

EMPIRICAL ANALYSES OF PLANT-CLIMATE RELATIONSHIPS FOR THE WESTERN UNITED STATES

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The Random Forests multiple-regression tree was used to model climate profiles of 25 biotic communities of the western United States and nine of their constituent species. Analyses of the communities were based on a gridded sample of ca. 140,000 points, while those for the species used presence-absence data from ca. 120,000 locations. Independent variables included 35 simple expressions of temperature and precipitation and their interactions. Classification errors for community models averaged 19%, but the errors were reduced by half when adjusted for misalignment between geographic data sets. Errors of omission for species-specific models approached 0, while errors of commission were less than 9%. Mapped climate profiles of the species were in solid agreement with range maps. Climate variables of most importance for segregating the communities were those that generally differentiate maritime, continental, and monsoonal climates, while those of importance for predicting the occurrence of species varied among species but consistently implicated the periodicity of precipitation and temperature-precipitation interactions. Projections showed that unmitigated global warming should increase the abundance primarily of the montane forest and grassland community profiles at the expense largely of those of the subalpine, alpine, and tundra communities but also that of the arid woodlands. However, the climate of 47% of the future landscape may be extramural to contemporary community profiles. Effects projected on the spatial distribution of species-specific profiles were varied, but shifts in space and altitude would be extensive. Species-specific projections were not necessarily consistent with those of their communities.

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

Introduction

Analyses of plant-climate relationships have proliferated as warming of the global climate has become indisputable (e.g., Thomas et al. 2001; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). While recent studies tend to be centered on the effects of global warming, vegetation-climate relationships have been used to address a diverse range of topics that include deciphering paleoecologic records (e.g., Monserud et al. 1998), predicting extinction rates in natural populations (e.g., Thomas et al. 2004), describing intra-specific genetic responses (Rehfeldt et al. 1999, 2002), and estimating the effect of climate variability on forest productivity (Loustau et al. 2005). Although considerable debate has taken place on the relative merits of mechanistic (e.g., Cumming and Burton 1996; Chuine and Beaubien 2001; Chuine et al. 2004) and niche-related (e.g., Iverson and Prasad 1998; Bakkenes et al. 2002) modeling, most analyses are correlative, largely because the complex of interacting factors governing physiological responses to climate is only beginning to be understood (Pearson and Dawson 2003). We use correlative models in an empirical evaluation of plant-climate relationships.

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Correlative approaches to bioclimatic modeling first employed the climatic envelope of Box et al. (1993, 1999), a Hutchinsonian hypervolume. With dimensions determined by climatic limits of distribution, the envelope encompasses the realized climate niche. Although it is used to outline the distribution of biomes (Prentice et al. 1992; Monserud et al. 1993), communities (Berry et al. 2002), species (Pearson and Dawson 2003), or populations (Tchebakova et al. 2005), the envelope generally overestimates the realized niche (Rehfeldt 2004), largely because distributions are controlled by interactions of variables that may not be intuitively obvious (Stephenson 1998). Overestimating the realized niche creates bias in the model that often is assumed to reflect potential niche space rather than modeling errors. Perhaps the greatest weakness of the envelope approach, therefore, is that the statistical fit of the models is difficult to judge. Like Iverson and Prasad (1998), Bakkenes et al. (2002), and Thuiller et al. (2003), we circumvent many of the problems associated with the climate envelope by using regression models to predict occurrence from presence-absence data.

Statistical approaches to modeling vegetation have been discussed elsewhere (e.g., Guisan and Zimmermann 2000; Moisen and Frescino 2002; Thuiller 2003; Thuiller et al. 2003). Although no consensus is available, a recurring concern involves the multicollinearity (Beaumont et al. 2005) of predictor variables, which leads toward overparameterization,

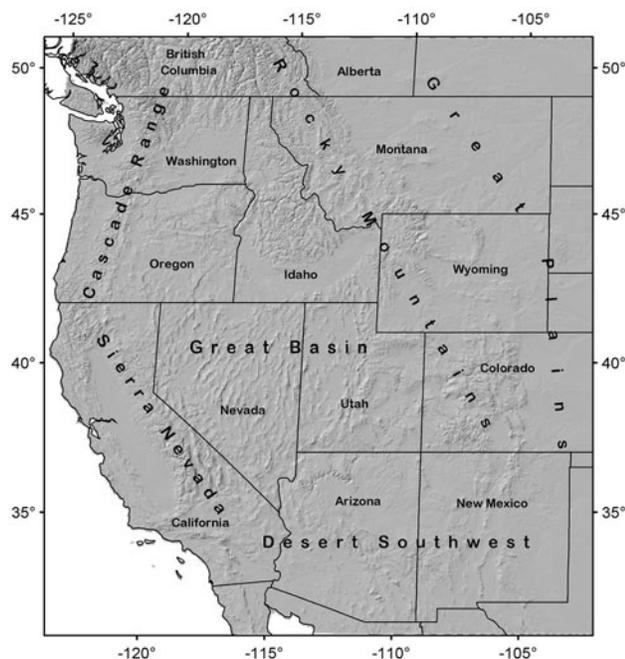


Fig. 1 Relief map for region of study naming geographic locations referenced in the text.

overfitting, and, ultimately, predictions of a precision lower than that suggested by the regression statistics (Graham 2003). To avoid overfitting, correlative modelers ordinarily reduce the array of potential predictors by incorporating independent variables of purported physiological relevance, labeled “biophysical variables.” The list includes water balance (Stephenson 1990, 1998; Berry et al. 2002); annual runoff, actual and potential evapotranspiration, and moisture indices (Bakkenes et al. 2002); soil temperatures (McKenzie et al. 2003); humidity index (Thuiller 2003); and radiation (Beaumont et al. 2005). By using a multivariate regression tree, Random Forests (Breiman 2001), that is immune to overfitting, we avoid issues concerning physiological relevance and instead concentrate on summer and winter temperatures, measures of available moisture, length of the frost-free season, and the interactions of temperature and precipitation, the variables long regarded as the primary factors controlling plant distributions (Holdridge 1947).

Spatial resolution of bioclimatic models is often a compromise between specificity and breadth but ultimately is dependent on the resolution of the environmental data (Thuiller et al. 2003). While coarse grids may suffice for global modeling, grids of 25 km (Shafer et al. 2001; Thompson et al. 2002) or 50 km (Bakkenes et al. 2002; Berry et al. 2002; Thuiller 2003) or county subdivisions (Iverson and Prasad 1998) are far too coarse for an ecological assessment in the mountainous West of the United States. Likewise, the grid of 180 m used by Thuiller et al. (2003) for a province of Spain is too fine for large regions. We employ a climate model that provides point estimates and a map on a grid of 1 km, a resolution useful for land management.

Our goals are (1) to develop bioclimatic models that predict the occurrence of plant communities and some of their

constituent species and (2) to project contemporary climate profiles into future climate space. We combine an immense volume of presence-absence data, powerful statistical models, and a relatively fine spatial scale to assess relationships across a broad and physiographically diverse region. The work of Iverson and Prasad (1998) is used as a foundation, but our assessment of plant-climate relationships is of a scope and thoroughness not yet attempted. By considering plant communities and some of their constituent species, we initiate a comparison of holistic and individualistic predictions. Our approach improves on that of others working in the same geographic region (Shafer et al. 2001; Thompson et al. 2002), who relied on range maps to delimit four-variate climate envelopes on 25-km grids and presented results not subject to statistical evaluation.

Methods

The analyses are limited to the western United States and southwestern Canada (fig. 1), lat. 31°–51°N, long. 102°–125°W, the region supported by the climate surfaces of Rehfeldt (2006).

Climate Estimates

The climate model of Rehfeldt (2006) uses the thin plate splines of Hutchinson (1991, 2000) to produce climate surfaces from normalized (1961–1990) monthly values of total precipitation and average, maximum, and minimum temperature from ca. 3000 geographically disparate weather stations. Hutchinson’s software can be used to predict (a) the

Table 1
Climate Variables Used as Independent Variables
in Regression Analyses

Acronym	Definition
MAT	Mean annual temperature
MTCM	Mean 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–September
TDIFF	Summer-winter temperature differential, MTWM – MTCM
DD5	Degree-days >5°C
DD0	Degree-days <0°C
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
GSDD5	Degree-days >5°C accumulating within 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

Note. Interactions used in the analyses are MAP × DD5, MAP × MTCM, GSP × MTCM, GSP × DD5, DD5 × MTCM, MAP × TDIFF, GSP × TDIFF, MTCM/MAP, MTCM/GSP, DD5/GSP, AMI × MTCM, SMI × MTCM, TDIFF/MAP, TDIFF/GSP, PRATIO × MTCM, and PRATIO × DD5.

Table 2

Biotic Communities of Brown et al. (1998), Their Numeric Codes, the Total Number of Data Points and the Number Used for Analysis, and the Actual and Adjusted Proportions of Observations Misclassified by the Random Forests Multiple-Regression Tree

Biotic community	Code	Data points		Proportion misclassified	
		Total	Sample ^a	Actual ^b	Adjusted ^c
Sitka coastal conifer forest	2	247	247	0.29	0.22
Rocky Mountain subalpine conifer forest	3	7824	5133	0.33	0.14
Rocky Mountain and Great Basin alpine tundra	4	724	724	0.73	0.45
Plains grassland	5	41,588	10,369	0.05	0.02
Rocky Mountain montane conifer forest	6	19,066	7655	0.28	0.11
Cascade-Sierran montane conifer forest	7	6657	4339	0.20	0.11
Oregonian coastal conifer forest	8	5445	4375	0.07	0.06
Cascade-Sierran subalpine conifer forest	9	2432	2431	0.22	0.16
Great Basin shrub-grassland	10	23,318	8195	0.17	0.05
Cascade-Sierran alpine tundra	11	194	194	0.79	0.55
Oregonian deciduous and evergreen forests	12	1530	1530	0.23	0.16
Great Basin conifer woodland	13	12,155	6048	0.35	0.17
Great Basin desertscrub	14	13,871	6889	0.19	0.08
Great Basin montane scrub	15	1195	1195	0.42	0.29
California evergreen forest and woodland	16	2480	2480	0.17	0.10
California chaparral	17	1221	1221	0.32	0.22
California valley grassland	18	2788	2788	0.08	0.12
Mojave desertscrub	19	4915	3442	0.07	0.05
Semidesert grassland	20	4964	3428	0.20	0.05
Southwestern (Arizona) interior chaparral	21	409	409	0.43	0.40
Sonoran desertscrub	22	6013	4183	0.05	0.02
California coastal scrub	23	794	794	0.06	0.08
Chihuahuan desertscrub	24	2795	2795	0.11	0.03
Madrean evergreen forest and woodland	25	461	461	0.53	0.18
Madrean montane conifer forest	26	114	114	0.33	...

^a Total observations in sample = 81,439 (ca. 50% of total data points).

^b Overall classification error = 19%.

^c Classification error after adjusting for misaligned geographic data = 9.4%.

climate at point locations, identified by latitude, longitude, and elevation, and therefore (*b*) the climate along gridded surfaces. Our analyses employ 35 variables, many of which are simple interactions of temperature and precipitation (table 1).

To update the climate surfaces for the effects of global warming, monthly output for the IS92a scenario (1%/yr increase in greenhouse gases after 1990) of the International Panel on Climate Change (IPCC 2001) was summarized from general circulation models (GCMs) produced by the Hadley Centre (HadCM3GGa1; Gordon et al. 2000) and the Canadian Centre for Climate Modeling and Analysis (CGCM2_ggga; Flato and Boer 2001) for the region of study. The GCM output was used to calculate the monthly change in climate between the normalization period and the decades beginning in 2030, 2060, and 2090 for each weather station used in developing the climate surfaces. Downscaling from the relatively coarse grids of the GCMs to the point locations of the weather stations was accomplished by using a weighted average of the monthly change in climate calculated for the GCM cell centers lying within 500 km of a station. The inverse of the distance from the station to the cell center was used for weighting. Because the two GCMs use different grid sizes, weighted means were calculated from the output of each GCM and were averaged to estimate the change in climate of each weather station. The splines were then refitted to calculate anew the variables of table 1.

Vegetation Data

Plant associations. Brown et al. (1998) have produced a hierarchical classification of the vegetation of North America that uses climate as a primary consideration. The western United States includes, for instance, at the second level of the hierarchy, four formations (tundra, forests and woodlands, scrublands, and deserts) that segregate along gradients of moisture stress, and at the third level, four climatic subdivisions (Arctic-alpine, boreal, cold temperate, and warm temperate). Biotic communities appear at the fourth level as the recurring associations recognized by indicator species. Twenty-five terrestrial biotic communities occur within our geographic window (table 2). A digitized outline of the spatial distribution of the communities was conveniently provided to us.

To prepare a data set for statistical analyses, a series of points was located systematically across the geographic window at intervals of 0.05° in latitude and longitude (a grid of ca. 6 km), producing a data set with ca. 164,000 terrestrial points. The sampling interval of 0.05° was a compromise between finer grids that would have been computationally impractical and coarser grids that would have increased the risk of not sampling small polygons. Altitudes were estimated for each point from the digital elevation model of GLOBE (GLOBE Task Team 1999), climate variables (table 1) were generated for each point from the climate surfaces, and the

Table 3

Allocation of Nine Species to Biotic Communities, Number of Field Plots in Which Each Species Was Present, the Number Contained within the 35-Variable Climatic Envelope, and the Number within the Envelope Expanded by ± 0.5 SD in All Dimensions

Species	Biotic community ^a	Number of plots		
		Present	Envelope	Expanded envelope
<i>Pseudotsuga menziesii</i>	6, 7, 8	20,171	96,087	103,142
<i>Pinus ponderosa</i>	6, 7	15,147	97,993	106,290
<i>Picea engelmannii</i>	3	5730	69,230	79,812
<i>Juniperus osteosperma</i>	13	4643	67,780	78,317
<i>Pinus edulis</i>	13	4544	52,194	62,648
<i>Larix occidentalis</i>	6, 7	4541	37,869	49,685
<i>Quercus gambelii</i>	6, 15	1942	37,600	53,127
<i>Carnegiea gigantea</i>	22	379	457	1541 ^b
<i>Pinus leiophylla</i>	25, 26	82	1141	2245 ^c

^a D. E. Brown, Botany Department, Arizona State University, Tempe, personal communication. Codes are defined in table 2.

^b Expanded by ± 10 SD in all dimensions.

^c Expanded by ± 1.5 SD in all dimensions.

biotic community expected at each grid point was obtained by interfacing the grid with the digitized communities.

Because the grid was systematic, the number of data points obtained for each community was proportional to the size of the community (table 2). One rare community, the Madrean conifer forest (no. 26), in fact, was represented initially by only six data points. To provide a suitable number of observations for analyses, these six were augmented by 108 point locations where G. E. Rehfeldt had obtained samples for research on the Madrean pines (Rehfeldt 1999). Data points for all other communities were obtained solely from the systematic grid.

Species. The analyses dealt with nine species chosen for their spatially disparate distributions and for their representation across a broad spectrum of the biotic communities (table 3): *Pseudotsuga menziesii*, *Pinus ponderosa*, *Larix occidentalis*, *Juniperus osteosperma*, *Pinus edulis*, *Quercus gambelii*, *Picea engelmannii*, *Pinus leiophylla*, and *Carnegiea gigantea*. All are woody plants except *C. gigantea*, the giant saguaro. The woody plants are common conifers of western forests except for *P. leiophylla*, which reaches its northern limit of a broad geographical distribution in the mountain islands of the desert Southwest. As our work progressed, it became obvious that one of these species, *J. osteosperma*, had been confused with its congeneric cohorts, *Juniperus scopulorum* and *Juniperus monosperma*. Analyses of *J. osteosperma* nonetheless are presented to illustrate the sensitivity of the approach to data errors.

The primary source of data for all species except *C. gigantea* was Forest Inventory and Analysis, USDA Forest Service. This organization maintains permanent plots that systematically sample woody vegetation on forested and nonforested lands (Alerich et al. 2004; Bechtold and Patterson 2005). Ca. 117,000 of these plots occur within our geographic window. We used presence-absence data from the initial plot installation that corresponded most closely with the period of the climate normals. Although the geographic location of these

plots is proprietary, we were allowed to generate estimates of climate variables directly from the inventory databases. Our analyses, therefore, were performed without knowledge of the geographic location of the plots. Forest Inventory, however, makes available a geographic position of their plots for which latitude and longitude have been compromised somewhat. None of the compromised data were used for our analyses, but several are used in an illustration of the climate profile of *J. occidentalis*. Inventory data from Canada are also proprietary and were not available for our analyses.

For three species (*P. menziesii*, *P. ponderosa*, and *L. occidentalis*), inventory data were supplemented with individual tree locations held in the archives of tree improvement or research organizations (see "Acknowledgments"). With the one exception noted above, data points plotted in the figures are from these supplements. Data provided by the British Columbia Ministry of Forests for *L. occidentalis* were the only records that were available for Canada; all other results pertaining to Canada are extrapolations. The locations of sites inhabited by *C. gigantea* were obtained from the Sonoran plant atlas (Turner et al. 1995) supplemented with a survey conducted by us.

Statistical Procedures

Exploratory analyses were made to compare several different algorithms. Although not presented, the comparisons included canonical discriminant functions, climate envelope correlations, and the logistic form of a generalized linear function. The technique yielding the lowest errors and best verification was Random Forests (Breiman 2001), a multivariate regression tree. Tree-based methods are data-partitioning algorithms that recursively split observations into groups to produce a tree with branches and nodes (Hastie et al. 2001). According to Breiman, Random Forests is a combination of trees with each tree dependent on the values of a random vector of predictors sampled independently and with the same distribution for all trees within the forest. Because the generalization error converges to a limit as the number of trees in the forest becomes large, colinearity and overfitting are not issues.

Of the versions of Random Forests that are available, we used R (R Development Core Team 2004), which is based on the original programming of Leo Breiman and Adele Cutler (Liaw and Wiener 2002). The algorithm builds a set of independent regression trees from an input data set. The trees in their aggregate are called a forest. The process begins with the drawing of a bootstrap sample consisting of ca. 64% of the total number of observations. This sample is used to build a tree, while the omitted observations, 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. Predictions are made by running an observation down all trees in all forests. A "vote" concerning the classification of that observation is then available from each tree. Votes from all trees in all forests are collected and can be presented as (a) a proportion of the favorable votes to the total or (b) the plurality.

Breiman (2001) cautions that the Random Forests output tends to be mechanistically indecipherable. To date, no techniques exist for quantifying threshold values of those variables acting to separate classes. Instead, the algorithm available in R produces two measures for evaluating the importance of independent variables, the mean decrease in accuracy and the mean decrease in the Gini index of class purity. Both rely on an iterative process of randomly permuting (noising up) a predictor in the out-of-bag sample. The sample is then run down the appropriate tree. Importance is measured by the increase in error attributable to permuting. The process is repeated for all variables, trees, and forests. For the cases we considered, the two indices were so strongly related that the most important group of variables from one index ordinarily would include those from the other. Although correlative models are not a desirable means of assessing mechanistic interactions, these indices, as described in the R documentation, are useful in assorting a large number of predictor variables or culling superfluous variables (Breiman 2001).

Community profiles. Preliminary analyses showed, first, that out-of-bag errors were lowest when the number of observations within classes was reasonably balanced and, second, that our computing systems would operate on only 80,000 data points, approximately one-half of the total available. To meet these criteria, we designed a sample consisting of (a) 100% of the data points for the 14 smallest communities and (b) 25%–80% of the available points for the largest communities, with the proportional representation negatively related to the size of the community (table 2). The culling of ca. 50% of the observations addressed the limit of 80,000 and occurred at the expense of the largest communities. When compared to several other sampling schemes, this procedure was the best at reducing classification errors for the smallest communities while having little effect on classification errors for the largest. The mean decreases in accuracy and the Gini index were used jointly to cull superfluous predictors. The final analyses used 12 predictors to build one forest with 100 trees.

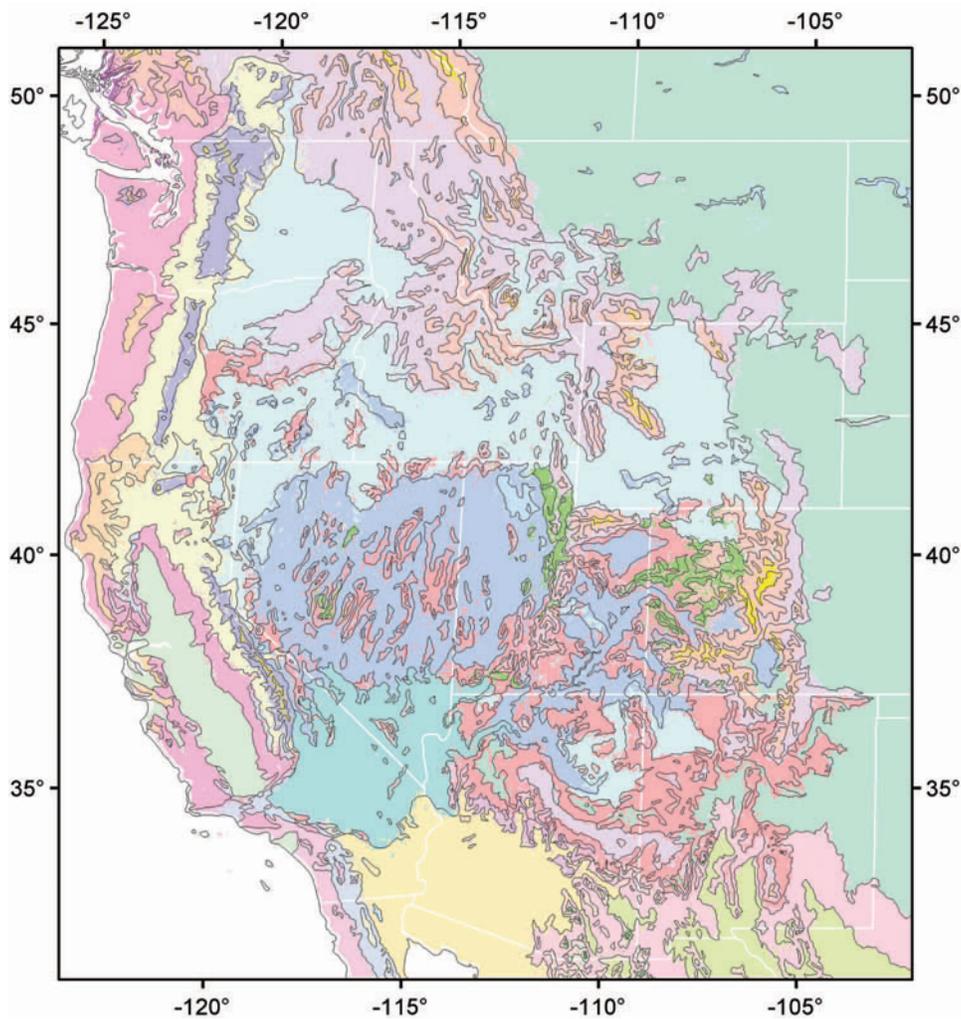


Fig. 2 Distribution of 25 biotic communities (black outlines) of Brown et al. (1998) superimposed on the distribution of communities (color) predicted from the Random Forests regression tree.

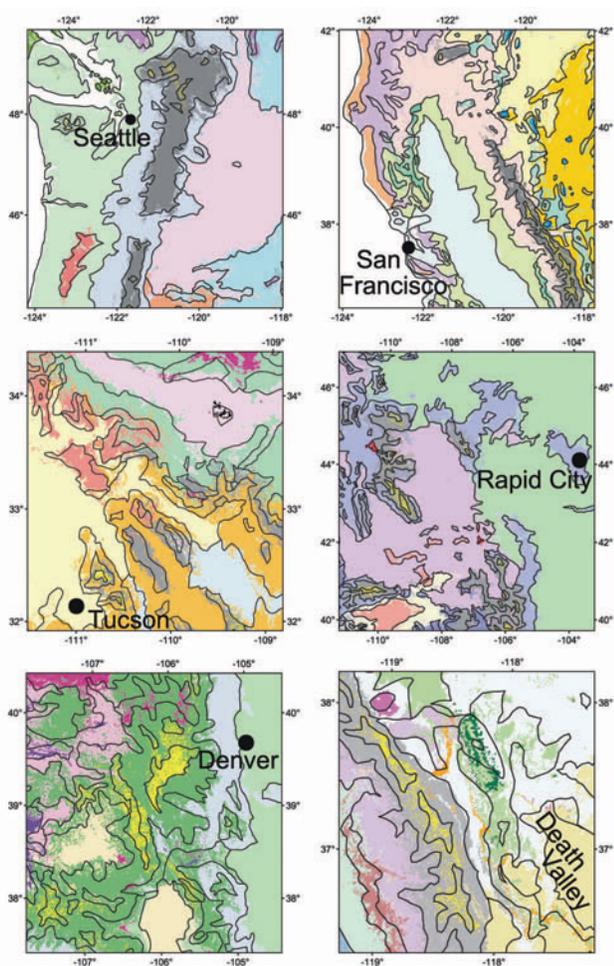


Fig. 3 Six panels from fig. 2 illustrating the fit of the model.

Species-specific climatic profiles. Preliminary analyses showed that (a) out-of-bag errors increased when the number of observations for which presence = yes was <40% of the total and (b) weighting the observations of presence = yes would drive errors of omission (presence = yes but prediction = no) toward 0 while reducing errors of commission (presence = no but prediction = yes) by 25%–50%. Our sampling protocol, therefore, was to (a) use 100% of the observations for which presence = yes, weighted by a factor of 2 or 3, and fix their proportion in the sample at 40%; (b) define an expanded climate envelope as a 35-variable hypervolume, the dimensions of which corresponded to the climatic limits of distribution of the species expanded by ± 0.5 SD; (c) select 50% of the sample from the observations of presence = no within the expanded envelope; and (d) select 10% of the sample from the observations outside the expanded envelope. This procedure thus used all available observations of presence = yes and concentrated the remainder of the sample in those climates for which separating presence from absence would be the most difficult. Weighting permitted a higher proportion of the total observations to be used for each forest.

This sampling protocol was followed without alteration for the seven widespread species for which the number of observations was abundant (table 3). For the most widespread species, *P. menziesii*, *P. ponderosa*, and *P. engelmannii*, a weight of 2 was used, but for *L. occidentalis*, *P. edulis*, *J. osteosperma*, and *Q. gambelii*, the weight was 3. Analyses consisted of five forests of 100 trees, using an independent sample for each forest.

To develop robust models for *P. leiophylla* and *C. gigantea* from few observations (table 3), we employed two-stage regression models. For the first stage, the Random Forests algorithm was used on a data set consisting of 40% observations of presence = yes and 60% observations of presence = no. The former group consisted of all available observations weighted by a factor of 3. The latter group consisted of a sample of observations from a 35-variable envelope expanded sufficiently to provide a pool of observations from which the sample drawn would represent ca. 10% of the total. To provide this pool, the envelope was expanded by ± 1.5 SD for *P. leiophylla* and ± 10 SD for *C. gigantea*. The second stage of the regression model consisted of the rule that the species would not occur outside the expanded envelope defined by those variables being used as predictors in the first stage. Analyses for both species consisted of 10 forests of 100 trees, using an independent sample of observations for each forest.

Because Forest Inventory did not record the vegetation at nonforested locations, ca. 3500 data points lying within the actual climate envelope of *C. gigantea* were excluded from the analysis. The species was assumed to be absent in the remainder of the Forest Inventory plots.

A visual assessment of the fit of the models was made by comparing predicted distributions of the climate profiles with the range maps of Little (1971, 1976) that are available as digitized files (USGS 2005). Regressions initially used a full complement of the 35 predictors. The indices of variable importance were then used to reduce the size of the data frame by ca. 50%. To further assure that the variables selected at random for each node would be of consequence, the mean decrease in accuracy was used in an iterative process that sequentially culled predictors to find a parsimonious model. The best model was identified when classification errors began increasing, usually with eight to 12 predictors. The most parsimonious model was used for the bioclimatic models, but for judging the relative importance of predictors, the iterations were continued until only three variables remained.

Mapping Predictions

Nearly 5.9 million pixels of 1-km resolution constitute the terrestrial portion of our geographic window. With the use of the digitized elevations of GLOBE (GLOBE Task Team 1999), the climate of each pixel could be estimated from the surfaces of Rehfeldt (2006). These estimates were then run down regression trees to predict vegetation.

For mapping biotic communities, the vegetation of a pixel was declared to be that of the community given the plurality of the 100 votes. Errors of estimate were calculated for all predictions that did not conform to digitized community boundaries. In summarizing these errors, we noticed that misclassification was related to poor alignment between the

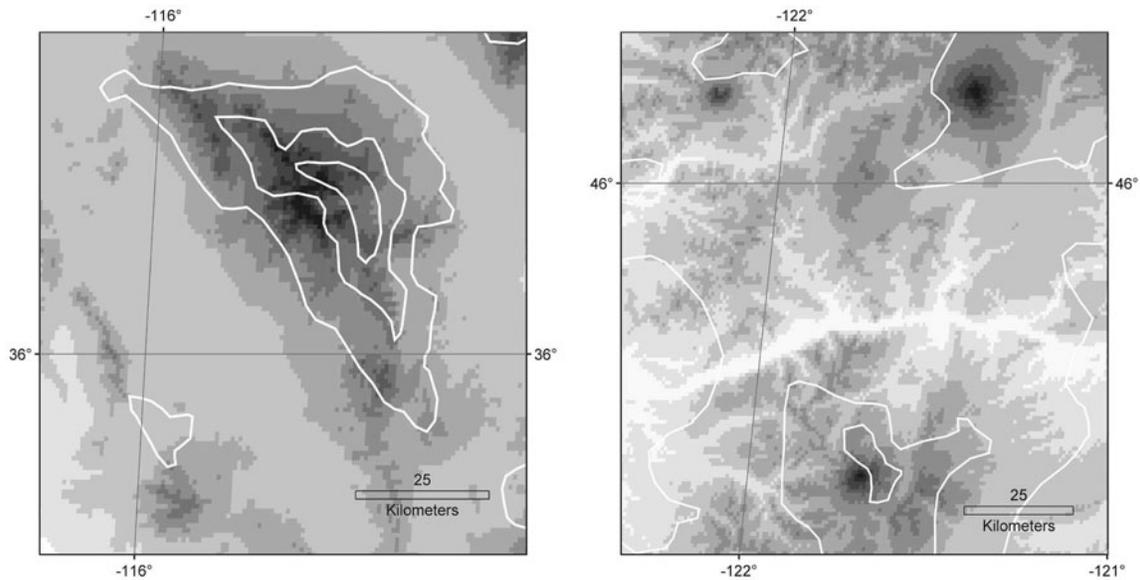


Fig. 4 Digitized outlines of biotic communities of Brown et al. (1998) superimposed on the digitized elevations of GLOBE (GLOBE Task Team 1999). Left, Mount Charleston, near Las Vegas, Nevada. Right, Columbia River Gorge and three volcanoes of the Cascade Range east of Portland, Oregon.

digitized community boundaries and the digital elevations on which climate estimates were based. Misclassification, therefore, was highest for those communities that tend to occur in small patches or irregular shapes. An adjustment to the classification error was made using a linear regression of classification error on the ratio of polygon perimeter to area, an index of the shape of the polygon.

In using the plurality of votes to map contemporary community profiles in future climatic space, each pixel was assorted into one of the 25 communities. This approach, however, could not provide for the contingency that future climates may be novel, having no analog among the contemporary communities. To consider this contingency, we examined the possibility that the projected climate of a pixel may be extramural to that of the community receiving the plurality of votes. To classify extramural climates, the climate envelope was used for truncation: if, for any single variable, the projected climate was outside the 35-variable envelope of the community receiving the voting plurality, the climate of the pixel was classified as extramural.

Bioclimatic profiles of the nine species were mapped using the votes cast in favor of a pixel being within the climate profile of a species. To illustrate the performance of the model along with the uncertainty in its predictions, votes were grouped into five classes, each consisting of 20% of the total. To predict occurrence, the climate of a pixel was declared suitable for a species when receiving a majority (>50%) of favorable votes.

Results

Fitting Climate Variables to the Occurrence of Biotic Communities

Maps (figs. 2, 3) comparing the predicted occurrence of communities with their digitized outline indicate that the fit

of the model was excellent. Yet classification errors averaged 19% (table 2). The errors, however, were dependent on the size of the polygons within which the communities occur. Errors were the largest for the small communities, averaging ca. 75% for the two tundra communities, 53% for the Madrean evergreen forest, and 45% for the Great Basin

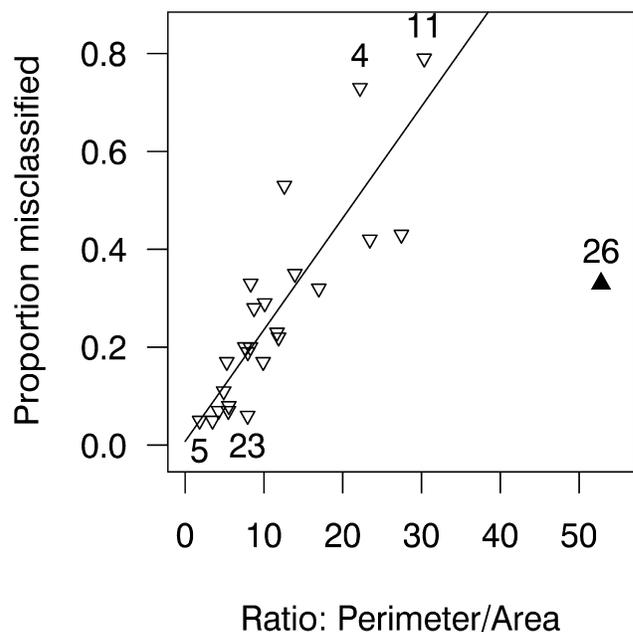


Fig. 5 Scatter of data points and linear regression of classification error on polygon shape, the ratio of the perimeter to the area of the average polygon. Numbers locate data points for selected biotic communities (see table 2). Community 26 was excluded from the regression.

Table 4

Statistical Output from Bioclimatic Models: Classification Errors from the Confusion Matrix and the Three Most Important Predictors According to the Mean Decrease in Accuracy

Species	Classification errors ^a		Important variables ^c
	Commission ^b (%)	Overall (%)	
<i>Pseudotsuga menziesii</i>	7.7	4.7	GSP, MAP × DD5, AMI × MTCM
<i>Pinus ponderosa</i>	7.0	4.3	MINDD0, AMI, TDIFF/GSP
<i>Picea engelmannii</i>	8.8	5.3	AMI, TDIFF/GSP, MAP × DD5
<i>Juniperus osteosperma</i>	6.3	3.8	FDAY, PRATIO, GSP × TDIFF
<i>Pinus edulis</i>	6.7	4.1	FDAY, GSP × TDIFF, PRATIO
<i>Larix occidentalis</i>	5.4	3.2	MMAX, PRATIO, MINDD0
<i>Quercus gambelii</i>	3.5	2.1	GSP × DD5, TDIFF/MAP, PRATIO × MTCM
<i>Carnegiea gigantea</i>	0.3	0.1	DD5 × MTCM, GSP × MTCM, PRATIO
<i>Pinus leiophylla</i>	6.5	3.8	GSP × DD5, PRATIO, MAP

^a Errors of omission (presence = yes, but prediction = no) are <0.5%.

^b Presence = no, but prediction = yes.

^c Variable acronyms are keyed to table 1.

montane scrub and the Southwestern interior chaparral, all of which occupy less than 0.1% of the geographic area. For large (e.g., Great Plains) or compact (e.g., Sonoran desert-scrub) communities, errors of classification were 5% (table 2).

This relationship between classification errors and the size of the community becomes obvious in figure 3. In the panels that include Rapid City and Denver, the separation of the largest community, the Great Plains, from those it borders is excellent. Boundaries between the predicted occurrences of communities also conformed well to the digitized map in regions where altitudinal segregation of communities was pronounced, from sea level to alpine tundra in the Seattle and San Francisco panels or from desert to subalpine in the Tucson panel. Differences between the observed and the predicted became most noticeable for communities that occur in patches or as stringers along altitudinal bands, as illustrated for the high elevations in the Denver panel and in the arid mountains of the Death Valley panel. This latter panel, for instance, consists of a patchwork of 12 communities, arranged largely along altitudinal transects from the Mojave desertscrub, the California chaparral, or the Great Basin desertscrub to the tundra of the White Mountains. As shown by this panel in particular and the figure as a whole, classification errors accumulate along community boundaries and are therefore related to polygon geometry.

Further inspection of the classification errors revealed misalignment between the digitized distribution of communities

and the digitized elevations, the latter of which were used for climate estimates. Misalignment of these files is apparent along the coastline in the Seattle and San Francisco panels of figure 3 but is even more obvious when the communities are superimposed on the digitized elevations. In figure 4 (left), the altitudinal zonation of communities is acentric to Mount Charleston, which rises out of the Mojave Desert near Las Vegas, Nevada, and the lesser peaks to the south. In figure 4 (right), the digitized boundaries are misaligned with three volcanoes in the Cascade Range east of Portland, Oregon; the boundaries are acentric to Mount St. Helens (upper left) and Mount Hood (bottom) and ignore Mount Adams (upper right) entirely. To be sure, the digitized community map is being used in a manner that demands greater accuracy than originally intended by its authors. Nonetheless, because community boundaries were used as the standard of excellence, any lack of synchronization between files will lead to misclassification, with the greatest errors associated with small patches of irregular shape. Error rates, therefore, should be largest for those communities with the largest amount of perimeter per unit area.

To test this hypothesis, classification errors were regressed on the ratio of the perimeter to the area of the community's average polygon. Because of the supplemental data that had been appended to the data points for community 26, data for this community were withheld from the regression. Not surprisingly, community 26 appeared as an outlier in an otherwise strong, linear relationship (fig. 5). The regression was statistically significant ($P < 0.05$), with an R^2 of 0.75. Because a circle is the polygon with the smallest ratio of perimeter to area and because the ratio increases as the radius of the circle decreases, a reasonable approximation of an error adjusted for polygon size and shape would be a value predicted by the regression in figure 5 for a circle with an area equal to that of the community's average polygon. By adjusting for misalignment of geographic data sets in this way, error rates would be reduced for all communities (table 2), but the reduction would be substantial for the tundra communities and the Madrean woodland, the communities that occur in the smallest patches. Recalculating overall error rates from the adjusted values and including the errors for community 26 would reduce the overall error to 9.4%, a reduction of about one-half.

Other sources of classification error include the broad ecotones that undoubtedly connect these communities. For example, all but six of the data points for the Madrean montane conifer community, number 26 (table 2), were plot locations that meshed precisely with the digitized elevations. Errors from misalignment of digitized data sets, therefore, would be small. Yet, classification errors were 33%. Of these, 65% involved the Madrean evergreen forest and woodland, a community ordinarily adjacent to the montane conifers in the altitudinal sequences of the desert Southwest. While ecotones are an obvious source of classification error, adjusting for them would have required a subjectivity we were not willing to pursue.

Although 12 variables were used to fit the model, only seven were of primary importance: PRATIO, TDIFF, PRATIO × MTCM, GSP × DD5, TDIFF/GSP, MAP × TDIFF, and MMAX (table 1). Of these, the first four were dominant.

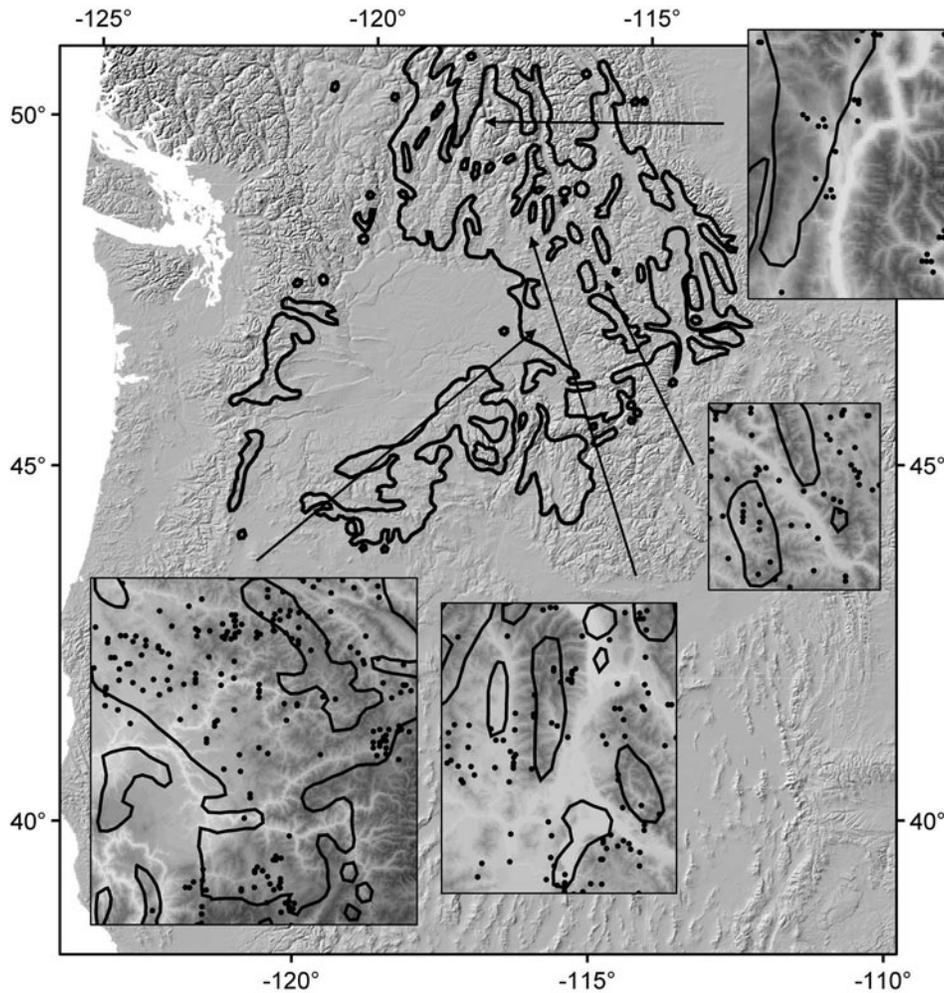


Fig. 6 Distribution of sites (dots) inhabited by *Larix occidentalis* in relation to the digitized range map (black outline; Little 1971).

Species-Specific Bioclimate Models

Of the species, the most abundant was *Pseudotsuga menziesii*, which had slightly more than 20,000 observations, and the least abundant was *Pinus leiophylla*, with only 82 observations (table 3). Because the sample drawn for each forest was based on a 40% contribution of the observations for which presence = yes, each regression tree produced for the former species, with presence = yes weighted twice, was based on ca. 100,000 observations, while those for the latter, with presence = yes weighted three times, was based on only 600. The table also shows that the climate envelope greatly overestimates the realized climatic niche. For *P. menziesii*, in fact, the 35-variable envelope contains ca. 96,000 of the observations, 82% of the total number of forested and nonforested lands within the Forest Inventory database.

Classification errors (table 4) from the fitting of the Random Forests algorithm ranged from 0.1% (*Carnegiea gigantea*) to 5.3% (*Picea engelmannii*). However, errors of omission, the most serious of the errors, were less than 0.15% (*Pinus ponderosa*), while errors of commission were less than 9%.

Using range maps for verification has limitations, largely because range maps include data errors that become apparent with modern mapping technology (fig. 6). Range maps also are two-dimensional representations of botanical limits of distribution that will encompass unsuitable sites, particularly with regard to altitude. Nonetheless, the range maps provide strong verification of the models (figs. 7–15). In the figures, the two darkest shades of green (>60% of the votes) tend to be centered well within the boundaries of the range map, while those with the lightest shades (20%–40%) are on the periphery. Insets are used in most of these figures for illustrating voting majorities and tend to reproduce the range maps. Each map is instructive.

Pseudotsuga menziesii. Correspondence between the predicted occurrence and the range map is nearly perfect (fig. 7), even for isolated populations (lower right inset). The inset at the upper right documents another instance (see fig. 6) of disharmony between the range map and the actual distribution.

Picea engelmannii. Correspondence between the predicted occurrence and the range map is strong (fig. 8), although

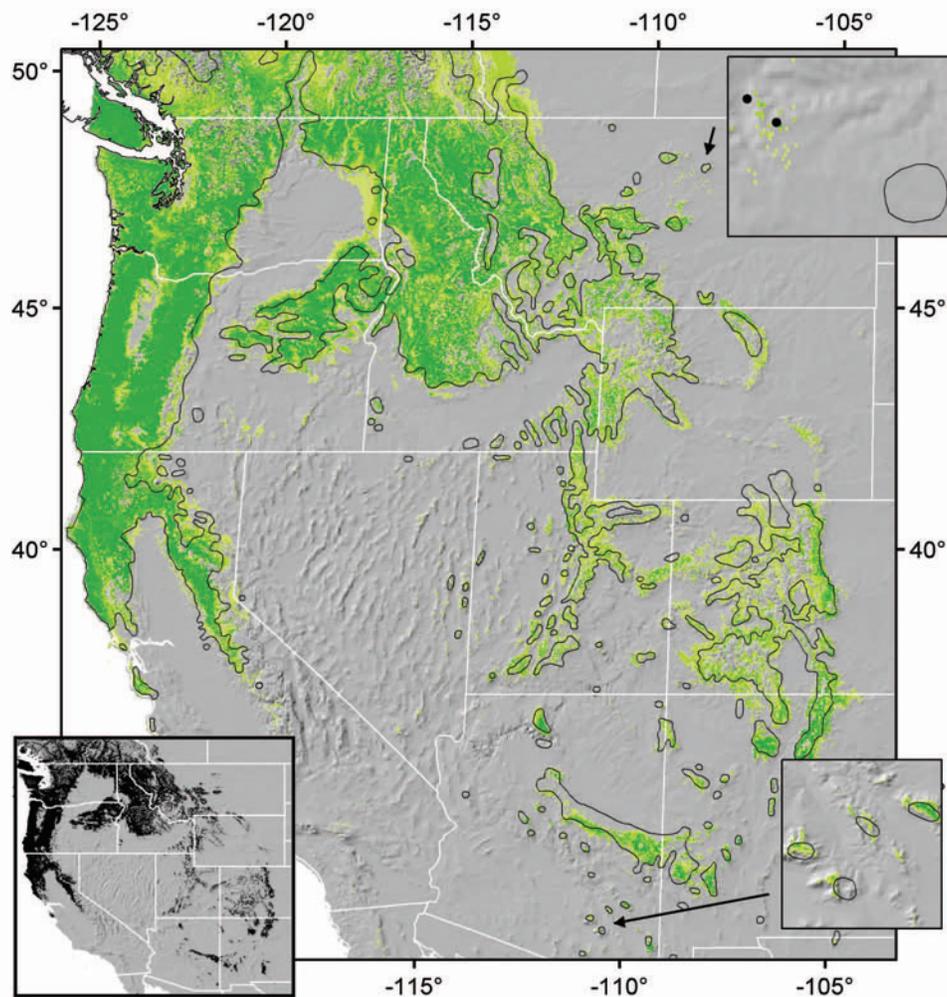


Fig. 7 Modeled bioclimate profile of *Pseudotsuga menziesii* overlaid with the digitized range map of Little (1971). Shades of green code the proportions of votes received by a pixel in favor of being within the climate profile: 0%–20%, no color; 20%–40%, lightest green; 40%–60%, light green; 60%–80% dark green; and 80%–100%, darkest green. Occurrence of the profile based on the majority of votes is in the lower left. Dots in the panel on upper right indicate sites known to be inhabited.

areas of disharmony are apparent, particularly in eastern Oregon, where the climate profile is predicted to occur outside of the boundaries of the range map. The model accurately predicted the occurrence of isolated populations such as those in the Chiricahua Mountains of southeast Arizona, the southernmost population of the species (inset at bottom center), and in the Sweetgrass Hills of Montana (upper right inset), where existing populations were not included on the range map. Still, the map produced from the majority of votes corresponds closely with the range map.

Pinus ponderosa. Concurrence between model predictions, the range map (fig. 9), and data points (lower insets) can be nearly perfect. Nonetheless, areas of disharmony exist, the most notable of which are in (a) the Willamette Valley of western Oregon (upper left inset), where *P. ponderosa* is present but where the model allocates few supporting votes, and (b) western Montana (upper right inset), where both the

range map and the predictions are poorly aligned with the species' sporadic distribution.

Larix occidentalis. Despite errors of prediction that are smaller than those for the three conifers considered above (table 4), predictions are less consistent with the range map (fig. 10). Errors in the range map notwithstanding (fig. 6), the model predicts that the species should be abundant in much of the northern Cascade Range of south-central British Columbia, where the contemporary distribution is limited to two small populations. For this species and for several considered below, climates approaching that of the profile are predicted at locations far removed from the contemporary distribution (lower right inset).

Quercus gambelii. The modeled climate profile is generally consistent with the range map (fig. 11), although the profile is predicted to occur where the species is absent, most noticeably (a) on the periphery of the range in northwest

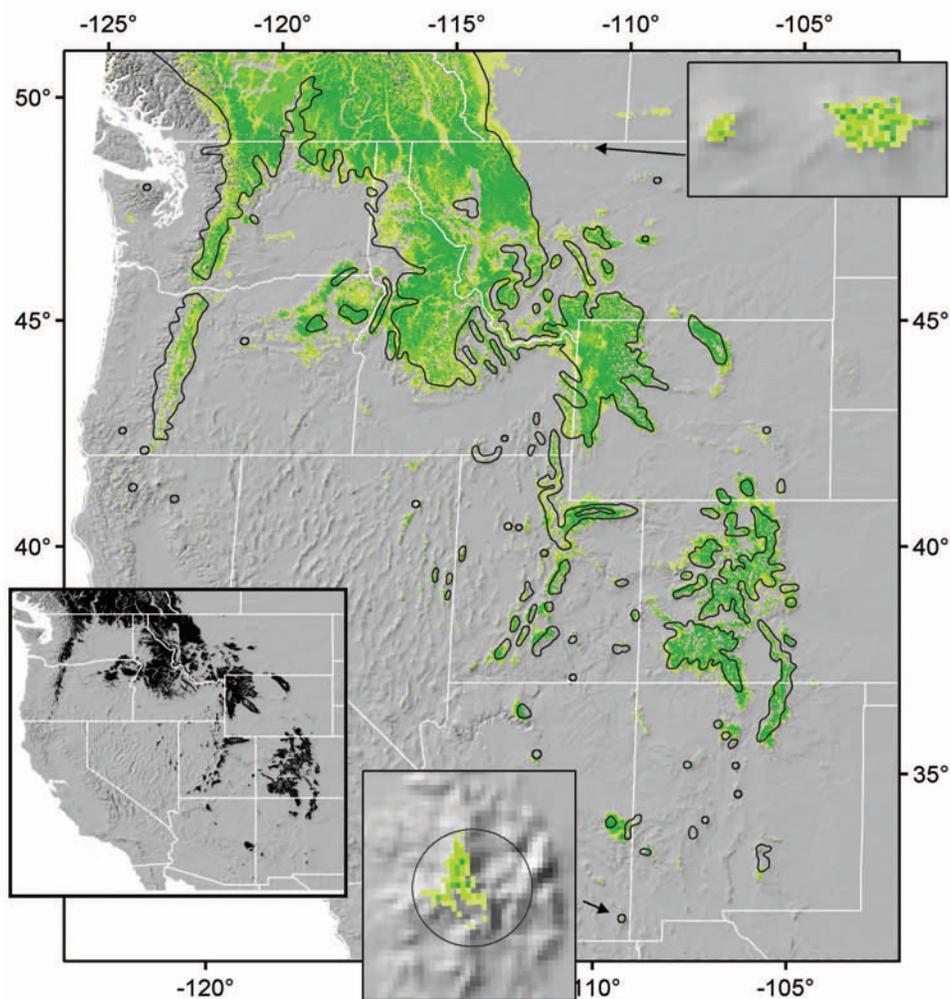


Fig. 8 Modeled bioclimate profile of *Picea engelmannii* (see fig. 7).

Arizona and (b) far to the north in the Salmon River drainage of central Idaho and the Bitterroot Mountains of western Montana (upper right inset).

Pinus edulis. Correspondence between predictions and the range map (fig. 12) is outstanding in its minutiae, whether in the center of distribution (upper left inset) or on the periphery (lower left inset). The profiles of this species, the previous one (*Q. gambelii*), and the next one (*J. osteosperma*), all species endemic to the Great Basin, are all predicted to exist far to the northwest in the Okanagan Valley of British Columbia.

Juniperus osteosperma. Insets (fig. 13) illustrate areas where *J. osteosperma* was likely confused with *Juniperus scopulorum* (upper right) and *Juniperus monosperma* (lower right). By predicting the presence of the *J. osteosperma* profile within these insets, the model demonstrates a sensitivity to such errors and thereby illustrates the power of Random Forests to classify data. Nonetheless, the predictions capture the essence of this juniper's distribution, particularly in the areas where it is abundant.

Carnegiea gigantea. Concurrence between the range map, data points, and predictions is precise (fig. 14). The species' altitudinal limit in the mountains surrounding Tucson (lower right inset) is ca. 1050 m, where the climate evidently becomes too cold (see Steenbergh and Lowe 1977). The model correctly describes (a) the general absence of the cactus in the lower Gila River drainage (lower left inset) and (b) the transition between the Sonoran and Mojave Deserts (upper center inset).

Pinus leiophylla. Predictions, the range map, and data points are in harmony (fig. 15), although the map of the majority of votes identifies locations proximal to the contemporary distribution that should be within the climate profile. The model also suggests that the climate may also approach that of the profile in valleys of the Clearwater and Salmon Rivers of Idaho far to the north.

The climate variables most important for predicting the occurrence of these nine species center around annual and summer precipitation, the periodicity of the precipitation, and the interactions of precipitation with temperature (table 4).

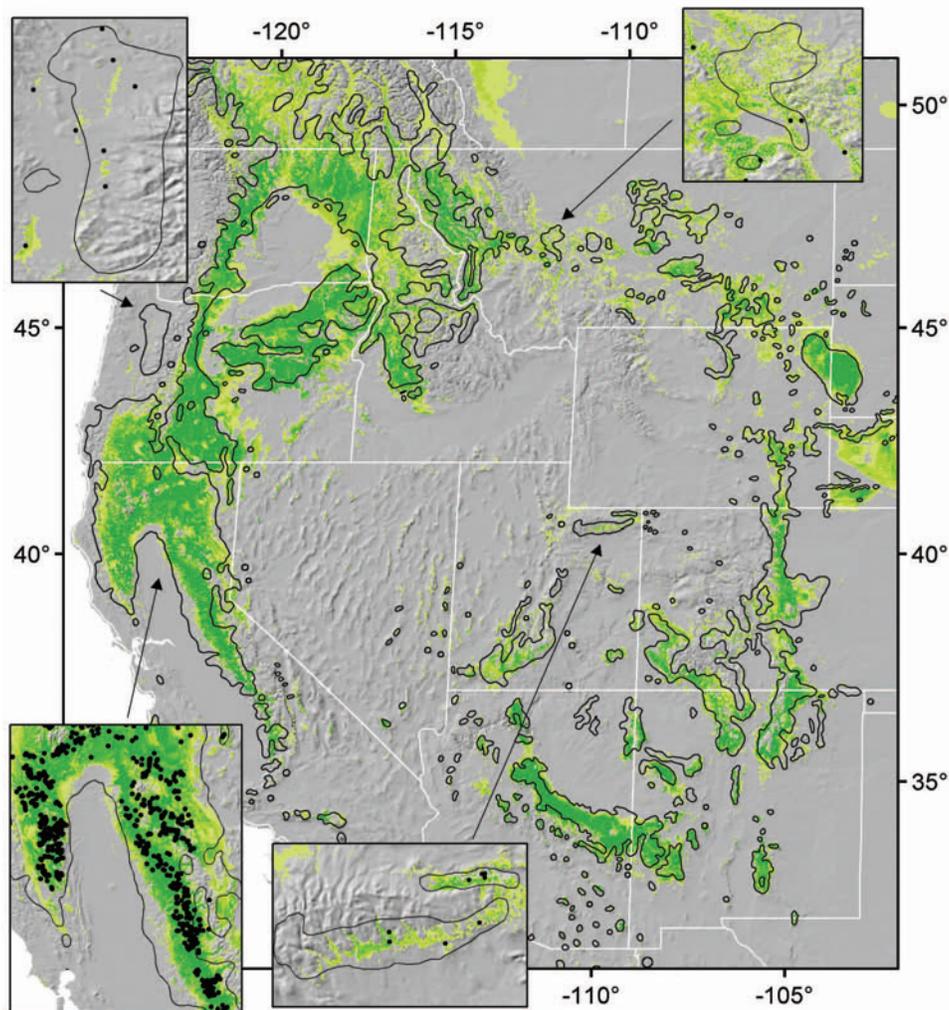


Fig. 9 Modeled bioclimate profile of *Pinus ponderosa* (see fig. 7).

Of the 27 variables listed as important (table 4), 21 involve precipitation directly or interactively, 13 incorporate mean annual precipitation, 16 incorporate summer precipitation, and only five involve the direct effects of either summer or winter temperature. PRATIO, the variable reflecting the periodicity of precipitation, appears in the models of six of the nine species.

Predicting Response to Global Warming

To illustrate the utility of the models for assessing response to a change in climate, we use the average global warming predictions from two GCMs that, for the current century, suggest that temperatures should rise by ca. 5°C and precipitation should increase by ca. 27% (126 mm) in our geographic window, but the ranges vary from 3.4°C to 6.5°C for temperature and from -11% (-38 mm) to 224% (1174 mm) for precipitation.

Community profiles. In using the plurality of votes to predict the future distribution of contemporary profiles, all pixels are assigned to one of the 25 communities. Votes cast

by the Random Forests algorithm, summarized for groups of similar communities (table 5), indicate that the area of the coastal forest profiles would change little but that most communities would increase in area, largely at the expense of the subalpine-tundra profiles but also at the expense of the Great Basin woodlands. The profile of one community, the Sitka coastal conifer forest, a minor component of the flora of the Northwest, would disappear early in the century. The spatial shifting of community profiles would be extensive, however, involving ca. 45% of our geographic window. By the end of the century, therefore, only 55% of the pixels in the window would exhibit the same community profile they do today.

Projected changes in area of community profiles follow disparate patterns across the century (table 5). While the area allocated to the Great Plains profile would remain relatively constant, that for the profiles of some communities (e.g., grasslands, Madrean) would decline in area early and increase later, and that for profiles of others (e.g., desertscrub) would increase early but decrease later, while those of still others would increase steadily in area (e.g., evergreen forests

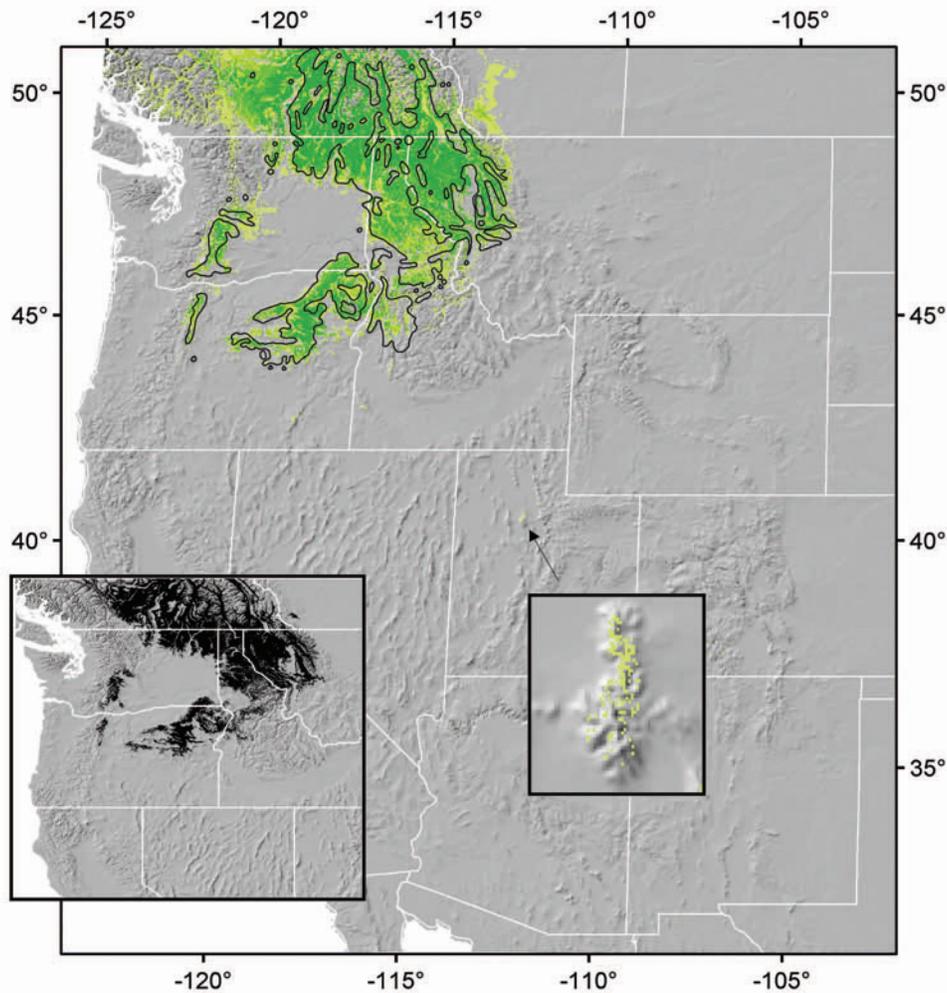


Fig. 10 Modeled bioclimate profile of *Larix occidentalis* (see fig. 7).

and chaparral), decrease steadily (e.g., subalpine tundra, Great Basin woodlands), or maintain early gains (montane and coastal forests). Because temperatures are increasing throughout the century, the disparate trends for these communities would result from a difference in response to changes in precipitation and, therefore, to the balance between temperature and precipitation.

However, these projections appear much different when one considers the extramural climates, the climates predicted to be outside the 35-variable climate envelopes that surround the contemporary climate profiles of these communities. Extramural climates account for 0.4% of the pixels in the contemporary climate but should increase to 12.3% in the decade beginning in 2030, 25.6% in that of 2060, and 47.2% by the end of the century (fig. 16). To be sure, the misalignment of geographic data sets would account for extramural predictions for the contemporary climate, but the exponential increase in the extramural climates projected for future decades means simply that by the end of the century, 47% of the West would exhibit profiles with no contemporary analogs

among the communities of today. For these extramural climates, predictions from correlative models of even superb statistical fit would be tenuous.

Extramural climates should be concentrated in the western Great Plains, the Southwest, and the Pacific Coast and should occur sporadically elsewhere (fig. 16). The extramural climates, therefore, would be disproportionately dispersed through the future distribution of the community profiles (table 5), accounting for less than 15% of the profiles of the montane forests and Great Basin woodlands but more than 88% of the evergreen forests and chaparral profiles. Particularly illustrative are the projections for the community recognized today as the coastal conifer forest (fig. 17). When judged according to the plurality of votes, the profile of this community should continue to occupy ca. 3.6% of the western landscape throughout the century, although 40% of the future area should be in locations other than where the profile occurs today (table 5), including sites far inland in the mountains of Idaho. But, by the end of the century, 61% of the future distribution predicted for this profile would be

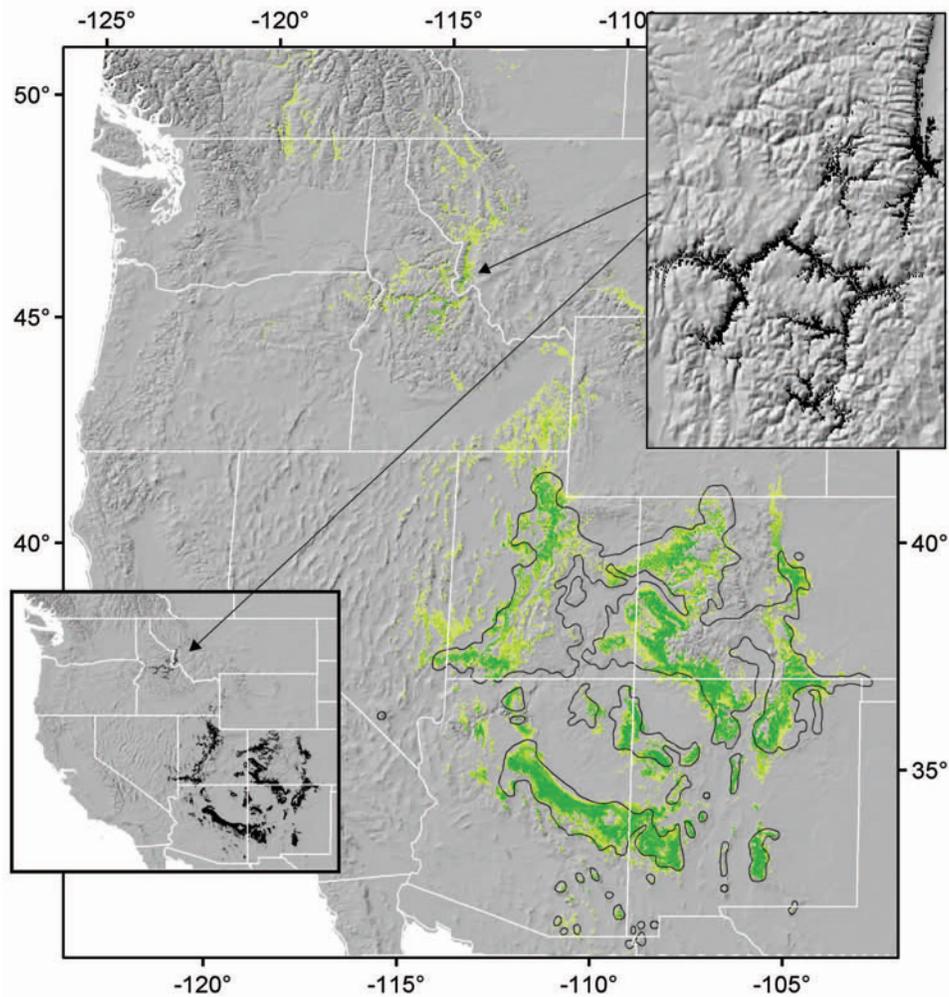


Fig. 11 Modeled bioclimate profile of *Quercus gambelii* (see fig. 7).

outside the contemporary climatic envelope (table 5), including some of the novel climates that had arisen earlier. Our statistics suggest, in fact, that only 29% of the contemporary distribution of this profile should remain in place and remain within the contemporary envelope.

When the extramural climates are taken into consideration, the proportion of the contemporary distribution of community profiles that would not be subject to disruption, that is, would remain in place and within the contemporary envelope, would become relatively small for all but the coastal forests (29%), the Great Plains (33%), and the montane forests (45%) (table 5; fig. 18). By the end of the century, the climate of only 22.2% of our geographic window could be expected to support the same communities it does today. The statistics (table 5) also indicate that by the end of the century, at least five of the biotic communities (2, 4, 11, 23, and 26; table 2) might cease to be recognizable, while an additional four may become precarious (12, 17, 18, and 25).

Species-specific profiles. Global warming, according to the IS92a scenario, is projected to have pronounced, wide-

spread, highly disruptive, and disparate effects on the climate profiles of these nine species (table 6; figs. 19, 20). Statistics describing the fate (table 6) of *C. gigantea* and *P. leiophylla* profiles are presented but pertain only to the northern portions of their distributions, are misleading, and are not considered further.

According to our projections, only the area occupied by the profile of *Q. gambelii* is expected to increase by the close of the century, that of *P. menziesii* should hold constant, but those of *L. occidentalis*, *P. edulis*, *P. engelmannii*, and *J. osteosperma* would be reduced drastically (table 6). Spatial shifts of the profiles would be extensive for all species, with the profile of *P. menziesii* being the least affected. Even so, only 54% of the contemporary distribution of the *P. menziesii* profile should remain in place throughout the century. Although the occurrence of extramural climates should not be a large factor, when considered in light of the proportion of profiles that would vanish from their contemporary locations, the combination would portend widespread disruption to the contemporary distribution of the climate profiles of these species

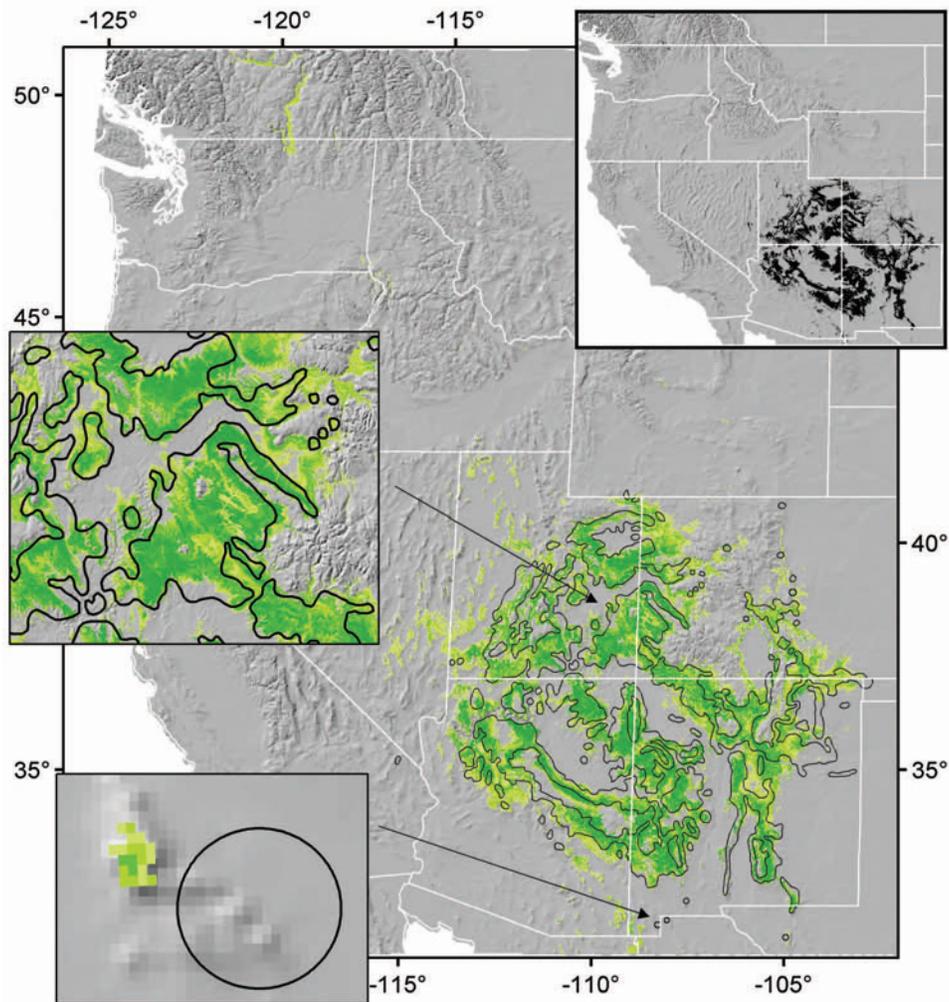


Fig. 12 Modeled bioclimate profile of *Pinus edulis* (see fig. 7).

(table 6). Shifts in spatial distribution of the profiles should be accompanied by increases in their altitudinal distributions of ca. 500 m in *P. menziesii*, *P. ponderosa*, and *P. edulis*, ca. 400 m in *L. occidentalis*, and ca. 300 m in *P. engelmannii* and *Q. gambelii*, but only ca. 100 m in *J. osteosperma*.

A comparison of tables 5 and 6 shows that projected effects on the profiles of the species are not necessarily consistent with those of their communities. On the one hand, projections for the profiles of *P. menziesii* of the coastal forests and *P. engelmannii* of the subalpine tundra (table 6) closely parallel those predicted for their respective communities (table 5). But on the other hand, *P. ponderosa* is a prominent indicator of the montane forests, while *L. occidentalis* is a lesser component of the same forests in the north, as is *Q. gambelii* in the south. Yet the profiles of these species are projected to respond to global warming much differently from each other (table 6) as well as from the community as a whole (table 5).

Projections for the profiles of *J. osteosperma* and *P. edulis*, both indicator species of the Great Basin conifer woodlands,

are particularly illustrative of the effects that disparate individualistic responses may have on communities of the future. The profiles of both species are expected to vanish across much of their contemporary distribution (table 6), in association with the demise of the woodlands (table 5). While the profiles of both species should become reduced in area, that of the pine is projected to collapse into Colorado and shift upward in altitude, while that of the juniper should shift laterally into Nevada (fig. 20). As a result, the co-occurrence of these two species should change from 35% (i.e., 35% of the sites where either species occurs should have both) to only 6% by the end of the century. Even though the profile of the Great Basin woodlands would persist throughout the century, these results suggest that the composition of these woodlands would change considerably.

Our projections also show that the climate profile for the northern portion of the distribution of *C. gigantea* now growing in southern Arizona would shift northward by ca. 500 km (fig. 20) and rise ca. 600 m in altitude. Likewise, figure 21 shows that the profile describing the northern tip of

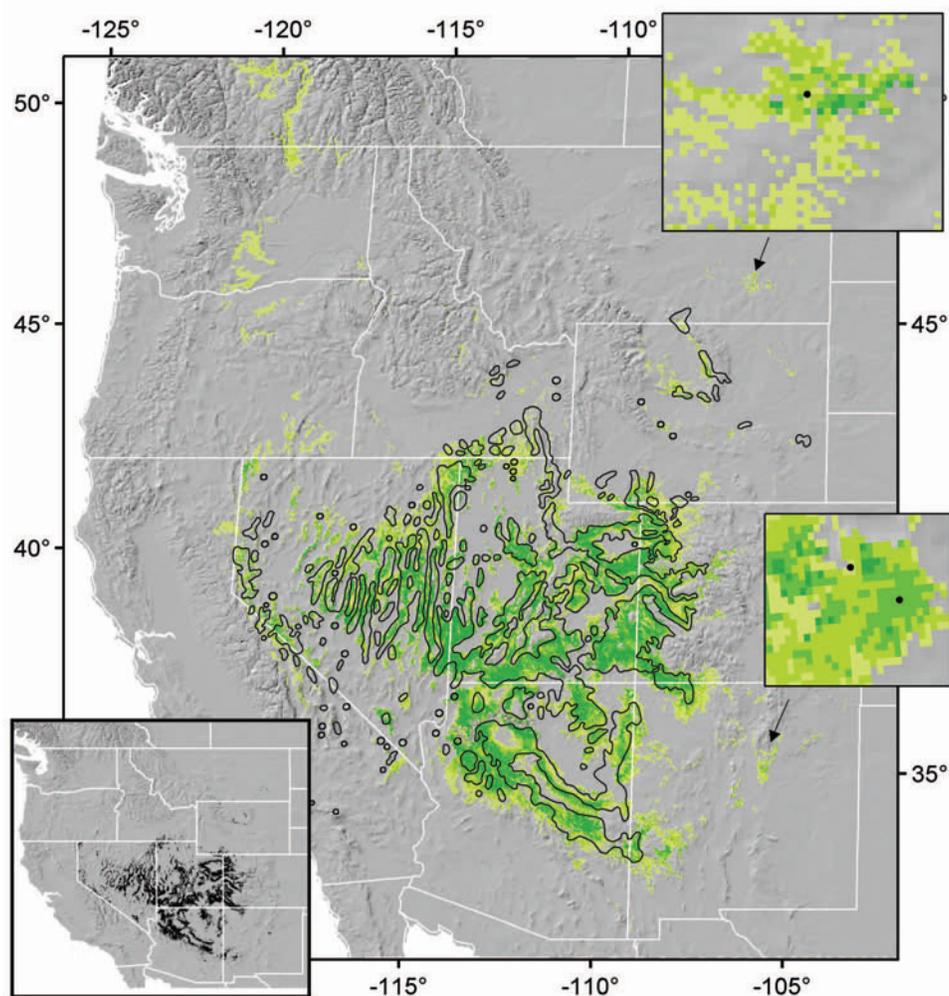


Fig. 13 Modeled bioclimate profile of *Juniperus osteosperma* (see fig. 7). Dots in the inserts show general location of Forest Inventory sites purported to be inhabited by *J. osteosperma* but more likely inhabited by *Juniperus scopulorum* (upper right) or *Juniperus monosperma* (lower right).

the broad geographic distribution of *P. leiophylla* should shift northward early in the century by as much as 400 km and upward by ca. 100 m; by 2060, it should shift northward by as much as 600 km and upward by 400 m; and by 2090, it should shift northward by 800 km and upward by ca. 600 m. A reasonable expectation for both of these species would be that by the end of the century, a portion of the extramural climates of the Southwest (fig. 16) should exhibit climate profiles typical of these species in the Mexican portions of their contemporary distributions.

Discussion

Plant-Climate Relationships

Communities. Climatic control of community composition and distribution is at the foundation of plant sociology. While a demonstration that the biotic communities of Brown et al. (1998) recur across the landscape in response to climate

might be anticipated, the degree to which the occurrence of the communities can be predicted from climate at a resolution as fine as 1 km seems remarkable indeed. The strength of the relationships of figures 2 and 3 was a pleasant surprise to Brown himself (D. E. Brown, Botany Department, Arizona State University, Tempe, personal communication).

The variables most important for separating the communities tend to parallel general differences in climate across our geographic window. Of greatest importance was the ratio of summer to annual precipitation, a variable reflecting general differences among maritime coastal climates, continental climates of the interior, and monsoonal climates of the Southwest. Another important predictor, the summer-winter temperature differential, separates maritime and continental climates, and together these two variables, along with their interactions with temperature and annual precipitation, accounted for five of the seven most important variables. The remaining variables, summer maximum temperatures and the interaction of growing season precipitation with degree-days

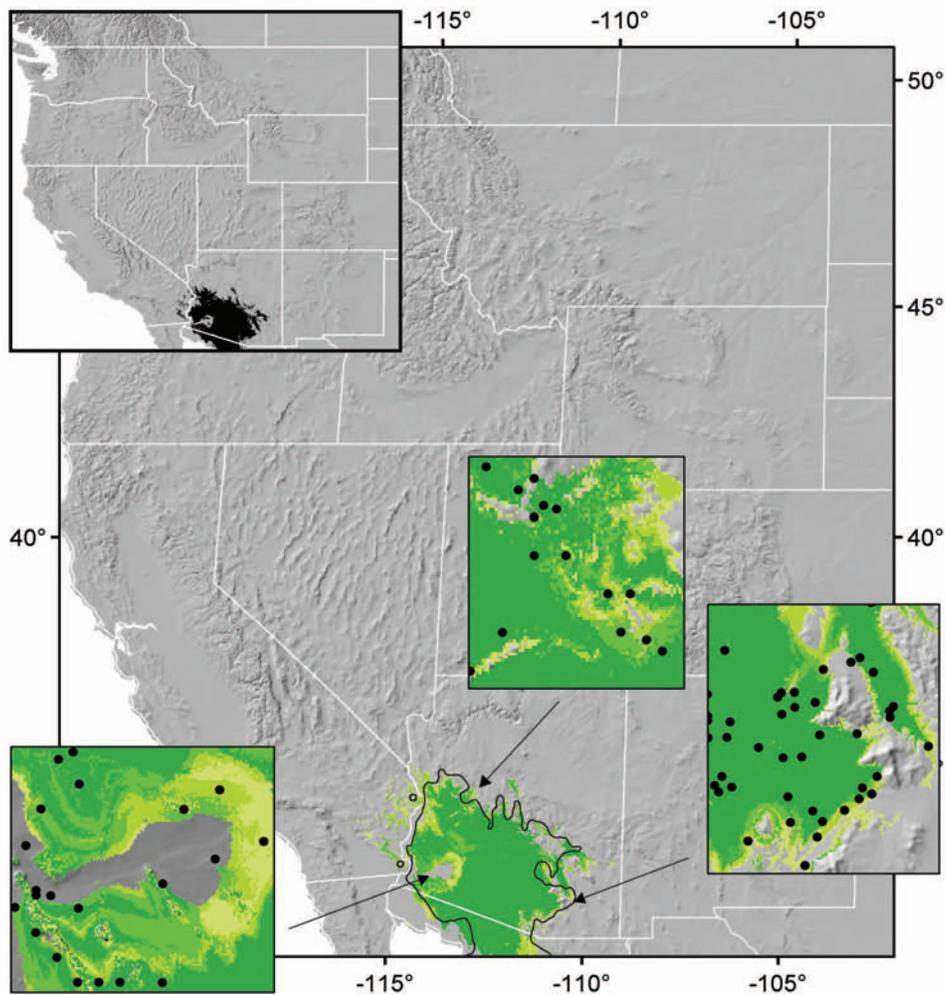


Fig. 14 Modeled bioclimate profile of *Carnegiea gigantea* (see fig. 7).

warmer than 5°C, undoubtedly contribute to the altitudinal gradients that are strongly related to vegetation (Daubenmire and Daubenmire 1968).

The climatic basis of the distinctive vegetation zones in the West has been the subject of conjecture for decades. Climate variables purported to control the distribution of plant communities, for instance, have included low temperatures for the upper altitudinal margins and moisture stress at the lower (Larson 1930), the length of the frost-free season (Baker 1944), the balance between temperature and precipitation (Haig et al. 1941), and summer droughts (Daubenmire 1956). Our list of important variables emphasizes the complex nature of the interactions through which these intuitive effects might be expressed.

Species. The Random Forests regression tree produced bioclimatic models of excellent fit. The errors of omission that accrue when a model falsely predicts absence approached zero, and errors of commission were less than 10%. While many ecologically plausible reasons exist for the errors of commission, experimental errors are the most plausible explana-

tion for errors of omission. For judging fit, therefore, errors of omission are the most serious, and for these errors to approach zero in our analyses demonstrates the power of the regression tree to properly classify data.

The models received strong verification when predicted distributions were compared to range maps (figs. 8–18), despite the drawbacks (fig. 6) of using range maps as a standard of excellence. Still, for several of the species but most notably *Larix occidentalis* (fig. 10) and *Quercus gambelii* (fig. 11), the comparisons pinpointed lands where the climate should be suitable but where the species was either absent or present at frequencies so low as to escape representation in field plots. From the statistical perspective, disharmony of this type produces errors of commission. Yet disharmony between range maps and predictions from well-fitted models is as likely to result from disequilibrium between the climate and plant distributions as from experimental errors. As discussed by Ackerly (2003), equilibrium is only temporary at best, largely because climate change is an ongoing process to which plant responses will always lag (Davis 1989; Huntley

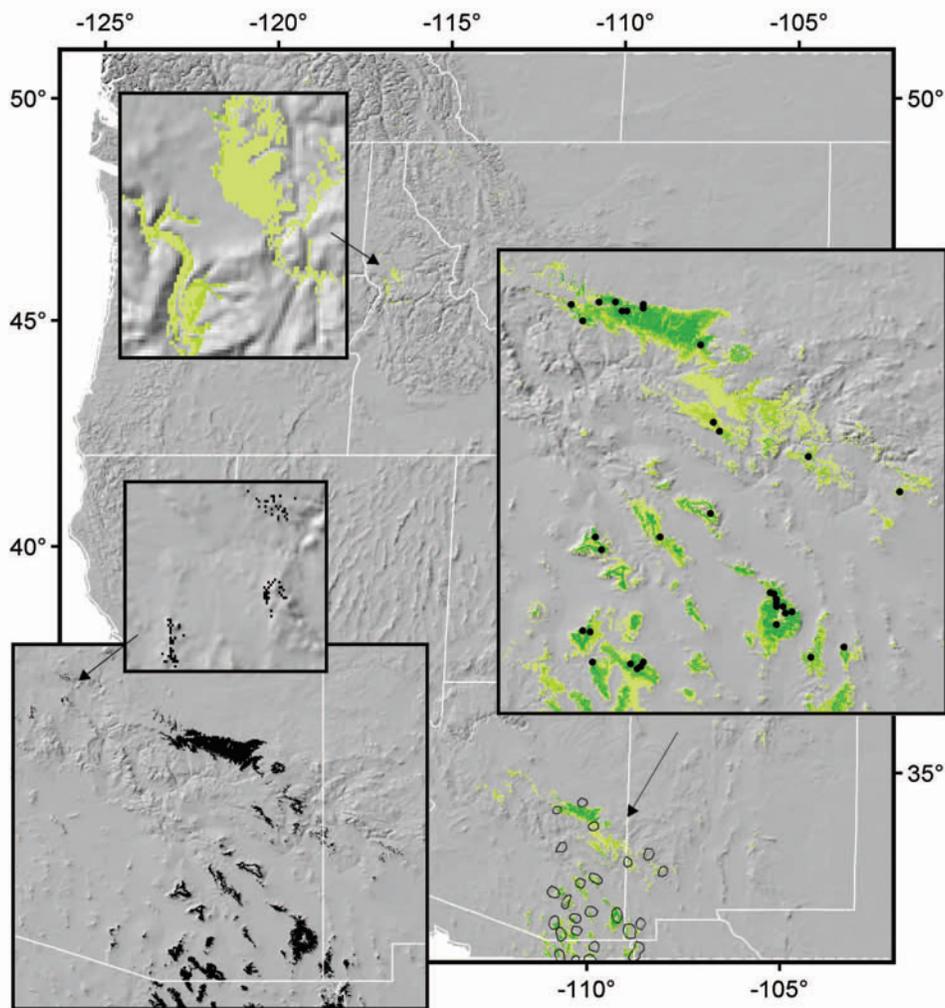


Fig. 15 Modeled bioclimate profile of *Pinus leiophylla* (see fig. 7).

1991). In judging whether errors of commission in our models originate from experimental errors or from plant-climate disequilibrium, it is instructive to note that provenances of *L. occidentalis* perform admirably when established beyond the limits of the species' distribution in the northern Cascade Range of British Columbia (B. J. Jaquish, British Columbia Ministry of Forests, Vernon, personal communication), precisely as the bioclimatic model predicts (fig. 10). A portion of the errors of commission (table 4), therefore, quite likely reflect unoccupied niche space resulting from a lag in the response of the vegetation to the warming trends of the twentieth century.

Even though correlative models are not suited to mechanistic interpretations, the relative importance of predictor variables nonetheless may reflect underlying physiological processes (Pearson and Dawson 2003). In our analyses, the climate variables of most importance for predicting occurrence of a disparate group of species were similarly disparate (table 4). Yet some commonalities exist: interactions of temperature and either annual or summer precipitation were

among the most important variables for all species except *L. occidentalis*; the ratio of summer precipitation to total precipitation was implicated for all but *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Picea engelmannii*; and the direct influence of the amount of winter cold was important for only *P. ponderosa* and *L. occidentalis*. On the whole, our list of important variables provides support to Cumming and Burton (1996), who used mechanistic models to conclude that forest types and their constituent species likely will respond to climate for different reasons.

Our list of important variables (table 4) does not necessarily corroborate intuitive expectations. On the one hand, winter cold and drought are thought to limit distributions of *Carnegiea gigantea* (Steenbergh and Lowe 1977), and our list tends to be supportive. Likewise, silvics manuals (e.g., Burns and Honkala 1990) suggest that the occurrence of *P. ponderosa* and *L. occidentalis* is limited largely by moisture stress and winter cold; again, table 4 is supportive. But on the other hand, the silvics manuals also state that *P. engelmannii* is limited to climates with cool summers and cold winters, but our

Table 5

Predicted Area Occupied by the Climate Profiles of Groups of Biotic Communities for the Present Climate in Relation to the Entire Western Landscape, the Change in Area Expected from Global Warming for Three Future Decades Relative to the Contemporary Distribution, the Extramural Percentage, and the Percentage of the Contemporary Area Expected to Have the Same Climate Profile throughout the Century

Grouping	Group composition ^a	Total area in 2000 (%)	Δarea (%)			Extramural by 2100 (%)	Remaining in place through 2100 ^c (%)
			2030	2060	2090 ^b		
Great Plains	5	24.4	2.2	-3.6	6.6 (1.6)	61	89 (33)
Grasslands ^d	10, 18, 20	18.4	-13.0	-0.8	17.9 (3.3)	53	33 (13)
Desertscrub	14, 19, 22, 24	17.3	31.2	22.9	3.0 (0.5)	53	25 (4)
Montane forests	6, 7	15.2	15.4	14.9	11.7 (1.8)	12	51 (45)
Great Basin woodlands	13, 15	8.2	-26.0	-9.6	-28.7 (-2.2)	3	17 (17)
Subalpine tundra	3, 4, 9, 11	7.7	-32.0	-71.8	-84.7 (-6.5)	19	10 (9)
Evergreen forest-chaparral	12, 16, 17, 21, 23	4.1	23.8	42.1	53.2 (2.3)	88	45 (5)
Coastal forests	2,8	3.6	4.1	4.8	0.1 (0.0)	62	60 (29)
Madrean	25, 26	0.3	-76.1	-20.3	10.2 (0.1)	86	0 (0)

^a Codes are defined in table 2.

^b Value in parentheses is percentage relative to total landscape.

^c Value in parentheses is percentage remaining in place and within the climatic profile.

^d Other than Great Plains.

listing includes three variables reflecting interactions of temperature and precipitation. Likewise, that *Pinus edulis* demands arid climates, cold winters, and adequate summer precipitation is not obvious in the variables chosen by our models.

Effects of Global Warming

Our projections rely not only on the accuracy of the bioclimatic models but also on the ability of the IS92a scenario to depict the accumulation of greenhouse gases and on the precision of the Hadley and Canadian GCMs to represent the cumulative effects of these gases on climate. To the extent that the scenario and the GCMs are correct, our models predict widespread disruption of natural ecosystems.

Predicted effects. Votes cast by the Random Forests algorithm portray a straightforward and intuitively appealing view of the effects of global warming on the future distribution of community profiles: those of the grasslands, chaparrals, and montane forests would increase largely at the expense of those of subalpine forests, tundra, and Great Basin woodlands (table 5). The approach toward a new equilibrium would require much of the vegetation to be in flux as climate profiles shift. By the end of the century, ca. 55% of the landscape would exhibit climates that are incompatible with the vegetation occurring there today. Projected effects on the distribution of the species-specific profiles, however, tend to support the individualism long recognized in paleoecological reconstructions (e.g., Overpeck et al. 1985; Huntley 1990; Jackson and Overpeck 2000; Ackerly 2003). In some cases (e.g., *P. menziesii* and *P. engelmannii*), species-specific predictions are consistent with those of their communities, but in other cases, (e.g., *Juniperus osteosperma* and *P. edulis*), predictions are inconsistent. While these responses generally are compatible with intuitive expectations and published works (Neilson 1995; Bachelet et al. 2001; Hansen et al. 2001), they nonetheless greatly oversimplify potential effects.

Nearly one-half (47%) of the western landscape is projected to be governed by climate regimes that are extramural, having no contemporary analogs among the communities of

today. Because contemporary limits of distribution are a product of competition as well as climatic tolerances, these extramural climates are particularly disconcerting. The validity of projections from correlative models depends in part on competitive relationships and therefore on climate profiles remaining constant. Yet the paleoecologic record demonstrates that competitive relationships do change; individualistic responses of species to past climates have produced assemblages of species with no modern analogs (Overpeck et al. 1985; Huntley 1990; Jackson and Overpeck 2000; Ackerly 2003). Consequently, predictions made by our correlative models for extramural climates are not defensible. With 55% of the future landscape governed by a climate profile unlike that which occurs there today and 47% of the future climate classified as extramural, one can estimate from the statistics in table 5 that only 22% of the future landscape would have been free of disruption, that is, expected to support the same vegetation that it has today. The conclusion, therefore, would be that the vegetation on much of the landscape would be in flux, but the future distribution of species and their associations could be predicted with confidence for only that portion not governed by extramural climates.

One can reasonably assume that a portion of the extramural climates (fig. 16) would have contemporary analogs outside our geographic window. Extramural climates predicted for the desert Southwest (figs. 16, 18), for instance, undoubtedly have contemporary analogs in the Sonoran and Chihuahuan desert and Madrean flora of Mexico (fig. 21). Likewise, extramural climates located on the western Great Plains probably have contemporary analogs in the grasslands toward the southeast. Yet whether contemporary analogs exist outside our geographic window for the extramural climates predicted for the Pacific Coast or the mountains of the interior is questionable. We are led, therefore, toward the conclusion that predicting the composition and distribution of future plant assemblages from contemporary climate profiles in a large and heterogeneous physiographic region may be impossibly complex (see also Neilson et al. 2005). As recognized

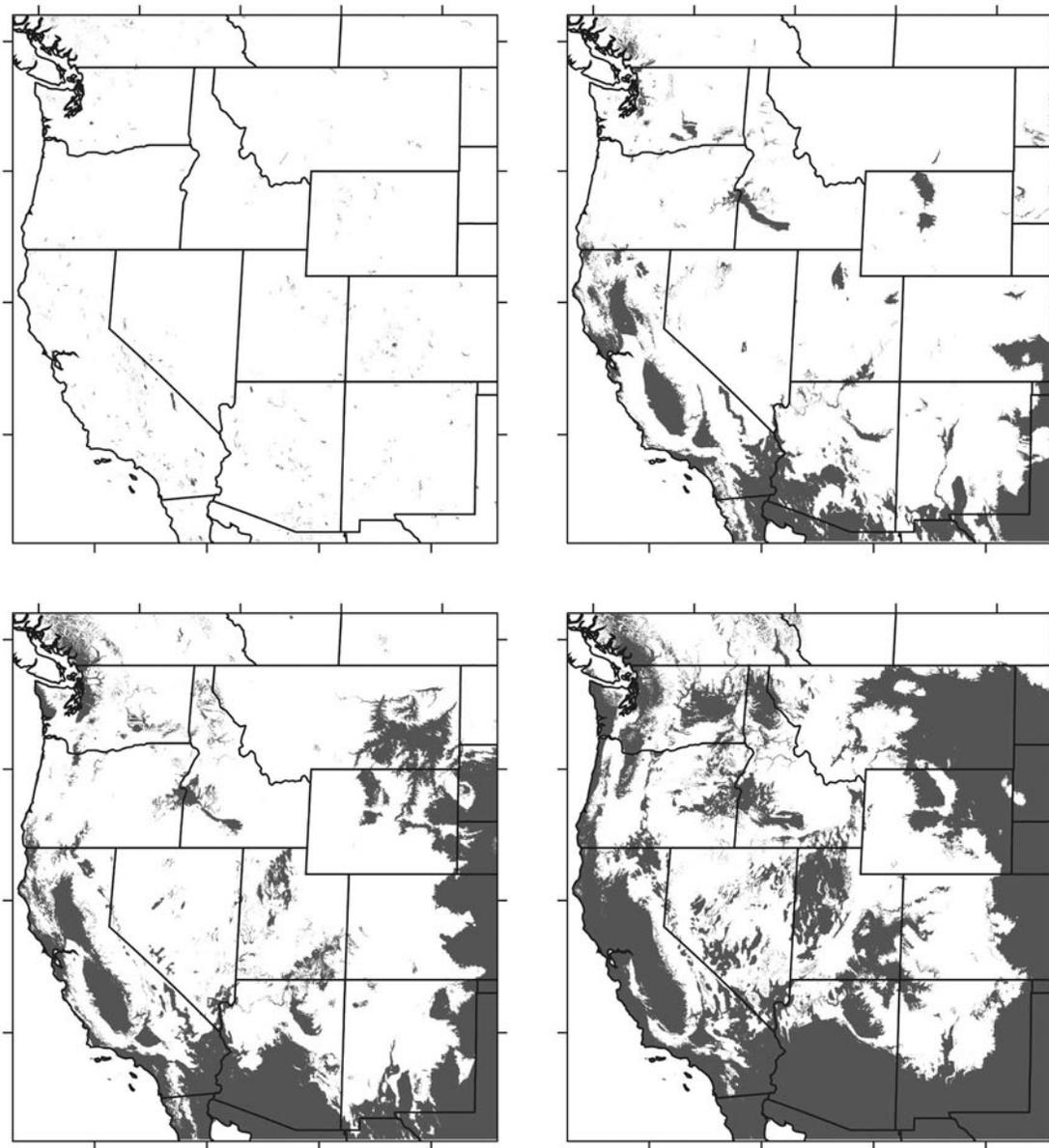


Fig. 16 Shading marks pixels predicted to be extramural to the contemporary climate profiles of 25 biotic communities of the western United States for the contemporary climate (upper left) and the climates of the decades beginning in 2030 (upper right), 2060 (lower left), and 2090 (lower right).

repeatedly in the paleoecologic record (Overpeck et al. 1985; Huntley 1990; Ackerly 2003), plant associations change, and, from our analyses, there is no reason to expect otherwise from the effects of global warming. Individualistic responses from species occurring as components of the same biotic community (table 6) provide additional compelling evidence that the associations themselves will change.

Yet for 47% of the West, predicted responses of the communities and their constituent species occur within contemporary climate profiles, and for this proportion our models should be applicable. The communities expected to be largely

unaffected by extramural climates are the montane conifer forests, the two Great Basin woodlands, the subalpine conifer forests, and the tundra (table 5). These communities are generally found in the mountain systems, account for ca. 35% of the landscape today, and should account for ca. 28% by the end of the century. For this portion, contemporary associations should persist as recognizable entities on future landscapes.

Synthesis. Our results join with many others (Melillo et al. 1995; Bachelet et al. 2001; Hansen et al. 2001; Shafer et al. 2001; Thompson et al. 2002; Neilson et al. 2005) to

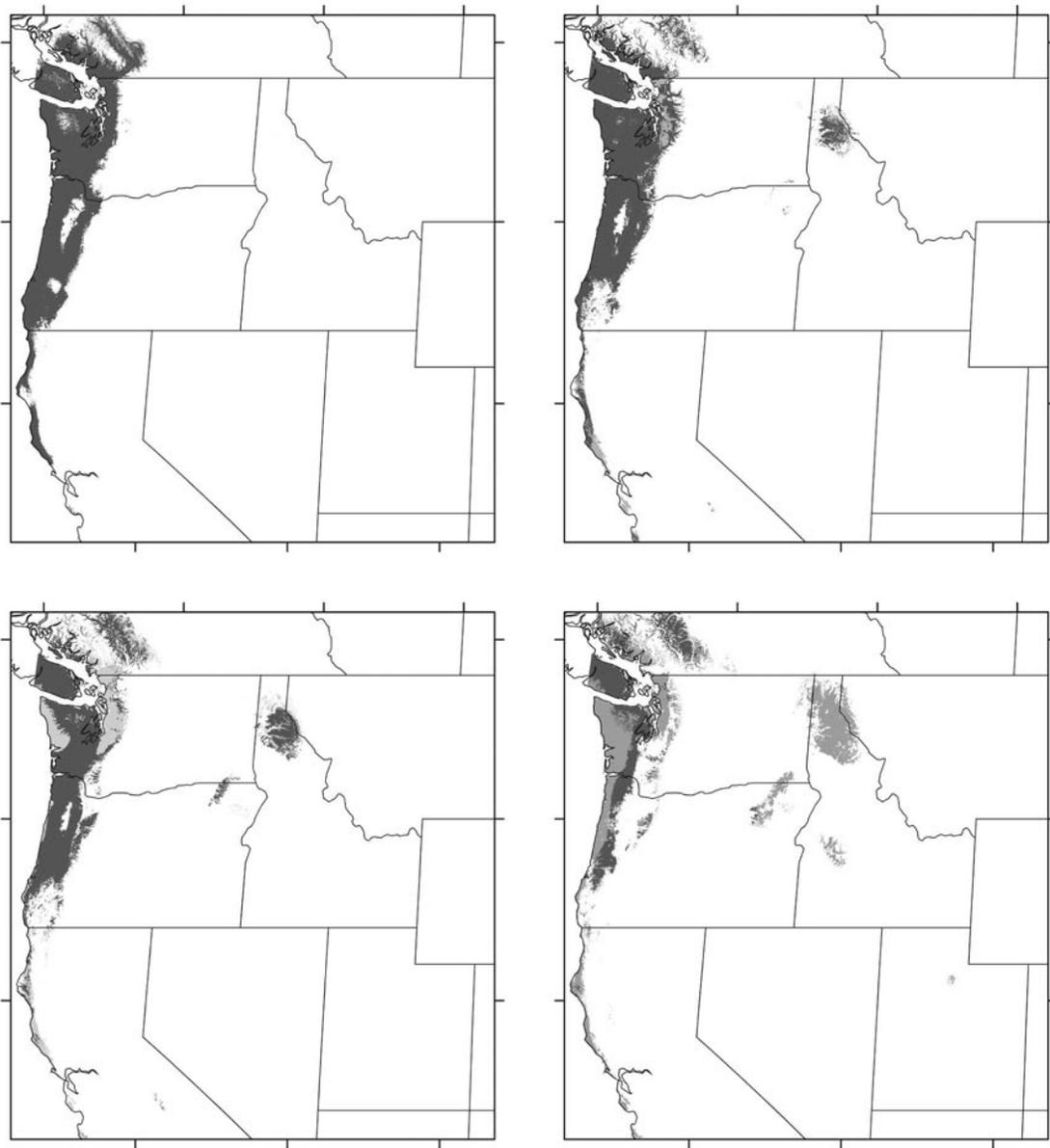


Fig. 17 Modeled community profiles using the plurality of votes for the Oregon coastal conifer forest for the contemporary climate (upper left) and for the decades beginning in 2030 (upper right), 2060 (lower left), and 2090 (lower right). Predictions shaded in light gray lie within the extramural climates of fig. 16.

predict a widespread disruption of native ecosystems from global warming. Even though the vegetation may retain general characteristics of deserts, grasslands, or forests, the future distribution of climates in all but the forested mountain systems is likely to support plant associations that differ from those of today. In fact, our estimate that only 22% of the future landscape should be governed by the same climate profile that it has today is itself a misleading statistic. It is well documented for most species, but particularly for woody plants, that adaptation to a heterogeneous environment is expressed in clines of genetic variability that have been molded

by climate. Consequently, a change in climate should precipitate intraspecifically a wholesale redistribution of genetic variability across the landscape to realign genotypes with their climatic optima (Rehfeldt et al. 1999, 2002, 2004). Realignment will undoubtedly invoke evolutionary processes, particularly recombination, migration, and selection. There seems little doubt, therefore, that essentially all lands in the natural landscape will be affected by global warming as now portrayed.

Although consistent in direction, our results differ in detail from those of most preceding analyses. Because our analyses

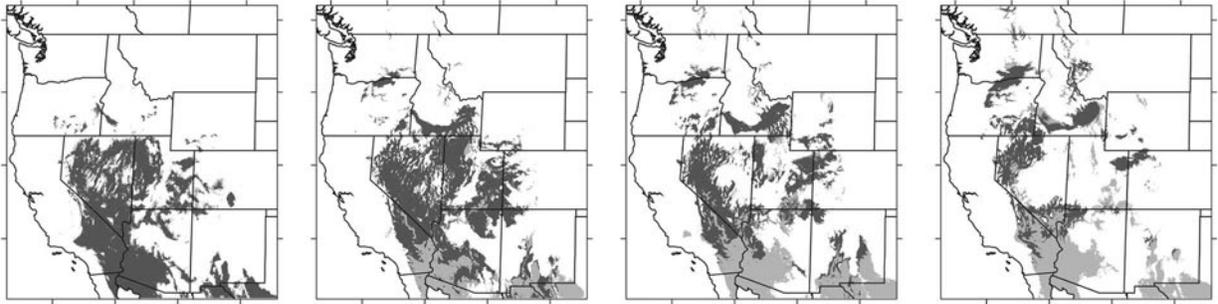
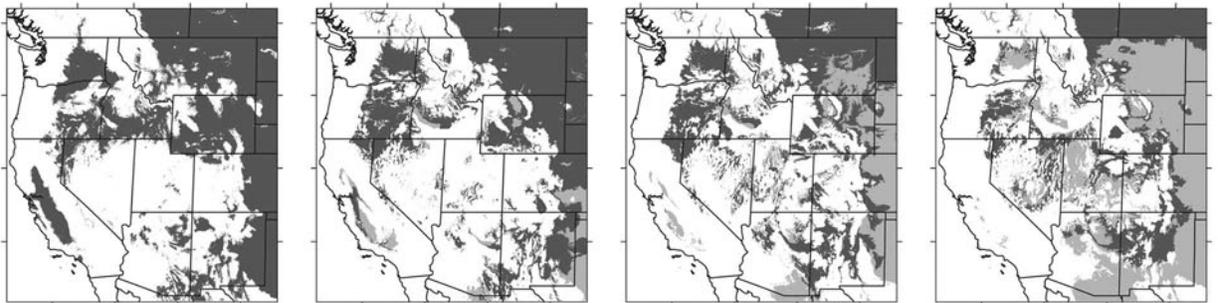
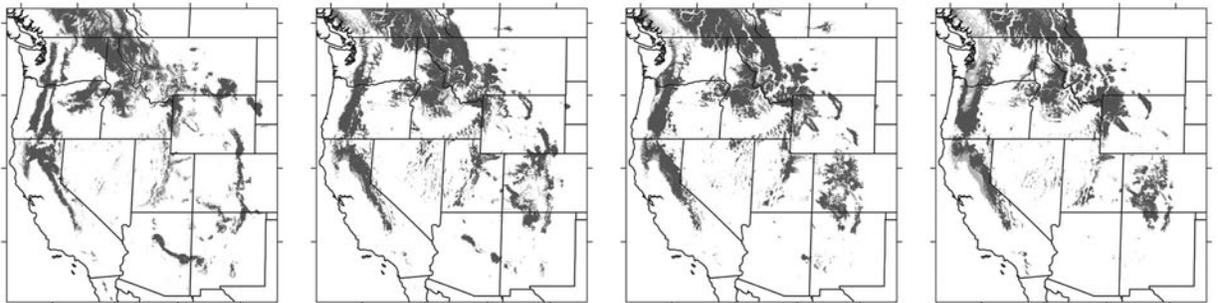
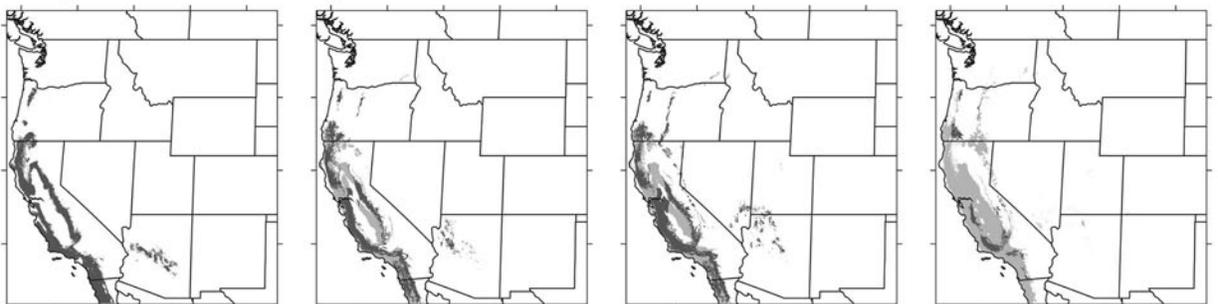
Desertscrub**Grassland****Montane Forest****Evergreen Forests and Chaparral**

Fig. 18 Modeled community profiles using the plurality of votes for four groups of communities (see table 5) for the contemporary climate and for the decades starting in 2030, 2060, and 2090 (left to right). Predictions shaded in light gray lie within the extramural climates of fig. 16.

are of a scope and thoroughness not yet considered and reach a statistical precision not attained by the general surveys conducted in the past, in-depth comparisons are not necessarily appropriate. At the level of the biome, for instance, our re-

sults (table 5) are in general agreement with those of Neilson (1995) and Bachelet et al. (2001): climate profiles of subalpine, alpine, and tundra vegetation should nearly disappear by the end of the century, while those of the montane forests

Table 6

Projected Effects of Global Warming on the Change in Area Expected in the Climate Profiles of Nine Species at Three Future Decades Relative to the Contemporary Distribution, Percentage of the Future Distribution Expected to Be Extramural, and the Percentage of the Contemporary Area Expected to Have the Same Climate Profile throughout the Century

Species	Δ area (%)			Extramural by 2100 (%)	Remaining in place through 2100 ^a (%)
	2030	2060	2090		
<i>Pseudotsuga menziesii</i>	11	7	-2	14	54 (38)
<i>Pinus ponderosa</i>	11	11	-13	18	36 (27)
<i>Picea engelmannii</i>	-33	-47	-72	5	23 (21)
<i>Juniperus osteosperma</i>	-42	-34	-68	6	11 (11)
<i>Pinus edulis</i>	-48	-54	-81	1	5 (5)
<i>Larix occidentalis</i>	-32	-41	-63	3	14 (14)
<i>Quercus gambelii</i>	45	81	23	6	25 (20)
<i>Carnegiea gigantea</i> ^b	-53	-53	-83	0	0 (0)
<i>Pinus leiophylla</i> ^b	-74	-25	-32	0	0 (0)

^a Value in parentheses is percentage remaining in place and not extramural.

^b Projections do not take into account the portion of the contemporary climate profile in Mexico.

would change little in area. Yet, our analyses suggest that forest profiles should decrease by ca. 5% rather than the 11% estimated by Hansen et al. (2001); profiles of scrublands and arid woodlands should decrease rather than increase; and those of grasslands, evergreen forests, and chaparral should expand rather than contract. As for individual species, our results concur with those of Shafer et al. (2001) and Thompson et al. (2002) in predicting a decline in the *P. engelmannii* profile but also conflict by predicting a decline in the climate profile of *P. ponderosa*, rather than an increase, and no change in the area of the *P. menziesii* profile, rather than a decrease.

Stasis. Correlative models predict the future distribution of contemporary climate profiles, but interpretations invariably avoid vegetation responses. Our models, for instance, predict that the climate profile of *P. edulis* should shrink in area by 48% by the decade beginning in 2030 (table 6), while those for the Great Basin woodlands in which the species occurs should be reduced by ca. 26% (table 5). Recent reports indeed document the demise of these woodlands, with mortality approaching 100% in some localities (Shaw et al. 2005). This correspondence between the actual and predicted demise indeed is suggestive of an initial response to global warming. Yet a prediction of importance equal to that concerning which climate profiles would be suitable for these lands in the future would be one concerning the rate at which the vegetation will respond. Although the rapid change predicted for global warming should accentuate the lag in response expected from change (Rehfeldt et al. 1999, 2002; Etterson and Shaw 2001; Jump and Peñuelas 2005), expectations regarding rates of recovery have yet to be addressed.

The subject of recovery is indeed complex. Needed are estimates for (1) rates of demise of the contemporary vegetation (see Rehfeldt et al. 2001), (2) species-specific climate profiles for the future landscape, as, for example, developed herein, (3) rates of immigration for species appropriate for the new profile (Clark et al. 1998; Higgins et al. 2003), and (4) estimates of the microevolutionary responses that will eventually convey adaptedness (Rehfeldt et al. 1999, 2002; Etterson and Shaw 2001; Savolainen et al. 2004). Among the issues lacking solutions are approaches to addressing compet-

itive relationships in novel climates and the effects of climate change on the insect and disease populations that are likely to participate in the demise of the contemporary vegetation. Yet reasonable estimates of the rate of response of natural vegetation, the rate that a new equilibrium is approached, and therefore the duration of the lag in response of the vegetation to the change are possible, even for a target seemingly destined for continuous motion.

In considering rates of adjustment to environmental change, one must also acknowledge the importance of human activities, whether proactive or inadvertent, in channeling vegetation responses. Fire suppression, for instance, has resulted in large-scale conversion of grasslands of the Southwest into shrub communities (D. E. Brown, personal communication), and consequently, a projected increase in the grasslands, for instance, undoubtedly would be compromised. Estimated rates of recovery, therefore, must also take into account the role of invasive species in either temporarily or permanently filling abandoned niche space created by the demise of the contemporary vegetation (Petit et al. 2004).

Mitigating the Effects of a Change in Climate

As the climate warms, plants eventually become less well attuned physiologically to their environment (Rehfeldt et al. 1999, 2001, 2002). As fitness deteriorates, evolutionary processes are activated so that adaptedness is maintained (see Davis et al. 2005). Maintaining adaptedness in natural populations requires, first, that species successfully track their climatic niche and, second, that genetic variability become reassorted so that genotypes reappear in the climates to which they are physiologically attuned (Rehfeldt et al. 1999). While the evolutionary process is demonstrably efficient at responding to a change in climate, the rate of climate change predicted for global warming poses a greater threat to natural populations than the amount of change (Huntley 1991; Rehfeldt et al. 1999, 2002; Etterson and Shaw 2001; Jump and Peñuelas 2005). Some (e.g., Noss 2001) advocate letting nature take its course, thereby relying on evolutionary processes to realign species, genotypes, and climate. Others, however, argue that rapid rates of change would create a lag

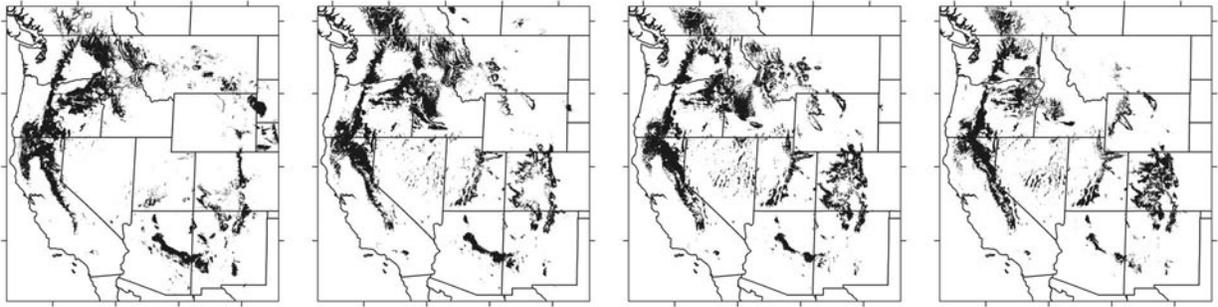
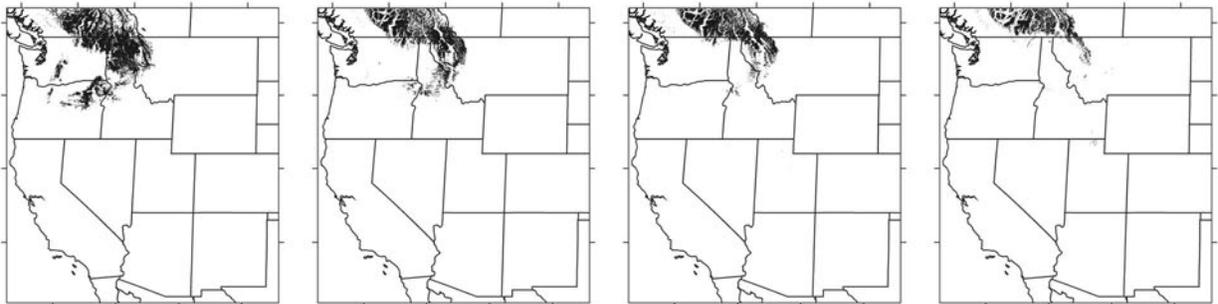
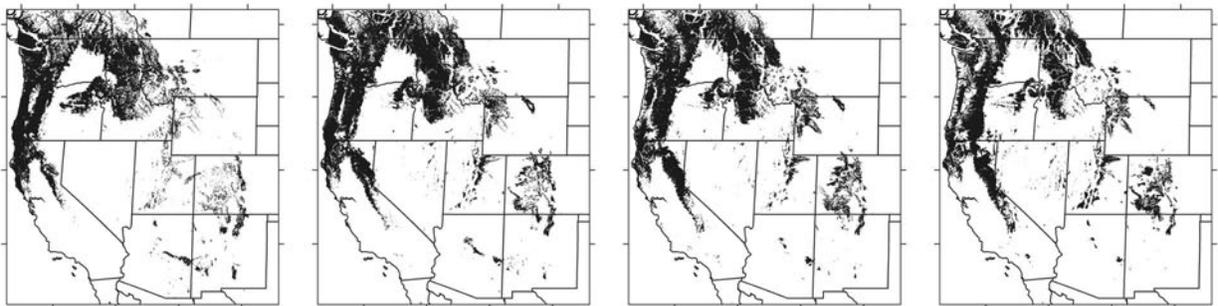
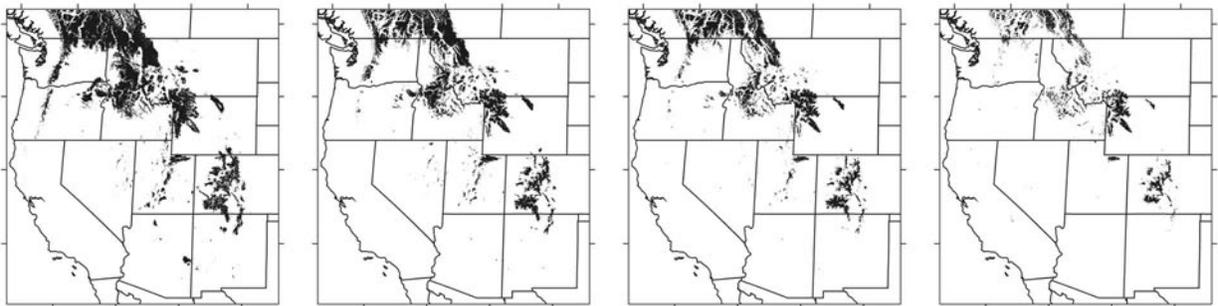
Pinus ponderosa*Larix occidentalis**Pseudotsuga menziesii**Picea engelmannii*

Fig. 19 Modeled climate profiles (votes > 50%) of four forest tree species for the contemporary climate and for the decades beginning in 2030, 2060, and 2090 (left to right).

in response so large that natural landscapes would be incapable of maintaining the production of goods and services that humans expect (Davis 1989; Huntley 1991; Rice and Emery 2003; Tchebakova et al. 2005). Mitigating effects of global

warming, therefore, would require mankind to proactively participate in evolutionary processes by planting the appropriate genotypes of the appropriate species at the novel location of their climatic optima (Tchebakova et al. 2005).

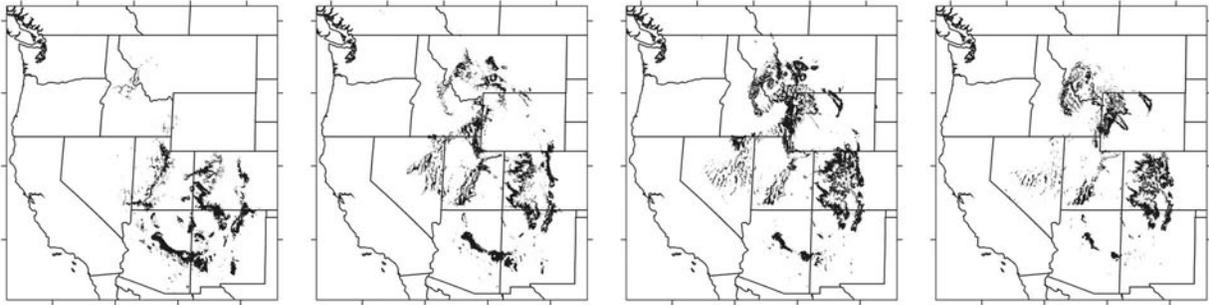
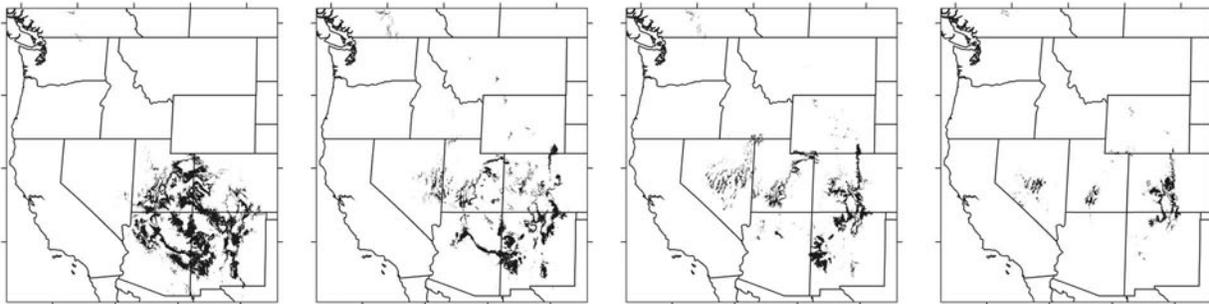
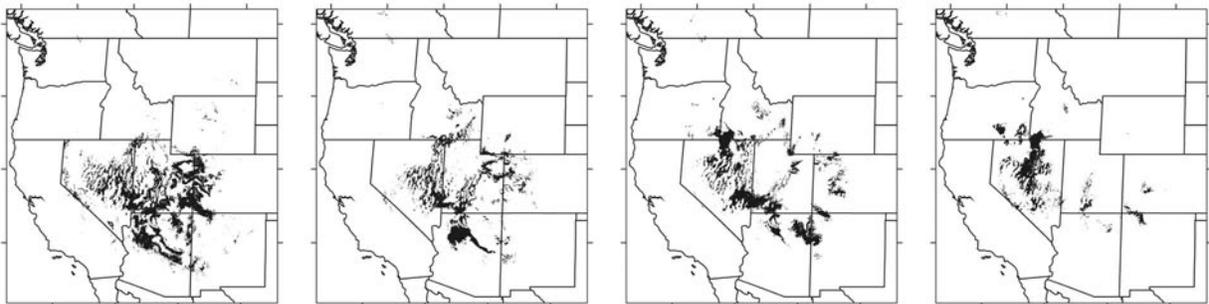
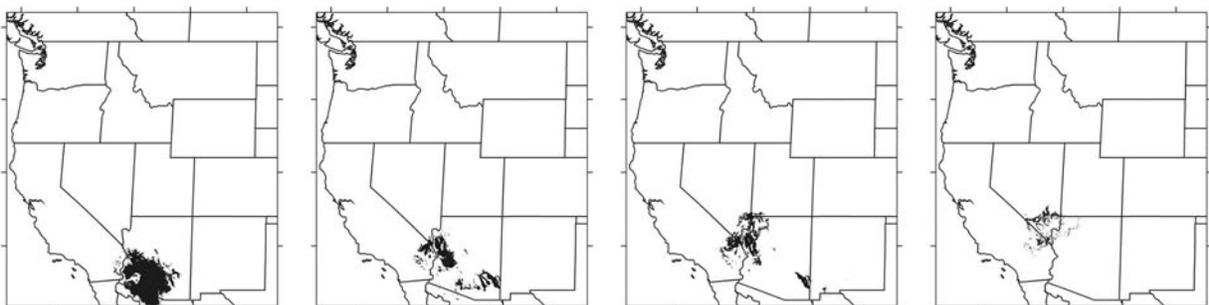
Quercus gambelii*Pinus edulis**Juniperus osteosperma**Carnegiea gigantea*

Fig. 20 Modeled climate profiles (votes > 50%) of four species for the contemporary climate and for the decades beginning in 2030, 2060, and 2090 (left to right).

Correlative models are well suited for designing programs to assist natural processes. Silvicultural practices interwoven into intensive forest management are devoted largely to regulating competition. The control of competition negates the

most serious objections for using correlative vegetation models for prediction, even for the extramural climates (fig. 16). Contemporary reforestation programs with goals of matching species and genotypes to the appropriate array of climates

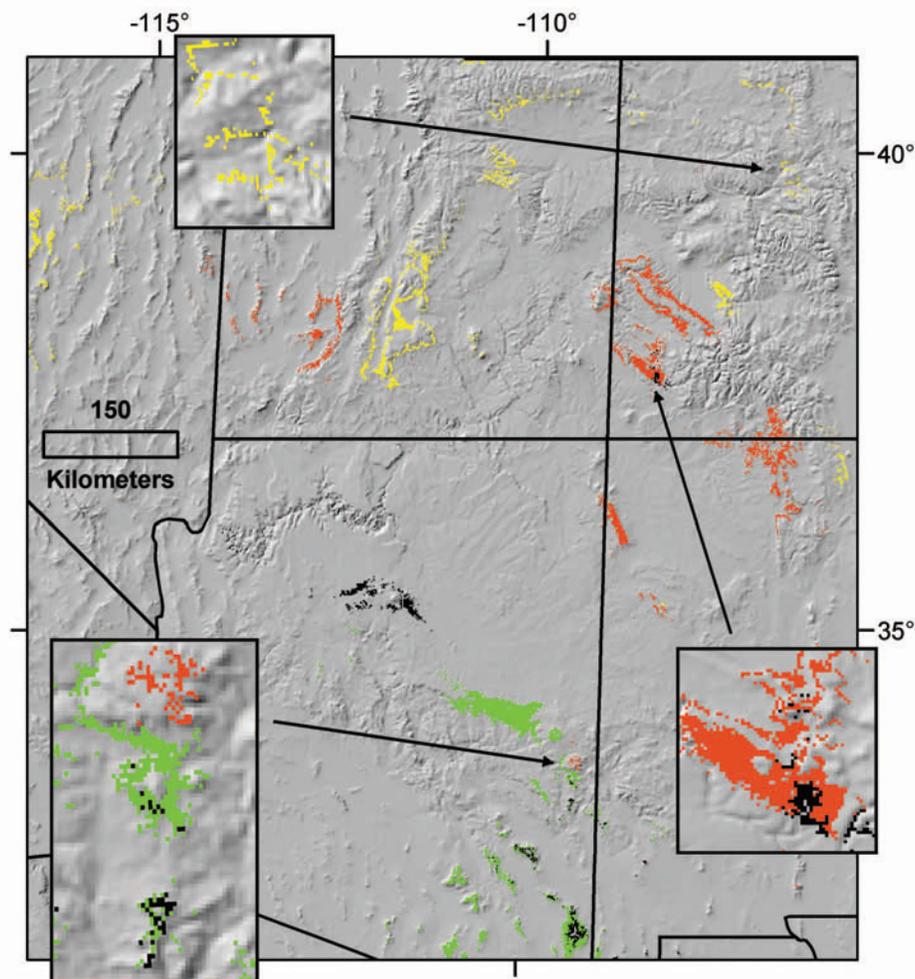


Fig. 21 Climate profile of *Pinus leiophylla* projected for the contemporary climate (green) and for the decades beginning in 2030 (black), 2060 (orange), and 2090 (yellow).

expected several decades in the future require for guidance models similar to those used to produce figures 19–21. Predictions from such models are suitable for pinpointing those locations expected to be climatically suitable for a species at a future date (see Booth 1990; Broadmeadow et al. 2005). A final step would be a query to a model of genetic variation to determine which genotypes would be appropriate (see Rehfeldt et al. 2004; Tchebakova et al. 2005). When mapped at a fine scale (fig. 21), predictions become a tool for land managers.

Conclusions

Bioclimatic models have been developed to predict the occurrence of plant communities and their constituent species. The models are of a scope, power, and precision that are currently unparalleled. Their fit and validation were superb. When applied to the subject of global warming, the models provided intuitively reasonable predictions but brought to the forefront as many questions as answers. Despite the avail-

ability of these powerful models, a thorough assessment of the effects of global warming is still distant. Analyses are particularly needed at the level of the landscape rather than continents or regions. Still, the accuracy of predictions from bioclimatic models ultimately is dependent on the aptness of the scenarios and the precision of the GCMs. Our models emphasize the importance of the periodicity of precipitation and of interactions between temperature and precipitation in controlling the distribution of communities and their species. Accuracy in assessing the ecological effects of global warming, therefore, will require that GCM modelers be as diligent with the effects of atmospheric pollution on precipitation as with temperature.

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