Modeled regional climate change and California endemic oak ranges

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In the coming century, anthropogenic climate change will threaten the persistence of restricted endemic species, complicating conservation planning. Although most efforts to quantify potential shifts in species' ranges use global climate model (GCM) output, regional climate model (RCM) output may be better suited to predicting shifts by restricted species, particularly in regions with complex topography or other regionally important climate-forcing factors. Using a RCM-based future climate scenario, we found that potential ranges of two California endemic oaks, *Quercus douglasii* and *Quercus lobata*, shrink considerably (to 59% and 54% of modern potential range sizes, respectively) and shift northward. This result is markedly different from that obtained by using a comparable GCM-based scenario, under which these species retain 81% and 73% of their modern potential range sizes, respectively. The difference between RCM- and GCM-based scenarios is due to greater warming and larger precipitation decreases during the growing season predicted by the RCM in these species' potential ranges. Based on the modeled regional climate change, <50% of protected land area currently containing these species is expected to contain them under a future midrange "business-as-usual" path of greenhouse gas emissions.

Quercus douglasii | species range displacement | *Quercus lobata* | regional climate model | conservation

Endemic species face relatively great risks from human activities because of their limited geographic distribution. For more than a century, ecologically and culturally valuable endemic oaks of California have experienced pressure from cutting for fuel, grazing, conversion of woodlands to vineyards and orchards, water resource development, competition with invasive grasses, and urban expansion (1). Here, we report how the regional manifestation of anthropogenic global climate change may present an even graver threat, complicating conservation planning for these and other restricted species (2, 3). Specifically, we highlight how predictions of future suitable habitat for endemic species can depend greatly on whether the scenario for climate change is derived from a relatively coarse-resolution global climate model (GCM) or a fine-resolution regional climate model (RCM).

California endemic oaks *Quercus douglasii* Hook. & Arn. and *Quercus lobata* Née (blue and valley oak, respectively) are sensitive to temperature and precipitation at many stages of their life history. Both experience the Mediterranean-like climate of much of California, with winter rain and summer drought. Blue oak occurs in the foothills of the Coast Ranges and western Sierra Nevada, forming both woodland and savannah habitat. It is winter-deciduous and drought-tolerant, remaining active well into the long, dry summers (4, 5). Tree-ring data show greater growth in years with greater mean annual precipitation, although there is geographic variation in the strength of this effect (6). Blue oak seedlings are sensitive to soil moisture availability, with higher mortality and lower growth where competition with annual plants leads more rapidly to growing season soil moisture deficits (7, 8). Valley oak occurs on deeper soils in the Great Central Valley and in riparian habitats of the foothills and has seen much of its

former habitat degraded or eliminated (4). Valley oak is also winter-deciduous but is less drought-tolerant than blue oak. It is highly sensitive at both seedling and adult stages to water stress (9). Higher acorn production by both species is correlated to warmer April temperatures (10), probably a result of greater pollen advection and therefore greater fertilization under warmer, less humid spring conditions (11).

Modern geographic distributions of blue and valley oaks also suggest that their ranges are constrained by climate factors (Fig. 1). We hypothesized that (*i*) the potential range of each species would be related to climate variables, (*ii*) climate change could alter the geographic location of suitable habitat for each species, and (*iii*) predicted future distributions would be sensitive to the spatial and temporal details of predicted future climate change. With respect to (*iii*), we were particularly concerned that predicted range shifts based directly on GCM-derived climate change scenarios could differ qualitatively and quantitatively from RCM-derived scenarios. Predicted climate change impacts to agricultural crop yields and agroeconomic activity (12–14) and to water yield in specific river basins (15) are known to depend on the scale of climate scenario used (GCM vs. RCM), suggesting that predictions for species range shifts could be similarly sensitive.

Methods

Climate Envelope Modeling. We used quadratic discriminant analysis to identify the multivariate climate and soil envelopes, and thereby suitable habitat, for each species. Discriminant analysis is similar to other statistical climate envelope approaches and has been used previously for predicting potential future species ranges with climate change (16). Discriminant analysis identifies the multivariate distance between a given cell and the centroids of all cells in the "oak-present" and "oak-absent" groups, assigning the cell to the closest centroid. We assumed unequal variances between groups and transformed explanatory variables when possible to achieve normal frequency distributions. We first built the statistical model based on modern climate and soils data and then applied the model to GCM- and RCM-based scenarios of future climate.

We selected four explanatory climate variables based on field observations of these species (5–11) and on factors likely to limit the ranges of deciduous trees (17): mean temperatures of the coldest and warmest months, total annual precipitation, and April–August precipitation. We selected three soil variables that reflect the importance of soil properties in regulating moisture availability, including available water-holding capacity, soil depth, and surface layer clay content.§ We used

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Fig. 1. Modern satellite-based distributions of blue oak (*A*) and valley oak (*B*).[¶] California ecoregions labeled in *B* are as follows: NW, northwest California; CR, Cascade Ranges; MP, Modoc Plateau; SN, Sierra Nevada; CV, Great Central Valley; ES, east of Sierra Nevada; CW, central west California; MD, Mojave Desert; SW, southwest California; and SD, Sonoran Desert.[¶]

satellite-based estimates of modern ($\approx$1990) blue and valley oak distributions[¶] and modern climate values derived from 1971–2000 weather station data interpolated to 4-km resolution[‖] as the basis for the discriminant models. (Links to digital versions of the annotated data sources may be obtained from the authors upon request.) Discriminant model-derived modern distributions somewhat overpredict oak presence relative to the satellite data (Table 1) but capture the geographic pattern of both species. The discriminant model predictions have better matches to historic range maps (18) (Table 1), suggesting that the model may be more representative of potential oak distributions before extensive habitat conversion.

We varied the criterion by which cells were assigned to the oak-present group by comparing thresholds of 50% and 80%. Using the higher probability threshold reduced the extent of modern potentially suitable oak habitat, resulting in better matches to the original satellite data and to range maps (Table 1). Raising the probability threshold from 50% to 80% also resulted in 28–40% less future suitable habitat, depending on the species and climate model output used. Therefore, the reported 50% threshold discriminant models, which overpredict modern potential habitat, may also overpredict future suitable habitat for any given future climate scenario.

We used output from a climate change experiment using the RCM RegCM2.5 and the GCM CSM (Climate System Model) (see below) to calculate differences between annual averages of the years 2080–2099 and 1980–1999 for the selected climate variables and added the anomalies to the modern climate 1971–2000 values. We thereby created a projected future California climate based on RCM output and a projected future California climate based on GCM output. We then used the discriminant models derived for each species to predict potential ranges after climate change, holding soil properties constant. We did not explore the third alternative of calculating a future California climate based on statistically downscaled GCM output. However, the relatively smooth, GCM-like signal for summer temperature change in California in a study using statistically downscaled GCM output (19) suggests that this approach may yield predictions that are more similar to those using GCM output than RCM output (see below).

[¶]Davis, F. W., Stoms, D. M., Hollander, A. D., Thomas, K. A., Stine, P. A., Odion, D., Borchert, M. I., Thorne, J. H., Gray, M. V., Walker, R. E., *et al.* (1998) *The California Gap Analysis Project: Final Report* (Univ. of California, Santa Barbara).

[‖]Daly, C., Gibson, W. & Taylor, G. (2002) *103-Year High-Resolution Precipitation Climate Data Set for the Coterminous United States* (Spatial Climate Analysis Service, Corvallis, OR).

Table 1. Skill of discriminant models in predicting the modern distributions of blue and valley oak

Model	Satellite data		Range maps	
	Percent correct	κ	Percent correct	κ
Blue oak				
(50%)	82	0.41	84	0.50
(80%)	87	0.48	87	0.53
Valley oak				
(50%)	71	0.10	81	0.52
(80%)	79	0.12	83	0.51

Numbers in parentheses indicate the likelihood threshold for assigning individual cells to the oak-present group in the discriminant model. Increasing the threshold from 50% to 80% likely improves the models' match to the satellite data and range maps, reducing the modern area predicted as suitable for blue oak (-24%) and valley oak (-27%). Percent correct reflects the percentage of all cells correctly assigned to oak-present and oak-absent groups. κ values account for the cells that would be assigned correctly by chance, where $\kappa < 0.4$ is poor agreement, $0.4 < \kappa < 0.55$ is fair agreement, $0.55 < \kappa < 0.70$ is good agreement, and $\kappa > 0.7$ is very good to excellent agreement (24).

Regional Climate Modeling. Most estimates of potential shifts in species' ranges with future climate change are based on relatively coarse GCM output (20–23). However, RCM-based climate scenarios may be better in California than GCM-based scenarios for several reasons. First, GCMs have topographically smooth landscapes, with each grid cell representing average land surface properties and climate over hundreds of kilometers, whereas RCMs can describe the land surface and topography at much higher spatial resolution. As a specific example, the Sierra Nevada Mountains and the Great Central Valley, which define climatologically distinct ecoregions in California, are represented in the RCM but not the GCM (24). Second, within regional models, with resolutions on the order of tens of kilometers, local topography, distance from the coast, and latitude can result in a more highly resolved, subregionally varying estimate of climate change (Table 2). Lastly, we used the RCM RegCM2.5, which has been used and validated for the western U.S. (25, 26) and compares more favorably to observations than a GCM for a range of temperature and precipitation variables in this region (26). RegCM has also been shown to produce elevationally dependent climate change consistent with observations in other regions (27), a climatic feature not well captured by relatively coarse-resolution GCMs.

We ran the RCM RegCM2.5 from 1980–1999 and 2080–2099, with atmospheric conditions at the domain boundaries derived from the National Center for Atmospheric Research global CSM (28). RegCM2.5 was run with a horizontal resolution of $\approx$40 km, compared with the 2.8° ($\approx$250 km) horizontal resolution of CSM. CSM is a fully coupled atmosphere, ocean, land, and sea-ice model that was run from 1870 to 2099 with observed increases in greenhouse gas concentrations until 1998 and increases thereafter from the ACACIA-BAU (A Consortium for the Application of Climate Impact Assessments Business-as-Usual) emissions scenario. ACACIA-BAU is a "business-as-usual" scenario of greenhouse gas emissions and climate policy similar to Intergovernmental Panel on Climate Change (IPCC) IS92a but with sulfate emissions more consistent with the Special Report on Emissions Scenarios (SRES) average (29). ACACIA-BAU CO_2 emissions rise from 7 to 19 gigatons of C·yr^{-1} between 1990 and 2100, an emissions trajectory slightly higher than the midrange IPCC SRES scenario A1B (30). CO_2 concentrations in CSM increased to $\approx$710 ppm by 2099 with this scenario, whereas the 2080–2099 RegCM2.5 CO_2 concentrations were kept constant at 660 ppm, the CSM midpoint for those years (28, 29). In CSM, mean global temperatures increased 1.9°C from 1990 to

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Table 2. Change in average climate variables between 1980–1999 and 2080–2099 from GCM and RCM output

Region	Model	Mean temperature of the coldest month, °C	Mean temperature of the warmest month, °C	Annual precipitation, mm	April–August precipitation, mm
California	GCM	2.53	2.52	−12.49	−5.27
	RCM	2.45	2.82	−5.18	−19.87
Northwest California	GCM	2.16	2.16	−30.69	−11.81
	RCM	2.27	2.98	31.11	−16.03
Cascade Ranges	GCM	2.51	2.49	−6.95	−2.03
	RCM	2.60	3.33	39.15	−20.45
Modoc Plateau	GCM	2.54	2.52	−3.65	−0.44
	RCM	2.64	3.65	39.81	4.26
Sierra Nevada	GCM	2.57	2.55	−2.12	−0.65
	RCM	2.66	2.90	−17.20	−46.43
Great Central Valley	GCM	2.45	2.43	−6.28	−2.36
	RCM	2.37	2.41	−3.63	−24.56
East of Sierra Nevada	GCM	2.71	2.71	−0.85	−0.58
	RCM	2.86	3.53	−18.16	−25.39
Central west California	GCM	2.25	2.23	−18.08	−7.44
	RCM	2.21	2.15	−20.35	−18.78
Mojave Desert	GCM	2.83	2.84	−14.07	−6.81
	RCM	2.68	3.07	−13.77	−10.82
Southwest California	GCM	2.58	2.58	−15.26	−7.41
	RCM	2.28	2.41	−31.38	−16.12
Sonoran Desert	GCM	2.80	2.79	−14.37	−7.31
	RCM	2.04	2.53	−38.06	−5.79
Blue oak	GCM	2.38	2.37	−12.65	−4.94
	RCM	2.37	2.56	2.71	−24.45
Valley oak	GCM	2.32	2.34	−13.27	−5.26
	RCM	2.32	2.49	0.04	−23.26

The first two rows reflect mean changes for all of California; subsequent rows reflect changes within the ecoregions identified in Fig. 1*B*. Blue oak and valley oak rows reflect changes within the modern potential habitat for those species, as determined by the discriminant model described in the text.

2100, a projection at the low end of the IPCC multiscenario, multimodel envelope (31).

Overall, CSM has a cold bias ($\approx$1–2°C annual average) and tends to be wet (up to 5 mm·d^{-1}) in western North America compared with observations (28, 29). Compared with observations, RegCM2.5 is cool (by 2–4°C on a monthly basis), wet during the rainy season (by 2.0 mm·d^{-1}), and dry in the late summer (by 0.6 mm·d^{-1}) (28). In California, RegCM2.5 slightly underestimates both the warmest and coldest month temperatures, whereas CSM overestimates the coldest month temperatures and underestimates the warmest month temperatures, as compared with observations. RegCM2.5 overestimates both annual (by $\approx$800 mm·yr^{-1}) and April–August (by $\approx$240 mm·yr^{-1}) precipitation, particularly in northwest California and the Sierra Nevada; CSM underestimates annual precipitation in northwest California and the Sierra Nevada (by $\approx$400 mm·yr^{-1}) and overestimates April–August precipitation in these subregions (by $\approx$200 mm·yr^{-1}). Overall, RegCM2.5 better captures the spatial patterns of temperature and precipitation throughout the state when compared with high-resolution observational data (32) (see Fig. 3, which is published as supporting information on the PNAS web site).

Because we used the change in climate between two time periods for projecting changes in suitable oak habitat, model bias is less relevant than model sensitivity to transient climate forcing, such as by greenhouse gases. When driven by the global atmospheric model HadAMH, RegCM reproduced slight winter warming trends in some subregions of Europe,

but not all, and a related winter drying trend in the Mediterranean region over the 20th century (33). For the European temperature trends, much of the model agreement with observations (or lack thereof) is attributed to global model forcing, whereas local feedbacks within the regional model appear to improve trend simulation for precipitation in some subregions (33). CSM, the global model we used as initial and boundary conditions, reproduces the pronounced global warming trend in the late 20th century, although it did not capture the rapid midcentury warming seen in observations (29). CSM also captures the slight positive trend in northern mid- to high-latitude precipitation over the 20th century but does not represent decadal variations in the El Niño southern oscillation very well, a point of concern for the tropics and our western U.S. region.

Conservation Area Calculations. To estimate the fraction of potential modern and future oak habitat overlapping with existing conservation areas, we combined digital maps of U.S. National Wilderness Areas** and of National Parks, California State Parks and Reserves, and private conservation areas†† into a single data layer. We then examined the change in the number of oak-present cells overlapping with all conservation areas

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**U.S. Geological Survey (2004) *National Atlas of the United States of America* (U.S. Geological Survey, Reston, VA).

††California Resources Agency (2003) *California Legacy Project* (California Resources Agency, Sacramento, CA).

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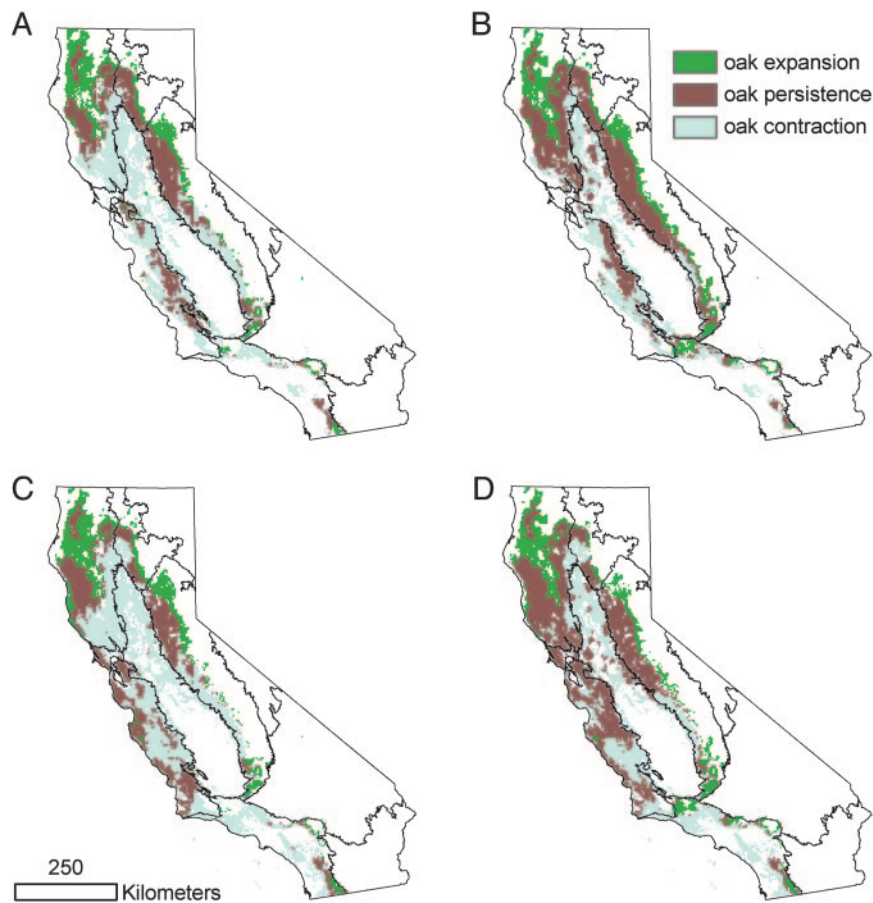
Fig. 2. Potential modern (light blue and brown) and future (brown and green) distributions of blue oak (*A* and *B*) and valley oak (*C* and *D*). *A* and *C* reflect distributional changes based on the RCM scenario; *B* and *D* reflect changes based on the GCM scenario.

between the modern and future scenarios. We used SYSTAT 8.0 for all statistical analyses and ARCGIS 8.3 for geospatial associations among climate, soil, species, and conservation area maps.

Results and Discussion

With RCM-based climate change, suitable habitat shrank to 59% and 54% of modern potential range sizes for blue and valley oak, respectively (Fig. 2 *A* and *C*). With GCM-based climate change, we saw more modest overall contractions to 81% and 73% of current range sizes (Fig. 2 *B* and *D*). For both species and model scenarios, we saw some expansion into northwestern California and the Sierra Nevada Mountains, with more persistence and expansion at the southern end of the species' range under the GCM cases. Under the RCM scenario, ≈39% of the predicted future habitat is new, whereas ≈30% is new under the GCM scenario.

The difference between RCM- and GCM-based predictions can be explained primarily by the larger predicted decreases in RCM April–August precipitation and by larger increases in temperature within the oaks' modern potential ranges, which include the Great Central Valley and Sierra Nevada regions (see Fig. 4, which is published as supporting information on the PNAS web site; see also Table 2). For example, in areas that lost blue oaks under the RCM case, annual precipitation changed <1%, April–August precipitation declined 43%, and both coldest month and warmest month mean temperatures increased by >2.3°C, resulting in a more heat- and drought-stressed environment during these winter-deciduous species' growing season. Mean temperature of the warmest month increases more in the

RCM than in the GCM, especially in Northern California, in the Sierras, and east of the Sierras. This discrepancy could be due to the fact that the RCM has more detailed topography than the GCM, resulting in greater warming at higher elevations, an effect that has been observed in the Alps (27). Changes in precipitation may also be elevation-dependent (27), but the larger decrease in summertime precipitation in the RCM is likely due to better resolution of spring circulation patterns. As a result of the large GCM grid cell size, storm systems may be more extensive in the GCM than in the RCM, with the most pronounced differences in the month of May. Additional factors that could yield stronger signals in temperature and precipitation in subregions of the RCM include more heterogeneous land cover, and therefore albedo and energy partitioning, and better resolution of convective activity and cloud cover.

Our predictions are based on only one RCM realization of potential climate change in the western U.S. Consistent with our RCM scenario, Leung *et al.* (34) found a nonsignificant warm season drying trend in California between 1995 and 2060 using an RCM, MM5, and a GCM, PCM. However, using another RCM, MAS, and GCM, HadCM2, Kim *et al.* (35) found a small increase in summer precipitation between control and enhanced CO_2 runs. Differences among scenarios may be due in part to GCM input but also to how the RCMs resolve circulation patterns and parameterize convective precipitation. Model scenarios yielding growing season precipitation increases may result in an expansion of suitable oak habitat rather than a contraction, as we found.

Our results indicating decreases and northward shifts in potential blue and valley oak habitat are consistent with

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modeled vegetation change in the California region predicted by dynamic vegetation models. Using the model MC1, Lenihan *et al.* (36) found that mixed evergreen woodland decreases in extent relative to the historic case under two different GCM scenarios for the 2070–2099 time period, losing out to mixed evergreen forest in one scenario (HadCM2) and to grassland in the other (PCM). Mixed evergreen woodland persists or expands slightly at the northern and upper elevation limits of its historical distribution. Also using MC1 but statistically downscaled output from four GCM scenarios, Hayhoe *et al.* (19) found overall decreases in the extent of mixed evergreen woodland with climate change by 2050 and 2100, primarily to expansion by grassland.

Our results showing impacts dependent on the scale of the climate model scenario are also consistent with studies of agricultural yield changes under RCM and GCM scenarios for climate change. In the midwestern U.S., yield differences between RCM and GCM scenarios were most pronounced where the climate models differed in precipitation, temperature, and humidity during key periods of the growing season, leading to differential water stress in some crops (13). Similarly, in the southeastern U.S., crop-specific sensitivity to RCM vs. GCM changes in growing season precipitation and temperature resulted in differences in predicted yield (12). The latter study also found that by adjusting planting dates for corn, the effects of decreased precipitation during the summer months in the RCM scenario were mitigated. For predicting impacts, this result underscores the importance of understanding the ability of agricultural and natural systems to adapt to climate changes, as well as the importance of using accurate climate change scenarios.

With our RCM-based results, we found that of the current conservation area encompassing current potential oak ranges, <50% (33% for blue oak and 40% for valley oak) also encompassed future suitable habitat, indicating that today's conservation areas may not provide protection for future oak habitat (data not shown). Future overlap between oak habitat and protected areas established to protect other species and ecosystems would depend on the ability of these two species to disperse northward and to compete with existing coniferous vegetation in the predicted future ranges. Climate-driven range shifts will be constrained by nonclimate factors that affect recruitment and establishment, including fire regimes, browsing by domestic and wild animals, acorn predation, and competition with annual grasses and conifers (37–39). For valley oak, small genetic "neighborhoods" also suggest limited genetic exchange across the modern landscape (40), indicating that the ability of this species to migrate significant distances in response to climate change may be limited. Given the above challenges to range shifts by these species, their persistence may be highly dependent on their ability to adapt to climate change *in situ*, perhaps by adjusting their growing season.

Our results show that conservation planning guided by GCM output or by the expectation of simple upward elevational shifts in distributions for these and other restricted species could be misdirected. In California, RCM-based patterns of warming and drying between April and August in the Sierra Nevada Mountains and Great Central Valley result in unexpected reductions and shifts in suitable habitat for two highly valued endemic species, a quantitatively different result than that obtained by using GCM output. This precipitation sensitivity is consistent with the observed importance of water stress to both species' growth and reproduction, leading us to believe that if the spatial variation in predicted climate change is more realistic in the RCM, these and other moisture-sensitive species may be particularly vulnerable to climate change in California. As conservation planners confront climate change, it will be critical that they employ a selection of RCM-based scenarios that resolve variation in climate response on scales relevant to restricted species and regional reserves. Similarly, planning for potential climate change impacts on biogenic trace gas emissions, water resource timing and availability, or agricultural yield and crop suitability should take into account regionally specific results from state-of-the-art RCMs.

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