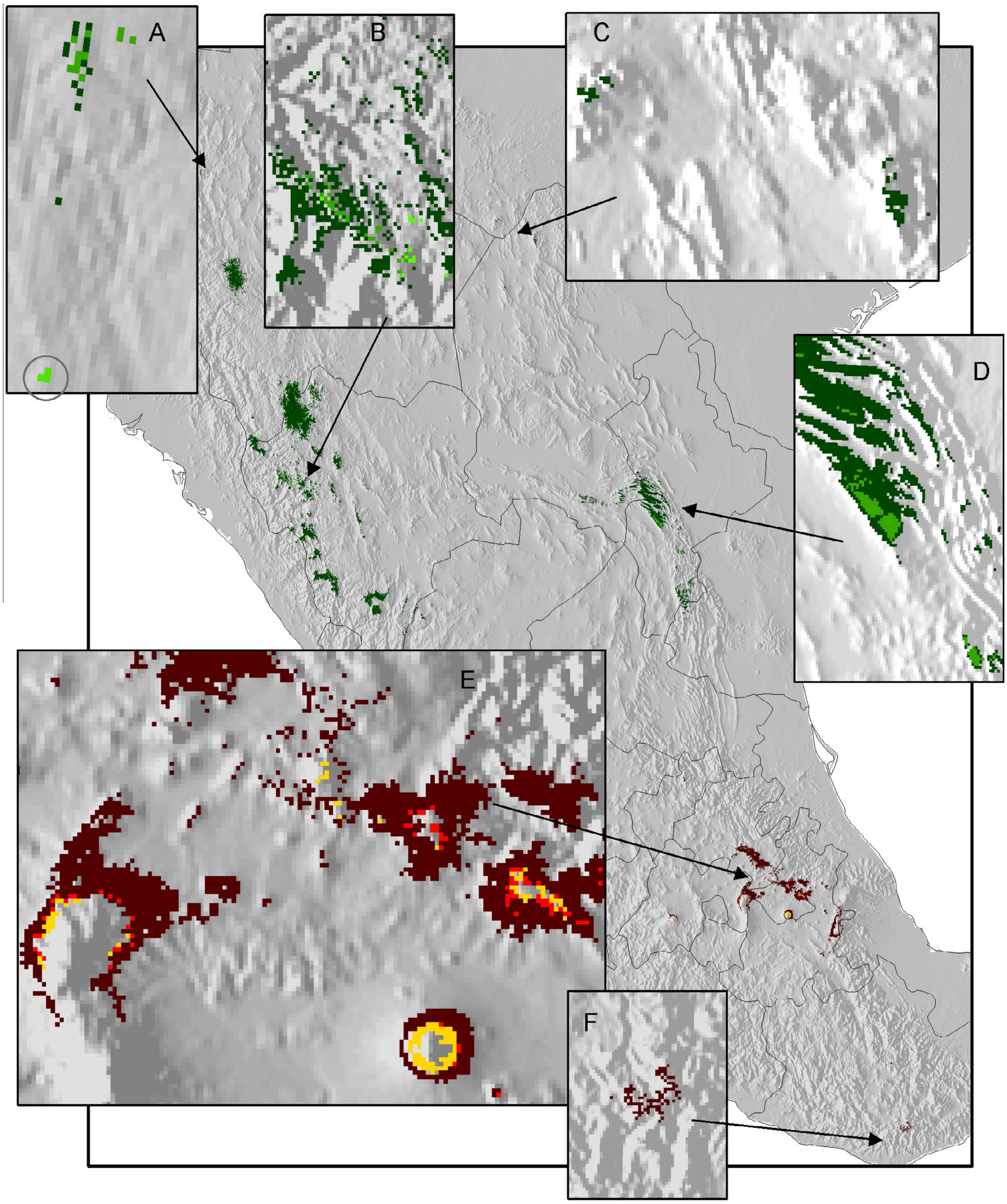

Fig. 7. Impact of climate change projected for *Pseudotsugs menziesii* var. *glauca* (green colorpath) of northern Mexico and the unnamed variety of southern Mexico (red colorpath). Darkest tones color grid cells present in the contemporary climate niche but lost in 2060 niche space; middle tones color grid cells expected to be within the climate niche at both time periods; and brightest tones color grid cells expected to be added to the 2060 climate niche.

highest elevations in the Sierra Madre Occidental and Oriental. Loss of niche space should be greatest in the Occidental, corresponding to increases in temperature on their interior slopes that are the largest in all of Mexico (see Sáenz-Romero et al., 2012a). Suitable habitat for the unnamed southernmost variety is projected to become scarce, being limited largely to increasingly higher elevations on the flanks of several volcanoes in the Transvolcanic Axis. This latter result is in common with projections for other conifers (Ledig et al., 2010; Rehfeldt et al., 2012; Sáenz-Romero et al., 2012b,c), but immigration may be problematic because of a lack of suitable soils (see Lauer, 1973). The plight of the Mexican variety is further exacerbated by ongoing demise of contemporary populations, high inbreeding, low seed production, and, as a result, little reproduction (Ventura-Ríos et al., 2010; Velasco-García et al., 2007).

These projected impacts are not necessarily intuitive. The climate niche of *P. ponderosa* extends further into arid climates than that of *P. menziesii* while that of *P. menziesii* extends further into mesic environments than that of *P. ponderosa* (see for instance, Rehfeldt et al., 2008). Consequently, responses to a warming climate seemingly should favor *P. ponderosa*, the species better able to tolerate xeric conditions. Impacts, however, appear to be much more complex. On the one hand, a pronounced loss of niche space seems likely in the eastern and southern portions of the current distribution of both *P. p.* var. *scopulorum* and *P. m.* var. *glauca,* largely because many of the highest mountains are already occupied by these taxa. As suitable niche moves upwards, there is no new habitat to replace that lost at lower elevations. But on the other hand, future climates in the interior northwest of USA and southwest Canada are projected to become increasingly better suited to the cedar-hemlock forests more typical of mesic conditions (Rehfeldt et al., 2012). While *P. menziesii* can be a part of this vegetation, *P. ponderosa* typically is not. As a result, the latter species may disappear in this region while the former may flourish (Figs. 5 and 6).

Uncertainties in making projections such as these are many and have been discussed thoroughly. Much of the uncertainty is focused on (a) the possibilities of future climates having no contemporary analogs, and (b) the accuracy of GCM output in portraying future climates. The first of these concerns the possibility that future climates may be suited to plant assemblages that do not occur today. Because the realized niche is determined in part by competitive interactions, this eventuality would presage novel competitive interactions which doubtlessly would alter limits of distribution. Impacts projected from models such as ours assume that competitive interactions remain the same such that the climate niche remains stable, that is, no-analog future climates will be unimportant. In analyses of North American biomes, Rehfeldt et al. (2012) mapped those future climates projected to be outside the range of climates occupied by contemporary vegetation. The results showed that by mid-century, no-analog commumities may be of local importance, such as in the inland northwest of the United States, but throughout much of the projected distribution of these two species, the occurrence of climates without contemporary analogs should not be widespread. Toward the end of the century, however, the occurrence of climates without contemporary analogs may increase substantially.

The uncertainty imposed by the many GCM formulations has several facets. For instance, we use an ensemble of GCM output from a single climate change scenario for the decade surrounding 2060. In using the ensemble, we likely invoke an array of climate variables not capable of being produced by any single GCM formulation. We do not consider this to be a limitation, however. Even though multi-model ensemble forecasts perform better than single GCM formulations in assessing plant distributions (Fordham et al., 2012), Hansen (2013) nonetheless warns that the various scenarios and time slices provided by the GCMs comprise a distribution of GCM output, but this distribution cannot be considered a distribution of future climates. Our goal was to project climatic niches into a future climate space representative of GCM output. For this goal, the ensemble met our needs.

Using the ensemble, however, does not allow presentation and discussion of the variation in projected impacts attributable to the various GCMs. This variation has been shown repeatedly to vary between large and enormous, depending on the time period being considered. For practical applications, modelers tend to find a reasonably suitable approach for assessing the agreement between various formulations so that impacts can be expressed and interpreted according to a GCM consensus. By using the ensemble, we merely define the consensus beforehand. Although this approach seemingly ignores the variation, we do not view this as a serious omission. Impacts to the vegetation attributable to the myriad permutations of GCMs, emissions scenarios, and time slices all can be viewed as timing options. That is, they tend to follow similar trajectories but differ temporally, occurring at different points along a common time line (see Fig. 4, Rehfeldt et al., 2009; Fig. 3, Rehfeldt et al., 2012; Fig. 4, Rehfeldt and Jaquish, 2010; Fig. 5., Joyce and Rehfeldt, 2013). Similar trajectories develop from the consistency among GCMs regarding temperature increases; the climate is warming. However, inconsistencies among GCMs surround precipitation projections. Because impacts to the vegetation are determined by the balance between temperature and precipitation, those attributable to a single GCM and scenario will be repeated at another time for a different GCM and scenario. For planning, therefore, one can assume that the climates portrayed by an ensemble are reasonably accurate in their trajectory, but are of questionable timing. In viewing the various combinations of GCMs, scenarios and time slices as timing options, accuracy of the predictions undoubtedly will be greater in the short-term than in the long-term.

Impacts of climate change on the varieties of *P. menziesii* and *P. ponderosa* and accompanying reforestation issues are considered in greater depth in PART 3, following a consideration of genetic variation within varieties in PART 2. The relevance of the latter presentation to the current results is primarily in reference to the areas in Figs. 5–7 for which the climate niche is considered to be stable; that is, the taxa are assumed to persist. In PART 2 we show these areas will contain genotypes becoming less and less suited to the climate in which they grow.

Acknowledgments

We appreciate the ground plot data made available by the Forest Management Branch, Alberta Sustainable Resource Development; the Mexican National Forestry Commission (CONAFOR); Colegio de Postgraduados, Texcoco, México; Forest Inventory and Analysis, U.S. Forest Service (http://www.fia.fs.fed.us); and Research Branch, British Columbia Ministry of Forest and Range. For unpublished records and personal knowledge on the occurrence of Mexican populations, we thank Jesús Vargas-Hernández (Conservemos México y sus Recursos Genéticos, Texcoco, México), Celestino Flores (Universidad Autónoma Agraria Antonio Narro, Coahuila), Christian Wehenkel (Universidad Juárez, Durango), and Antonio Plancarte-Barrera (Alen del Norte, Oaxaca). We appreciate the sound technical support of Nicholas Crookston (USDA, Forest Service, Moscow, Idaho USA). The manuscripts in this series have benefited greatly from diligence of five anonymous reviewers.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684.

Breiman, L., 2001. Random forests. Machine Learn. 45, 5–32.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. P. Natl. Acad. Sci. USA 102, 15144–15148.

Conkle, M.T., Critchfield, W.B., 1988. Genetic variation and hybridization of ponderosa pine. In: Ponderosa Pine: the species and its management. Washington State University Cooperative Extension. pp. 27–43.

Crookston, N.L., Rehfeldt, G.E., 2008. Climate estimates and plant-climate relationships. USDA Forest Service, Rocky Mountain Research Station, Moscow ID. Web Site: <http://forest.moscowfsl.wsu.edu/climate/> (assessed 2011–2012).

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88, 2783–2792.

Dansereau, P., 1957. Biogeography. An Ecological Perspective. Ronald Press, NY.

Davis, M.B., 1989. Lags in vegetation response to greenhouse warming. Climatic Change 15, 75–82.

Davis, M.B., Botkin, D.B., 1985. Sensitivity of vegetation and its fossil pollen record to rapid temperature change. Quatern. Res. 23, 327–340.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 2009 (40), 677–697.

Fordham, D.A., Wigley, T.M.L., Watts, M.J., Brook, B.W., 2012. Strengthening forecasts of climate change impacts with multi-model ensemble averaged projections using MAGICC/SCENGEN 5.3. Ecography 35, 4–8.

Globe Task Team, 1999 . The Global Land One-kilometer Base Elevation (GLOBE) Digital Elevation Model, version 1.0. Website <http://www.ngdc.noaa.gov/seg/topo/globe.shtml> (accessed 2008).

Gray, L.K., Hamann, A., 2013. Tracking suitable habitat for tree populations under climate change in western North America. Climatic Change 117, 289–303.

Gugger, P.F., Sugita, S., Cavender-Bares, J., 2010. Phylogeography of Douglas-fir based on mitochondrial and chloroplast DNA sequences: testing hypotheses from the fossil record. Mol. Ecol. 19, 1877–1897.

Hamann, A., Wang, T., 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87, 2773–2786.

Hansen, J.A., 2013. An old story, but useful lesson. <http://www.columbia.edu/~jeh1/mailings/2013/20130926_PTRSpaperDiscussion.pdf> (accessed Oct. 3, 2013).

Hansen, J., Sato, M., Ruedy, R., 2012. Perception of climate change. Proc. Natl. Acad. Sci. USA 109, 14726–114727.

Iverson, L.R., Prasad, A.M., Mathews, S., 2008. Modelling potential climate change impacts on the trees of northeastern United States. Mitig. Adapt. Strat. Glob. Change 13, 487–516.

Joyce, D.G., Rehfeldt, G.E., 2013. Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): Guidelines for land managers. For. Ecol. Manage. 295, 173–192.

Krakowski, J., Stoehr, M.U., 2009. Coastal Douglas-fir provenance variation: patterns and predictions for British Columbia seed transfer. Ann. For. Sci. 66, 811.

Krakowski, J., Stoehr, M.U., 2011. Douglas-fir provenance survival and growth in the British Columbia south submaritime seed planning zone. Know. Manage. Br. Nat. Resource Sec., Extension Note, Victoria, BC, 105.

Latta, R.G., Mitton, J.B., 1999. Historical separation and present gene flow through a zone of secondary contact in ponderosa pine. Evolution 53, 769–776.

Lauer, W., 1973. The altitudinal belts of the vegetation in the central Mexican highlands and their climatic conditions. Arctic Alpine Res. 5, 99–113.

Lavergne, S., Mouquet, N., Thuiller, W., Ronce, O., 2010. Biodiversity and climate change: evolutionary and ecological responses of species and communities. Annu. Rev. Ecol. Evol. Syst. 41, 321–350.

Ledig, F.T., Kitzmiller, J.H., 1992. Genetic strategies for reforestation in the face of global climate change. For. Ecol. Manage. 50, 153–169.

Ledig, F.T., Rehfeldt, G.E., Sáenz-Romero, C., Flores-López, C., 2010. Projections of suitable habitat for rare species under global warming scenarios. Am. J. Bot. 97, 970–987.

Little Jr., E.L., 1971. Atlas of United States trees, vol. 1. Conifers and important hardwoods. U.S. Department of Agriculture. Miscellaneous Publication, 1146.

Mátýas, C., 1994. Modeling climate change effects with provenance test data. Tree Physiol. 14, 797–804.

Mátýas, C., Yeatman, C.W., 1992. Effect of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb.) populations. Silvae Genetica 41, 370–376.

Morgenstern, E.K., 1996. Geographic Variation in Forest Trees. UBC Press, Vancouver, BC.

Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Inder, R.S., Ste-Marie, C., 2012. Placing forestry in the assisted migration debate. Bioscience 62, 835–842.

R Development Core Team, 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.

Rehfeldt, G.E., 1994. Evolutionary genetics, the biological species, and the ecology of the interior cedar-hemlock forests. In: Proceedings of the Conference: Interior Cedar-Hemlock-white Pine Forests: Ecology and Management, Spokane, WA, March 2–4. Department of Natural Resource Sciences, Washington State University, Pullman, WA.

Rehfeldt, G.E., Crookston, N.L., Sáenz-Romero, C., Campbell, E.M., 2012. North American vegetation model for land-use planning in a changing climate: a solution to large scale classification problems. Ecol. Appl. 22, 119–141.

Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analyses of plant–climate relationships for the western United States. Int. J. Plant Sci. 167, 1123–1150.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2008. Quantifying the abundance of co-occurring conifers along inland northwest (USA) climate gradients. Ecology 89, 2127–2139.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For. Ecol. Manage. 258, 2353–2364.

Rehfeldt, G.E., Jaquish, B.C., 2010. Ecological impacts and management strategies for western larch in the face of climate-change. Mitig. Adapt. Strat. Glob. Change 15, 283–306.

Rehfeldt, G.E., Jaquish, B.C., Sáenz-Romero, C., St Clair, J.B., López-Upton, J., Leites, L.P., Joyce, D.G., 2014b. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Reforestation. For. Ecol. Manage. 324, 147–157.

Rehfeldt, G.E., Leites, L.P., St Clair, J.B., Jaquish, B.C., Sáenz-Romero, C., López-Upton, J., Joyce, D.G., 2014a. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: clines in Growth Potential. For. Ecol. Manage. 324, 138–146.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, R.A., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biol. 8, 912–929.

Rehfeldt, G.E., Wykoff, R.A., Ying, C.C., 2001. Physiologic plasticity, evolution, and impacts of a changing climate in *Piuns contorta*. Climatic Change 50, 355–376.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A., 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. Ecol. Monogr. 69, 375–407.

Reyes-Hernández, J.V., Vargas-Hernández, J.J., López-Upton, J., Vaquera-Huerta, H., 2006. Phenotypic similarity among Mexican populations of *Pseudotsuga* Carr. Agrociencia 40, 545–556.

Sáenz-Romero, C., Rehfeldt, G.E., Crookston, N.L., Duval, P., Beaulieu, J., 2012a. Spline models of contemporary, 2030, 2060 and 2090 climates for Michoacán state, México; impacts on the vegetation. Rev. Fitotec. Mex. 35, 333–345.

Sáenz-Romero, C., Rehfeldt, G.E., Duval, P., Lindig-Cisneros, R.A., 2012b. *Abies religiosa* habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. For. Ecol. Manage. 275, 98–106.

Sáenz-Romero, C., Rehfeldt, G.E., Soto-Correa, J.C., Aguilar-Aguilar, S., Zamarripa-Morales, V., López-Upton, J., 2012c. Altitudinal genetic variation among *Pinus pseudostrobus* populations from Michoacán, México; two location shadehouse test results. Rev. Fitotec. Mex. 35, 111–120.

Sorensen, F.C., Weber, J.C., 1994. Genetic variation and seed transfer guidelines for ponderosa pine in the Ochoco and Malheur National Forests of central Oregon. USDA Forest Service Research Paper PNW-RP-468.

St Clair, J.B., Mandel, N.L., Vance-Borland, K.W., 2005. Genecology of Douglas Fir in western Oregon and Washington. Ann. Bot. 96, 1199–1214.

St Clair, J.B., Howe, G.T., 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Glob. Change Biol. 13, 1441–1454.

Thomas, C.D., 2010. Climate, climate change and range. Boundaries. Diversity Distrib. 16, 488–495.

van Vuuren, D.P., Edmonds, J.A., Kainuma, M., Riahi, K., Thomson, A.M., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S., 2011. The representative concentration pathways: an overview. Climatic Change 109, 5–31.

Velasco-García, M.V., López-Upton, J., Angeles-Pérez, G., Vargas-Hernández, J.J., Guerra de la Cruz, V., 2007. *Pseudotsuga menziesii* seed dispersion in populations of Central México. Agrociencia 41, 121–131.

Ventura-Ríos, A., López-Upton, J., Vargas-Hernández, J.J., Guerra de la Cruz, V., 2010. Caracterización de *Pseudotsuga menziesii* (Mirb.) Franco en el centro de México; Implicaciones para su conservación. Rev. Fitotec. Mex. 33, 107–116.

Wei, X.-X., Beaulieu, J., Khasa, D.P., Vargas-Hernández, J.J., López-Upton, J., Jaquish, B., Bousquet, J., 2011. Range-wide chloroplast and mitochondrial DNA imprints reveal multiple lineages and complex biogeographic history for Douglas-fir. Tree Genet. Genomes 7, 1025–1040.

Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. For. Ecol. Manage. 299, 35–51.