Modeling Species' Realized Climatic Niche Space and Predicting Their Response to Global Warming for Several Western Forest Species With Small Geographic Distributions

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Abstract

The Random Forests multiple regression tree was used to develop an empirically based bioclimatic model of the presence-absence of species occupying small geographic distributions in western North America. The species assessed were subalpine larch (*Larix lyallii*), smooth Arizona cypress (*Cupressus arizonica* ssp. *glabra*), Paiute cypress (syn. Piute cypress) (*Cupressus arizonica* ssp. *nevadensis*), and Macfarlane's four-o'clock (*Mirabilis macfarlanei*). Independent variables included 33 simple expressions of temperature and precipitation and their interactions. These climate variables were derived from a spline climate model for the Western United States that provides point estimates (latitude, longitude, and altitude). Analyses used presence-absence data largely from the Forest Inventory and Analysis, USDA Forest Service database. Overall errors of classification ranged from 1.39 percent for Macfarlane's four-o'clock to 3.55 percent for smooth Arizona cypress. The mapped predictions of species occurrence using the estimated realized climatic niche space were more accurate than published range maps. The Hadley and Canadian general circulation models (scenario IS92a for 1 percent increase GGa/year) were then used to illustrate the potential response of the species' contemporary realized climatic niche space to climate change. Predictions were mapped at a 1-km^2 resolution. Concurrence between species' geographic distribution and their contemporary realized climatic niche rapidly disassociates through the century. These models demonstrate the heightened risk for species occupying small geographic ranges of displacement into climatic disequilibrium from rapid climate change and provide tools to assist decisionmakers in mitigating the threat.

Keywords: Bioclimatic models, climatic distributions, climatic niche, global warming, Random Forests multiple-regression tree, response to climate change, narrow endemic.

Introduction

Climate is a principle factor that controls where species occur in nature (Woodward 1987). As the climate changes so then does the distribution of species. Long-lived plant species have adapted repeatedly to past climate change (see Ackerly 2003). When climate change exceeds species' tolerance limits, continued survival is dependent on the species ability to genetically adapt or migrate, or both, to suitable climate. These processes have contributed successfully to the persistence of long-lived plant species in response to past climate change (Davis and Shaw 2001). Their effectiveness under future climate change may be exacerbated by the increased rate of change predicted to occur over the present century. Projections for change in global climate rival historical periods of climate change at an accelerated rate (Houghton and others 2001). The accelerated rate of change threatens to displace current plant species distributions into climatic disequilibrium resulting in an increased potential for extinction of all or portions of species' ranges (Thomas and others 2001).

The objective for these analyses was to develop bioclimatic models that predict the occurrence of species with small natural distributions in the Western United States and project where suitable climates for the natural occurrence of these species may occur in the future in response to global warming. Three species were selected for the purposes of this analysis. The first was subalpine larch (*Larix lyallii* Parl.), a high-elevation, deciduous conifer inhabiting the Pacific Northwest. The second included two subspecies of Arizona cypress (*Cupressus arizonica* Greene), the smooth Arizona cypress (*C. arizonica* var. *glabra* (Sudw.) Little), which is endemic to central Arizona, and the Paiute cypress
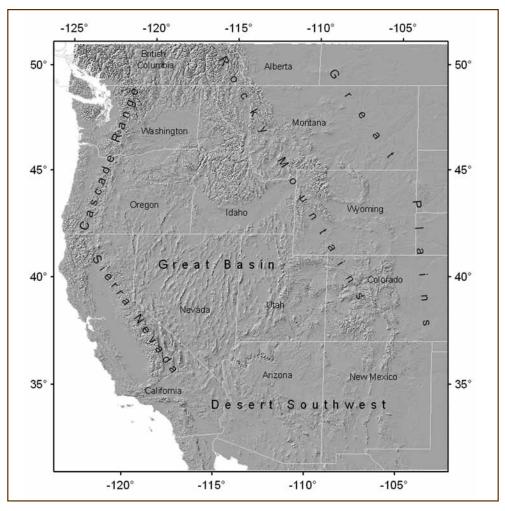
Figure 1—This shows the Western United States and southwestern Canada (from Rehfeldt and others 2006).

(syn. Piute cypress) (*C. arizonica* ssp. *nevadensis* Abrams E. Murray), which is endemic to the southern tip of the Sierra Nevada. The third was Macfarlane's four-o'clock (*Mirabilis macfarlanei* Constance & Rollins), a long-lived, deep-rooted perennial species that inhabits mid-to low-level canyon grasslands near the Oregon-Idaho northern border and is listed as endangered by the Bureau of Land Management (BLM) (USFWS 1996).

Methods

Study Area

The area of study consisted of the region supported by the climate surfaces of Rehfeldt (2006). This area encompasses the Western United States and southwestern Canada, latitudes 31° to 51° N and longitudes 102° to 125° W (Figure 1).

Climate Estimates

Spline climate model (Rehfeldt 2006) was used to estimate climate at point locations (latitude, longitude, and altitude). The model is based on monthly minimum, maximum, and average temperatures and precipitation normalized for the period of 1961-90. This data was obtained from more than 3,000 weather stations dispersed throughout the conterminous Western United Sates and southwestern Canada. Hutchinson's (1991, 2000) thin plate splines were used to develop geographic surfaces for monthly data. The result produced 48 surfaces representing minimum, maximum, and average temperature and precipitation for each month

Table 1—Climate variables and their acronyms used as independent variables in regression analyses (from Rehfeldt and others 2006)

Acronym	Definition
MAT	Mean annual temperature
MTCM	Average temperature in the coldest month
MMIN	Minimum temperature in the coldest month
MTWM	Mean temperature in the warmest month
MMAX	Maximum temperature in the warmest month
MAP	Mean annual precipitation
GSP	Growing season precipitation, April through September
TDIFF	Summer-winter temperature differential, MTWM-MTCM
DD5	Degree-days > 5 °C
DD0	Degree-days < 0 °C
GSDD5	Accumulated growing-season degree days > 5 °C, April through September
MINDD0	Minimum degree-days < 0 °C
SDAY	Julian date of the last freezing date of spring
FDAY	Julian date of the first freezing date of autumn
FFP	Length of the frost-free period
D100	Julian date the sum of degree-days > 5 °C reaches 100
AMI	Annual moisture index, DD5/MAP
SMI	Summer moisture index, GSDD5/GSP
PRATIO	Ratio of summer precipitation to total precipitation, GSP/MAP

Interactions: MAP x DD5, MAP x MTCM, GSP x MTCM, GSP x DD5, DD5 x MTCM, MAP x TDIFF, GSP x TDIFF, MTCM/MAP, MTCM/GSP, AMI x MTCM, SMI x MTCM, TDIFF/MAP, TDIFF/GSP, PRATIO x MTCM, PRATIO x DD5

of the year. For our analyses, these surfaces were used to estimate 33 climate variables that represent a range in climate variables from simple sums to complex interactions of temperature and precipitation (Table 1).

An updated version of the spline climate model was used to predict the effects of global warming for decades beginning in 2030, 2060, and 2090. The model used a regional summary of the IS92a scenario (1 percent per year increase in greenhouse gases after 1990) of the International Panel on Climate Change (Houghton and others 2001) from General Circulation Models (GCMs) produced by the Hadley Centre (HadCM3GGa1) (Gordon and others 2000) and

the Canadian Centre for Climate Modeling and Analysis (CGCM2_ghga) (Flato and Boer 2001). These two models are generally well respected, and averages of their predictions should provide an illustration of the potential effects of global warming.

Vegetation Data

Species were selected for this analysis based on their small geographic range and the availability of point location data to the authors. Species presence data were acquired from Barnes (1996) for Macfarlane's four-o'clock, Arno (1970), Khasa and others (2006), and Forest Inventory and Analysis, USDA Forest Service (FIA) database for subalpine larch, and unpublished field data from Forest Service RMRS, Moscow Forestry Sciences Laboratory, for smooth Arizona cypress and Paiute cypress (see Rehfeldt 1997). The FIA plot data were used to identify locations where the species did not occur. Their database was developed from a systematic sampling of woody vegetation permanent plots on forested and nonforested lands (Alerich and others 2004, Bechtold and Patterson 2005) within the United States. In accordance with FIA proprietary restrictions, plot locations are not available for publication. However, we were given access to their database to generate climate estimates for each plot directly from uncompromised field data. The resulting data sets include a tabulation of the presence-absence of species at approximately 117,000 locations.

Statistical Procedures

The Random Forests classification and regression tree package (Breiman 2001, Liaw and Wiener 2002, R Development Core Team 2004) was used to model species presence and absence. This tree-based method of regression uses a nonparametric approach and is resistant to overfitting, as multicolinearity and spatial correlation of residuals are not issues (Breiman 2001). Consequently, the algorithm was well suited for our analyses, which used variables among which intercorrelations could be pronounced.

An analysis data set was constructed for each species that initially included all predictor variables. Observations in this data set include all the observations with presence = yes weighted by a factor of 3. These observations made up

Table 2—Number of field plots in which each species was present, the number of locations contained within the 33-variable climatic envelope, the number of standard deviations for each climate variable in which the envelope was expanded, and the number of locations within the expanded envelope

| Species | Number of plots | | | |
	Present	Envelope	Standard deviations	Expanded envelope
Subalpine larch (*Larix lyallii*)	168	683	± 4.2	12,809
Smooth Arizona cypress (*Cupressus arizonica* ssp. *glabra*)	22	156	± 3.5	1,782
Paiute cypress (*Cupressus arizonica ssp. Nevadensis*)	49	537	± 11.6	3,811
Macfarlane's four-o'clock (*Mirabilis macfarlanei*)	27	107	± 3.0	1,910

40 percent of the total for a species (Table 2). The remaining observations (60 percent) of presence = no were selected by a stratified random sample of locations from two strata constructed using threshold values of the 33 predictor variables that define a climatic envelope for the species. The first stratum is the space formed by an expanded climatic envelope, where the expansion is defined by increasing the range for the threshold values of each climatic variable. The climate envelopes were expanded by factors large enough to produce about 20 times the number of locations sampled. The second stratum included locations outside the expanded envelope.

Regression analysis used 10 independent forests of 100 independent regression trees. Random Forests builds each tree using a separate boot-strap sample of the analysis data resulting in about 36 percent of the observations being used to compute classification error.

A set of regressions were run. The first regression used 33 climate predictors. Random Forest produces indices of variable importance (mean decrease in accuracy). The 12 least important variables were dropped after the first run. The regression procedure was then rerun nine more times with the remaining predictors, whereby the least important 1 to 3 predictors were dropped at each run until classification errors began to increase. The Random Forests run with the fewest variables selected prior to detecting an increase in classification error was considered the most parsimonious bioclimatic model for the species.

Mapping Procedure

Rehfeldt's climate surfaces (2006) and those updated to convey global warming were used to estimate the climate for nearly 5.9 million pixels (1 km^2 resolution) representing the terrestrial portion of the study area. The average altitude was made available from Globe (1999). The estimated climate and projected climates of each pixel were run down the 100 regression trees in the final set and the number of trees that predict the species is present and the number predicting absence were tabulated. A single-tree prediction is termed a vote. The votes were grouped into six categories: < 50, 50-60, 60-70, 70-80, 80-90, 90-100 percent. We consider any pixel in the first group as not having suitable climate for the species and define pixels in the other five categories as the species' realized climatic niche space. The fit of the mapped projections were assessed visually by comparing them with locations where the species were observed or Little's range maps (1971, 1976) that are available as digitized files (USGS 2005), or both.

Results

We found that reasonably parsimonious bioclimatic models are driven by either three or four climate variables (Table 3). Overall out-of-bag classification errors from fitting of the Random Forests algorithm ranged from 1.39 percent for Macfarlane's four-o'clock to 2.2 percent for subalpine larch. The models predicted species occurrence where species were known to occur with perfect accuracy (0 errors of omission); the error therefore is due to commission,

Table 3—Statistical output from bioclimatic models: classification errors from the confusion matrix, and the important predictors according to mean decrease in accuracy; variable acronyms are keyed to Table 1

Species	Classification errors (%)			Important variables
	Omission[a]	Commission[b]	Over all[c]	
Subalpine larch (*Larix lyallii*)	0	3.94	2.2	GSP × TDIFF, MAP × MTCM, MMIN
Smooth Arizona cypress (*Cupressus arizonica ssp. glabra*)	0	6.37	3.55	PRATIO, GSP × TDIFF, TDIFF
Paiute cypress (*Cupressus arizonica ssp. Nevadensis*)	0	3.09	1.73	MMIN, MAP × DD5, MTCM × GSP, PRATIO
Macfarlane's four-o'clock (*Mirabilis macfarlanei*)	0	2.55	1.39	MINDD0, MAP × TDIFF, TDIFF

[a] Errors of omission (species presence = yes but model prediction presence = no).
[b] Error of commission (species presence = no but model prediction = yes).
[c] Combined overall error from omission and commission statistics.

predicting the presence of a species when, in fact, it was absent. The use of digital elevation model (DEM) and GIS to make predictions on a 1-km grid introduces additional error and uncertainty. The use of Little's range maps to validate the models' mapped projections also introduced the possibility of error. Range maps are known to contain errors (see Rehfeldt and others 2006) but perhaps more importantly, they only provide two-dimensional limits of the species distribution and do not indicate where species actually occur within the species boundaries. Even so, a visual comparison between these range maps and our predictions can be used for general validation of the models.

Subalpine Larch

A visual comparison of Little's range map shows that the projection of the bioclimatic model overestimates the distribution of subalpine larch in the western portion of southwestern British Columbia and portions of the central Rocky Mountains (Figure 2A). Error associated with Canadian projections may have been exacerbated by the lack of species presence-absence data for that region. Nonetheless, the model does an excellent job of predicting the United States distribution. Here the majority of the pixels receiving the greatest proportion of votes occur well within the range limits.

Mapped projections for the effect of global warming on distribution of subalpine larch's realized climatic niche space in decades 2030 (Figure 2B), 2060 (Figure 2C) and

2090 (Figure 2D) indicate a rapid decline in distribution (Table 4). For area studied, about 62 percent of the contemporary realized climatic niche space is projected to disappear by the end of decade 2030 (Table 4). Only about one-third of the remaining proportion is expected to occur in pixels suitable for the species today. By decade 2030, the mean elevation of the realized climatic niche space is projected to occur 100 m higher in altitude, and the minimum elevation is expected to rise almost 300 m by the end of the century. Also, by the end of the century, only 3 percent of the contemporary realized climatic niche space is expected to remain and should be relegated to a few high mountain peaks in south-central Idaho, southwestern Montana, the northern Cascade Range in Washington and to the Grand Teton Range in northwestern Wyoming. Note that suitable climate space in the Grand Teton Range is projected to first occur in decade 2030 and persist in decades 2060 and 2090.

Smooth Arizona Cypress and Paiute Cypress

The predicted contemporary realized climatic niche space for smooth Arizona cypress and Paiute cypress better described actual distributions than Little's range map (Figures 3A, 4A). Although a few populations were not mapped in the realized climatic niche, we suspect that this omission was due to either a mapping resolution that was too coarse or to field locations that were not accurate enough.

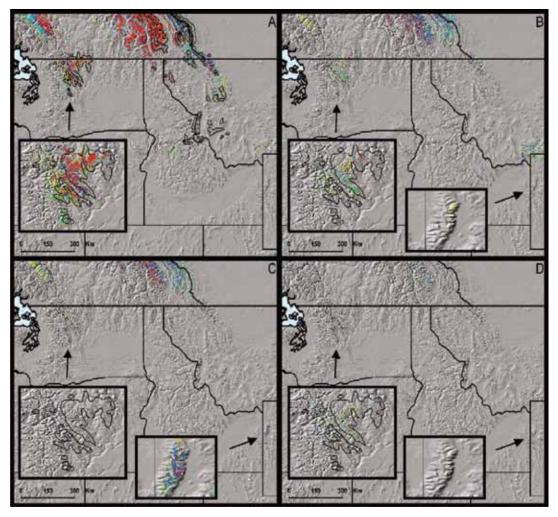In response to global warming under the IS92a scenario, the realized climatic niche space of Arizona smooth

Figure 2—Modeled realized climatic niche for subalpine larch (*Larix lyallii*) and its predicted response to climate change for decades beginning in (B) 2030, (C) 2060, and (D) 2090. Areas in (A) outlined in black depict species boundaries defined by Little (1971). Colors code the proportions of votes received by a pixel in favor of being within the climate profile: no color 0%–50%; yellow 50%–60%; green 60%–70%; light blue 70%–80%; dark blue 80%–90%; and red 90%–100%.

cypress should shift about 200 to 350 km northwest of its contemporary location (Figures 3B, 3C, 3D). The area occupied should increase by about 1.5 and 2 times its contemporary size in decades 2030 and 2060, respectively (Table 4). In decade 2090, the area decreases to 1.2 times the contemporary size as the distribution shifts to northern Nevada and southwestern Colorado. In all three future decades, the contemporary realized climatic niche space is expected to be prominent in valleys where the Arizona, Nevada, and Utah borders meet. This includes the Virgin Mountains in Nevada, an area where naturalized populations of the subspecies have been observed (Charlet 1996).

Only 14 percent of the climate space is expected to remain in place in its contemporary location through the decade of 2030, and none is to remain in place for decades 2060 and 2090. By the end of the century, average elevation is projected to increase 611 m.

By decade 2030, the Paiute cypress realized climatic niche space will lie outside its contemporary distribution. The realized climatic niche space is projected to shift nearly 40 km to the east along the southeastern slopes of the Sierra Nevada (Figure 4B). Overall, the area of its distribution should shrink about 86 percent (Table 4). Altitudes, however, should increase by about 100 m. The realized
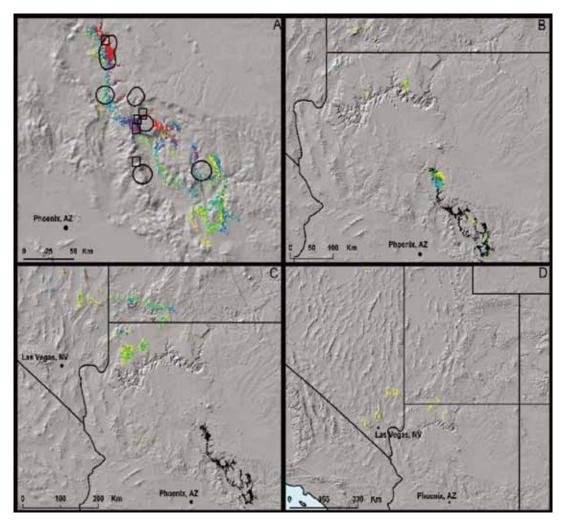
Figure 3—(A) Modeled realized climatic niche for smooth Arizona cypress (*Cupressus arizonica* ssp. *glabra*) and its predicted response to climate change for decades beginning in (B) 2030, (C) 2060, and (D) 2090. Areas in (A) outlined in black depict species boundaries defined by Little (1971) and squares indicate sites known to be inhabited. Colors code the proportions of votes received by a pixel in favor of being within the climate profile: no color 0%–50%; yellow 50%–60%; green 60%–70%; light blue 70%–80%; dark blue 80%–90%; and red 90%–100%.

Table 4—Projected change in area of species realized climatic niche space in response to climate change during three decades, and, in parenthesis, the percentage realized climatic niche space expected to match their contemporary distribution

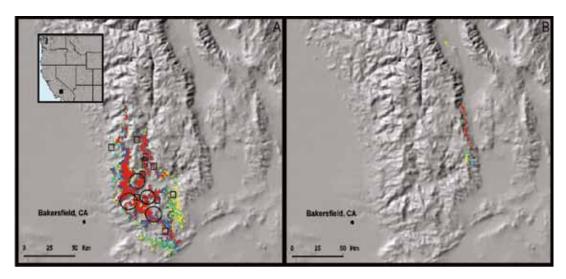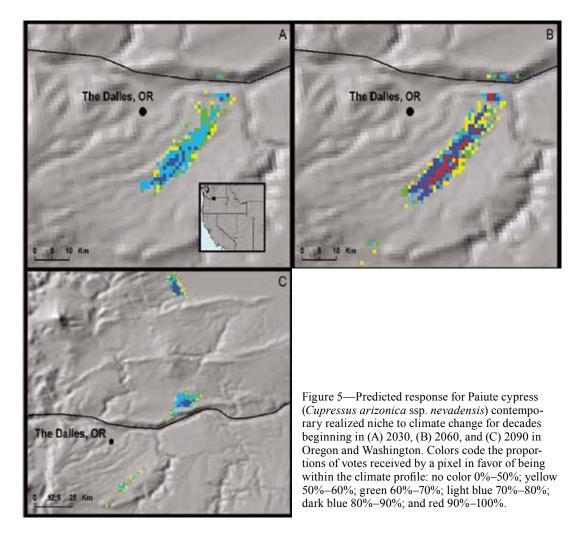|	Year of projected change		
Species	**2030**	**2060**	**2090**
	Percent		
Subalpine larch (*Larix lyallii*)	-62 (26)	-76 (21)	-97 (3)
Smooth Arizona cypress (*Cupressus arizonica* ssp. *glabra*)	+158 (14)	+210 (0)	+115.7 (0)
Paiute cypress (*Cupressus arizonica* ssp. *nevadensis*)	-86 (0)	-91 (0)	-95 (0)
Macfarlane's four-o'clock (*Mirabilis macfarlanei*)	+807 (23)	+1912 (2)	+3343 (0)

Figure 4—(A) Modeled realized climatic niche for Paiute cypress (*Cupressus arizonica* ssp. *nevadensis*) and its predicted response to climate change for the decade beginning in (B) 2030, in California. Areas in (A) outlined in black depict species boundaries defined by Little (1971) and squares indicate sites known to be inhabited. Colors code the proportions of votes received by a pixel in favor of being within the climate profile: no color 0%–50%; yellow 50%–60%; green 60%–70%; light blue 70%–80%; dark blue 80%–90%; and red 90%–100%.

Figure 5—Predicted response for Paiute cypress (*Cupressus arizonica* ssp. *nevadensis*) contemporary realized niche to climate change for decades beginning in (A) 2030, (B) 2060, and (C) 2090 in Oregon and Washington. Colors code the proportions of votes received by a pixel in favor of being within the climate profile: no color 0%–50%; yellow 50%–60%; green 60%–70%; light blue 70%–80%; dark blue 80%–90%; and red 90%–100%.
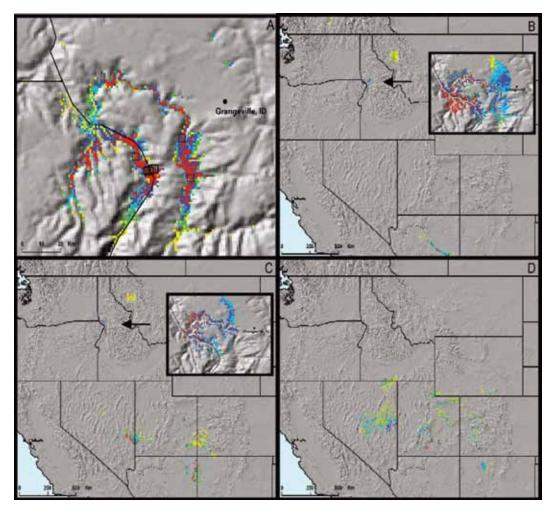
Figure 6—(A) Modeled realized climatic niche for Macfarlane's four-o'clock (*Mirabilis macfarlanei*) and its predicted response to climate change for decades beginning in (B) 2030, (C) 2060, and (D) 2090. Squares in (A) indicate sites known to be inhabited. Colors code the proportions of votes received by a pixel in favor of being within the climate profile: no color 0%–50%; yellow 50%–60%; green 60%–70%; light blue 70%–80%; dark blue 80%–90%; and red 90%–100%.

climatic niche space should also appear nearly 1100 km to the north near The Dalles, Oregon, by the decade of 2030 (Figure 5A) where it is projected to persist throughout the century (Figures 5B, 5C). In fact, by 2060, the realized climatic niche space of this subspecies occurs exclusively in Oregon and should occupy an area less than 90 percent of its contemporary distribution. The mean elevation for these new sites in Oregon and Washington are about 200 to 300 m lower in elevation than the contemporary distribution.

Macfarlane's Four-O'clock

Through most of the century, climate suitable to Macfarlane's four-o'clock should remain near its contemporary location (Figures 6B, 6C). The realized climatic niche, however, is expected to climb the canyon's slopes along the Snake, Imnaha, and lower Salmon Rivers in decade 2030 (Figure 6B). In the decade of 2060, it should occur in these canyons at altitudes nearly 142 m higher than today (Figure 6C), but, by the end of the century, it should disappear in these particular canyons but reappear within the Snake River watershed in southern Idaho (Figure 6D). Elsewhere in the West, however, the profile of this species should expand rapidly and increase in altitude (Table 4, Figures 6B, 6C, 6D), increasing by a factor of 8, 19, and 34 times the contemporary realized climatic niche space in decades 2030, 2060, and 2090, respectively (Figure 6, Table 4).

Discussion

Our bioclimatic models predict the occurrence of species and attempt to identify suitable habitats. As shown, these models can also be updated with predicted future climates to project the redistribution of species' contemporary realized climatic niche. The validity of these projections are dependent on the accuracy of the bioclimatic models as well as how closely the predicted future climate using the IS92a scenario from the Canadian and Hadley GCMs matches the actual climate of the future.

The climate variables identified as important for predicting species occurrence differed among the species and subspecies analyzed. These differences suggest that they will respond uniquely to climate change. Despite these differences, it appears that their small geographic distributions predispose them to a shared threat of more rapid onset of climatic disequilibrium in comparison with species occupying large-scale distributions. Analyses of species occupying larger scale distributions tend to report greater areas of unaffected distribution and show less separation between existing distributions and the geographic occurrence of suitable climate (Bakkenes and others 2002, Iverson and Prasad 1998, Rehfeldt and others 2006). The extent of disequilibrium predicted by these studies may, however, be an underestimate owing to the potential for maladaptation to climate within species (Rehfeldt 2004, Rehfeldt and others 1999, Rice and Emery 2003).

As natural systems attempt to regain equilibrium with the novel distribution of climates, distributions will shift. Redistribution rates, however, will be influenced by genetic structure, autecology, life history, reproductive capabilities, and ecophysiology (see, for instance, Ackerly 2003). Consequently, all of these factors should be taken into consideration in interpreting projections from bioclimatic models. The physiology of subalpine larch, for instance, appears to be consistent with the climatic profile described by our models. Its realized niche seems dependent on a superior hardiness and resistance to winter desiccation (Burns and Honkala 1990). Subalpine larch, however, does not compete well with other evergreen species (Arno and Hammerly 1984). Hence, the continued warming trend will likely eliminate subalpine larches from the Western United States through competitive exclusion. Common garden studies with smooth Arizona cypress and Paiute cypress by Rehfeldt (1997) revealed genetic variability equivalent to that conveyed by broadly distributed conifer species. This indicates populations within the species may only be adapted to a portion of its present or future realized climate space. In addition, both smooth Arizona cypress and Paiute cypress are fire dependent. Fire management practices may have had a substantial influence on limiting their distribution (Marshall 1963). Consequently, for these subspecies of *Cupressus arizonica*, our estimate of the realized climatic niche space may underestimate the breadth of climatically suitable area. Finally, Macfarlane's small distribution is attributed to reduced compatibility between its floral biology and pollinators (Barnes 1996). The rates that the range may expand would depend, therefore, on the presence of compatible pollinators.

Bioclimatic models represent tools that can be used to assist decisionmakers in managing threats associated with global warming. These models can be updated with predicted future climate to identify locations where suitable climate should occurs. These predictions can be used by managers to assist the natural processes by transferring species to the future location of climate suitable for their survival. Ideally the application of bioclimate models for this purpose should use multiple general circulation models and climate change scenarios to reduce uncertainty associated with predicted future climate (see Rehfeldt and Jaquish 2010). To be sure, additional modeling is needed that integrates a general understanding of climate, climate change, and plant-climate relationships. Interpretation of results by resource managers also requires integration of additional layers of information such as land use (see Hannah 2006).

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