

Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*)

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Abstract

Anticipating species movement under climate change is a major focus in conservation. Bioclimate models are one of the few predictive tools for adaptation planning, but are limited in accounting for (i) climatic tolerances in preadult life stages that are potentially more vulnerable to warming; and (ii) local-scale movement and use of climatic refugia as an alternative or complement to large-scale changes in distribution. To assess whether these shortfalls can be addressed with field demographic data, we used California valley oak (*Quercus lobata* Nee), a long-lived species with juvenile life stages known to be sensitive to climate. We hypothesized that the valley oak bioclimate model, based on adults, would overpredict the species' ability to remain in the projected persisting area, due to higher climate vulnerability of young life stages; and underpredict the potential for the species to remain in the projected contracting area in local-scale refugia. We assessed the bioclimate model projections against actual demographic patterns in natural populations. We found that saplings were more constricted around surface water than adults in the projected contracting area. We also found that the climate envelope for saplings is narrower than that for adults. Saplings disappeared at a summer maximum temperature 3 °C below that associated with adults. Our findings indicate that rather than a complete shift northward and upward, as predicted by the species bioclimate model, valley oaks are more likely to experience constriction around water bodies, and eventual disappearance from areas exceeding a threshold of maximum temperature. Ours is the first study we know of to examine the importance of discrete life stage climate sensitivities in determining bioclimate modeling inputs, and to identify current climate change-related constriction of a species around microrefugia. Our findings illustrate that targeted biological fieldwork can be central to understanding climate change-related movement for long-lived, sessile species.

Keywords: bioclimate modeling, climate change, microrefugia, oak recruitment, valley oak (*Quercus lobata*)

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Introduction

Species already are responding to climate change through detectable shifts in distributions (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003) and changes in community composition (Brown *et al.*, 1997; Moritz *et al.*, 2008). Species bioclimate models, empirical models based on geographic correlations between species distributions and climate, have been a principal approach to anticipating climate-related species range shifts (Heikkinen *et al.*, 2006) and are one of the few tools available to land managers to guide climate adaptation strategies (Heller & Zavaleta, 2009). Bioclimate models are robust predictors of climate change impacts for certain species (Araújo *et al.*, 2005), and some studies confirm that expected regional-scale range shifts northward and upward in elevation are occurring with warming (Rosenzweig *et al.*, 2008). However,

other species may have more complex distributional responses to climate change that models currently cannot anticipate. There has been considerable debate about bioclimate model assumptions, limitations and reliability (Pearson & Dawson, 2003; Thuiller, 2004; Hampe, 2004; Guisan & Thuiller, 2005; Martinez-Meyer, 2005; reviewed in Heikkinen *et al.*, 2006; Austin, 2007; Botkin *et al.*, 2007; Thuiller *et al.*, 2008) and calls for more ground validation and incorporation of ecological complexity (Araújo *et al.*, 2005; Araújo & Luoto, 2007; Keith *et al.*, 2008). While basic bioclimate models can provide relatively rapid assessment of potential changes in species distributions, the risks of inaccurate predictions are significant in the context of efforts to facilitate species persistence and movement through management actions (Hoegh-Goldberg *et al.*, 2008).

We propose two ways to refine and improve predictions of species response to climate change using field data. First, we argue that consideration of life stage-specific climate vulnerability, so far absent in bioclimate modeling, can improve the reliability and precision

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of model predictions, particularly for long-lived, sessile species. In these species, due to the suite of global changes that have occurred over the past century, current early life stages may experience distinct environmental conditions from those that current adults experienced in their early life stages. Moreover, early life stages may not tolerate the same range of conditions as adults, have been shown to respond differently to environmental gradients than adults (Collins & Carson, 2004), and therefore may respond differently to climate change, shaping changes in the species distribution distinct from predictions based on adult climate tolerances. Therefore, analyses based primarily on adults, the focus of most bioclimate models, could mask the responses of early life stages to climate change. Ongoing climate change (Ladochy *et al.*, 2007) has created the opportunity to test models with field data on emerging changes in distributions (Araújo *et al.*, 2005), through a comparison of spatial patterns of adults that established under historic climate conditions and recruits that currently are establishing in warmer conditions.

A second question that can be addressed by refining bioclimate models with field data concerns whether species can persist in microrefugia, microclimates that support small populations of species beyond the boundaries of the climatic limits of their main distributions (Rull, 2009; Dobrowski, 2010). Most places already are undergoing warming (IPCC, 2007), and comparing adult distributions to recruitment patterns in bioclimate model-projected contracting areas (areas from which a species is expected to retreat in response to climate change), can help identify potential climate microrefugia. While there has been extensive work on understanding the role of climate refugia during the Quaternary period (Keppel *et al.*, 2011), as far as we know, no studies on the impacts of current climate change have documented species constriction into local-scale climate refugia. Identifying and protecting potential microrefugia under current climate change is a new priority for conservation and adaptation planning (Keppel *et al.*, 2011), and Hampe & Petit (2005) suggest that the 'rear edge', or projected contracting area, of climate-based range shifts represents an understudied aspect of species response to climate change that is disproportionately important (based on paleoecological studies) to potential recolonization and the maintenance of genetic diversity. While paleoecological studies have addressed the role of regional-scale topographic refugia, other local factors such as areas of high groundwater availability that affect species through mechanisms like plant drought stress may function similarly and deserve examination.

Valley oaks (*Quercus lobata* Nee), a species endemic to California, United States and of high conservation concern, provide an excellent model system for exploring the potential for life stage analysis to refine bioclimate model projections and for microrefugia to allow persistence within pockets of former species distributions. As valley oaks are a long-lived, non-mobile species, it is possible to compare the current distribution of adults (which indicates the past distribution of saplings that survived to adulthood) with the current distribution of saplings (which bounds the possible extent of the future adult distribution). Young valley oaks also may be especially vulnerable to drought effects of climate change (Matzner *et al.*, 2003; Tyler *et al.*, 2006) exacerbated by ongoing anthropogenic changes in California oak woodlands (Gordon *et al.*, 1989; Grulke *et al.*, 2007; Ladochy *et al.*, 2007; Howard and Merrifield, 2010). The species is thought to be highly dependent on groundwater (Jepson, 1910; Lewis & Burgy, 1964; Griffin, 1973), and drought stress microrefugia may play an important role in conservation.

California has warmed an average of 1 °C over the past century (Ladochy *et al.*, 2007), producing discernible signals of this trend in the state's biota (Kelly & Goulden, 2008; Moritz *et al.*, 2008; Tingley, 2009). Thus, we expected to detect field-based evidence of a similar warming-based shift in valley oak woodlands. A regional bioclimate model has been developed for valley oaks using soil and climate parameters associated with adult distribution data (Kueppers *et al.*, 2005). It projects a decrease in extent and a general northward and upward expansion of the species distribution. We conducted a multi-scale observational field study to assess the correspondence between the valley oak bioclimate model projections (Kueppers *et al.*, 2005), and observed patterns of natural sapling recruitment in 30 study sites across the species distribution (Fig. 1).¹ We used data on valley oak sapling distributions within each site to evaluate whether saplings are constricted in extent relative to adults and whether, in particular, emerging microrefugia are related to groundwater availability. Finally, we compared the potential implications of an adult- vs. early-life stage focus in generating model predictions. We tested a set of hypotheses (1) that the valley oak bioclimate model would be consistent with regional-scale patterns of sapling recruitment: sites with saplings would be concentrated in the model-projected expanding and persisting areas and reduced in the projected contracting area. (2a) That the model would underpredict the potential for valley oaks to

¹We use scale terms as follows: regional scale, on the order of 100s of kms; landscape scale, on the order of 10s of kms; and local scale, on the order of 1 km.

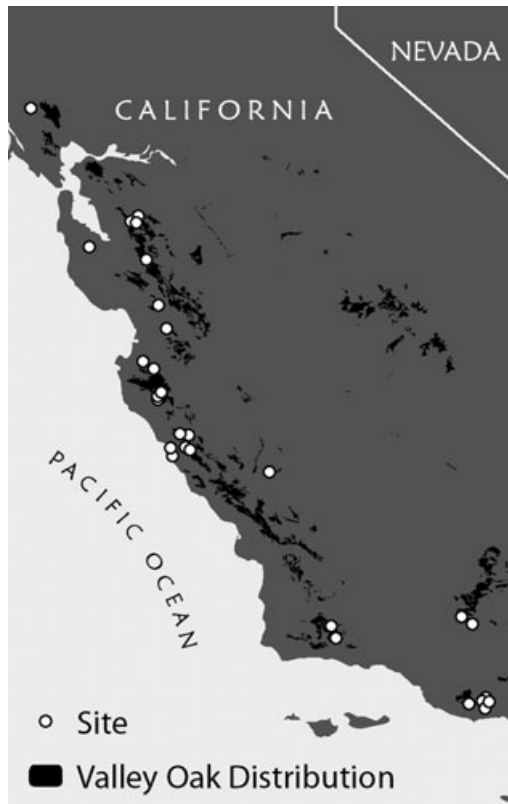


Fig. 1 Map of central and southern valley oak distribution (black), and study sites (white circles) California, United States. Map credit: A. Cole.

remain in the projected contracting area: sites with sapling recruitment would not be reduced and sapling recruitment would be higher in pockets of local-scale refugia in the projected contracting area; and (2b) that the model would overpredict the potential for valley oak survival in the projected persisting area: the overall climate envelope for saplings would be narrower than that for adults.

Materials and methods

Study system

The distribution of valley oak (*Q. lobata*) includes the California Coast Ranges, Central Valley and Sierra Nevada foothills (Griffin & Critchfield, 1972), all in a Mediterranean climate with rainy winters and prolonged summer droughts. The 30 sites across this distribution that comprised the field portion of our study included grazed and ungrazed sites (projected contracting areas: 14 ungrazed, 5 grazed, 1 unknown; projected persisting and expanding areas: 7 grazed, 3 ungrazed), an elevation range of 300–1400 m and a gradient of 45–100 cm average annual precipitation. Site community compositions included mixed valley oak, blue oak (*Quercus douglasii*) and live oak (*Quercus agrifolia*), mixed oak/conifer, and pure valley

oak woodlands, all with valley oak as the dominant tree species. Most sites had a non-native, annual grass understory (*Bromus* spp., *Avena* spp.), which has replaced an understory historically dominated by native perennial bunch grasses and forbs (Beetle, 1947; Barry, 1981; Gordon *et al.*, 1989). Valley oak sapling recruitment is thought to be rare in this system (reviewed in Tyler *et al.*, 2006; Zavaleta *et al.*, 2007).

We chose study sites based on interviews with land managers to help identify stands with sapling recruitment ($N = 20$); and where previous surveys had been conducted, identified through the literature ($N = 10$) (Fig. 1). Sites ranged from 0.5 to 1 km² in area. We identified 26 sites as ‘recruiting’, with more than 1 sapling [1.3–9 cm at base diameter and >0.5 m in height (Zavaleta *et al.*, 2007)] occurring within a 1 km² area. We excluded from our study: areas that were highly disturbed or within 5 m of roads or fencelines, and areas with mixed *Q. lobata* and *Quercus garyana* adults, which have morphologically indistinguishable saplings. We limited our analyses only to areas within the bounds of our land manager interviews, mainly in the central and southern parts of the distribution. The term ‘adult distribution’ in this paper refers to this subset of the valley oak distribution (Fig. 1). Thus, our conclusions are most applicable to oak woodland and savanna in the central and southern portions of the distribution (Fig. 1).

Field surveys

In all sites, to map valley oak saplings and to establish areas with and without recruitment, a field crew conducted a sweep of the entire site and took GPS coordinates for all valley oak saplings ($N = 4219$). To interpret relationships between recruitment and groundwater availability, we mapped springs and streams within each site. For all mapping, we used a Trimble GeoXH 2005 (Sunnyvale, CA, USA), accurate to 0.5 m. In 14 of the 30 sites, we were able to identify discrete, proximate recruiting and non-recruiting areas within the site, allowing for within-site comparative analysis. Non-recruiting areas were defined as areas at least 50 m from any valley oak sapling but within 50 m of a mature adult tree. To assess whether proximity to surface water was related to successful recruitment, we took GPS coordinates of randomly located saplings in recruiting areas and at random points in non-recruiting areas, with approximately one mapped point per 1500 m² of space. Surveys were conducted between late May and August of 2009.

Valley oak bioclimate model

To identify areas of the species distribution projected to expand, persist or contract with climate change, we used a regional bioclimate model for valley oaks projecting a change in distribution by 2100, based on a business-as-usual emissions scenario, similar to the IPCC A1B scenario (Kueppers *et al.*, 2005). The model used multivariate climate and soil envelopes as inputs to determine suitable habitat and based current distribution data on the California GAP analysis, relatively robust locality data for this species (Kueppers *et al.*, 2005). We chose this model over others based on global

climate models because of the former's sensitivity to sub-regional climatic changes from topographic and maritime effects. The model places land areas into one of three climate change projection categories for valley oaks: contracting areas, which are in the current potential distribution but projected to lose valley oaks completely; persisting areas, which are in the current potential distribution and in which valley oaks are expected to remain; and expanding areas, those not in the current potential distribution but into which valley oaks are expected to expand. Areas classified into the three model categories (expanding, persisting, and contracting) differ in current climate. Current mean maximum August temperatures and annual average precipitation for areas within the three categories are as follows: contracting: 32.4 °C, 61.1 cm; persisting: 30.1 °C, 103.4 cm; and expanding: 28.4 °C, 143.4 cm (30 year normals, PRISM Climate Group).

GIS and analysis

To explore correspondence of the valley oaks bioclimate model and the distribution of sapling recruitment, we overlaid layers of the model-projected expanding, persisting and contracting areas of the range (scale: 4 km²; Kueppers *et al.*, 2005) and the current valley oak adult distribution (scale: 1 : 100 000 km; California GAP analysis, UCSB 1998, updated 2002). We then generated a null expected proportion of recruiting sites that should occur in each of the three model-projected category areas, based on the proportion of the area of the current adult distribution in each. We used a chi-square test to determine whether the expected and observed (based on the GPS coordinates of our field site locations) distributions of recruiting sites differed. We also conducted binomial tests separately on each category to compare the expected likelihood of sites with recruitment in each model-projected category, with the proportion of observed sites falling into each model-projected category. The expanding category for both analyses above included areas within 5 km of a projected expanding edge. Much of the model-projected expanding area did not contain valley oaks, and a 5 km buffer allowed us to examine demography at the potentially expanding edge of the current distribution.

To evaluate whether patterns of recruitment in relation to surface water differed in the model-projected expanding/persisting and contracting areas, we compared the distances of saplings and adults to surface water in each model-projected category at two scales. To analyze local-scale hydrologic features, we created our own layer of GPS data on streams and springs at each site. We compared the distance to streams and springs for recruiting and non-recruiting points, in each of the model-projected categories (contracting $n = 164$ points; persisting/expanding $n = 119$ points), using a two-sample, two-tailed *T*-test. For this and subsequent analyses, we combined the projected expanding and persisting areas because they showed qualitatively similar trends.

To compare proximity to water bodies of recruiting and non-recruiting areas at the regional scale, we measured distances to key hydrologic features: rivers, lakes and reservoirs, and ground water basins, for all saplings ($N = 4219$)

and for an equal number of randomly generated points throughout the adult distribution. To map these large hydrologic features, we used the US Water Bodies dataset (USGS and US EPA, ESRI, 2008), the US Rivers and Streams dataset (USGS and US EPA, ESRI, 2008), and the California ground-water basin maps (CA DWR) (scale: 1 : 100 000 for all). We compared the distances of saplings and randomly generated points to each of these hydrologic features in the contracting and persisting/expanding model-projected categories, using a two-sample, two-tailed *T*-test with a Bonferroni *post hoc* correction.

To determine whether saplings had a narrower climatic envelope than adults, we compared climate parameters in our GIS layer of known valley oak recruitment (based on our field data) to the current adult distribution (California GAP analysis, UCSB 1998, updated 2002). We compiled the PRISM 30-year means (1960–1990, scale: 1 km²) of annual average precipitation, shown to be important to valley oak distribution (Kueppers *et al.*, 2005) and maximum August temperatures, which likely represent the highest levels of drought stress experienced by recruits, associated with both the adult distribution and our sapling layers. We generated a distribution of mean maximum August temperature and annual average precipitation associated with the adult distribution and with the recruiting sites, using a GIS grid of 750 m² cells (based on the average size of our field sites). We compared mean climate values in the recruiting areas ($N = 52$ cells with saplings) to climate values across the adult distribution. For this analysis, to reduce the potential confounding effects of unequal sample size, we resampled 1000 random draws of 52 cells from the adult distribution. We generated a *P*-value by evaluating where the mean of the 52 recruiting values fell within the distribution of means of the 1000 resampled draws of 52 cells from the adult distribution.

To evaluate whether minimum and maximum climate thresholds were different between the sapling and adult climate envelopes, we compared the lowest and highest values of maximum August temperatures and average annual precipitation associated with saplings ($N = 4219$) to randomly chosen points throughout the adult distribution ($N = 4219$). From this we identified the climate values above and below which saplings were not found and calculated the percentages of the adult distribution outside of those values. To estimate how the current valley oak bioclimate model might change if the model inputs were based on climate parameters associated with saplings instead of those associated with adults, we subtracted from the adult-based model inputs all areas above the observed maximum August temperature associated with saplings, and calculated the percent reduction of the area of adult-based inputs.

In all analyses, we transformed data as necessary to address violations of homogeneity of variance and normality. We analyzed the effect of timing of field survey on all variables to ensure that patterns were not due to seasonal differences. We used ArcGIS 10 (ESRI 2010) and Trimble GPS Pathfinder Office software (Trimble Navigation Limited, Sunnyvale, CA, USA). All statistical analyses were performed using SYSTAT 12 (Systat Software Inc., San Jose, CA, USA).

Results

The distribution of recruiting sites across the bioclimate model-projected categories (expanding, persisting and contracting) did not differ from the null expected proportion of recruiting sites in each category, based on the proportion of the area of the current adult distribution in each projection category ($N = 26$ sites with recruitment, 26 random locations) ($P > 0.05$) (Fig. 2). When we compared the expected and observed numbers of recruiting sites in each category separately the results were as follows: the number of recruiting sites in the projected expanding area was different and more than expected, binomial probability = 0.013; the number of recruiting sites in persisting areas was different and less than expected, binomial probability = 0.027; the number of recruiting sites in the projected contracting area was not significantly different than expected, binomial probability = 0.86. Our study was not designed to analyze grazing effects on recruitment, however, in our sites the presence of grazing did not predict whether or not a site had sapling recruitment (B. C. McLaughlin and E. S. Zavaleta, unpublished data).

Constriction of saplings to microrefugia

At the local scale, the model-projected contracting and persisting/expanding areas had different associations between oak recruitment and surface water. In the projected contracting area, saplings were closer than adults to surface water ($P = 0.005$, $T = 2.79$, $N = 164$, $df = 163$); in the projected persisting/expanding areas, we did not detect significant differences in distance to surface water between adults and saplings (Fig. 3).

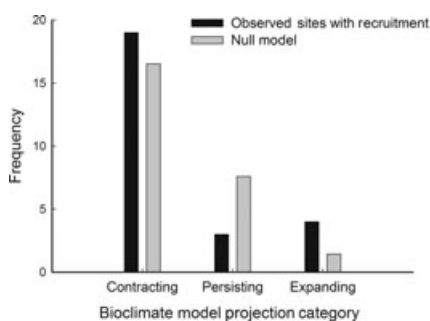


Fig. 2 Black bars represent sites with observed valley oak sapling recruitment ($N = 26$) in each of the bioclimate model-projected categories. Gray bars represent 26 locations chosen at random from the valley oak adult distribution, in proportion with the area of the distribution in each of the bioclimate model-projected categories (expanding, persisting and contracting), representing the null model of the expected distribution of recruitment across projected categories. No error bars exist for this figure because the y -axis represents known counts.

At the regional scale, in the projected contracting area, saplings were closer to rivers ($P < 0.00001$, $T = 24.2$, $df = 5362$, $N = 5364$), lakes and reservoirs ($P < 0.00001$, $T = 23.6$, $df = 5362$, $N = 5364$), and groundwater aquifers ($P < 0.00001$, $T = 20.9$, $df = 5362$, $N = 5364$) than the adult distribution (Fig. 4a–c). In the projected persisting/expanding areas, saplings were further away from rivers ($P < 0.00001$, $T = -9.3$, $df = 2667$, $N = 2669$), lakes and reservoirs ($P < 0.00001$, $T = -18.5$, $df = 2667$, $N = 2669$), and groundwater aquifers ($P < 0.00001$, $T = -19.1$, $df = 2667$, $N = 2669$) than the adult distribution (Fig. 4a–c).

Sapling climate envelope

Sapling recruitment was more climatically restricted than the adult distribution, to areas with higher average annual rainfall ($P < 0.05$) and lower maximum summer temperatures ($P < 0.01$) (Fig. 5a and b). The range of maximum August temperatures and average annual precipitation associated with recruiting sites was narrower than that associated with the adult distribution (Fig. 6), (recruiting sites: minimum = 23.5 °C, 35.4 cm, maximum = 34.6 °C, 108.6 cm; adult distribution: minimum = 22.5 °C, 19.8 cm, maximum = 37.6 °C, 144.8 cm). For maximum August temperature, the climate envelope of saplings was shifted to the cooler area of the adult distribution: 13.2% of the adult data points occurred at temperatures above the maximum value associated with saplings, and 0.001% of the adult data points occurred at temperatures below the minimum value associated with saplings (Fig. 6a). For average annual precipitation, the climate envelope of saplings was shifted toward the wetter area of the adult distribution: 7% of the adult data points occurred at precipi-

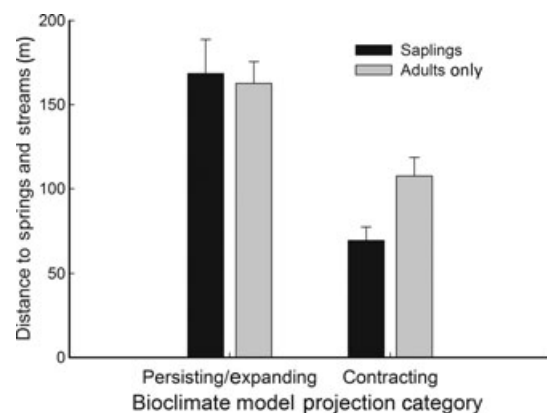


Fig. 3 Distance to streams and springs for field plots with and without valley oak sapling recruitment in the projected persisting/expanding and contracting areas, as identified by the valley oak bioclimate model. Bars represent \pm standard error.

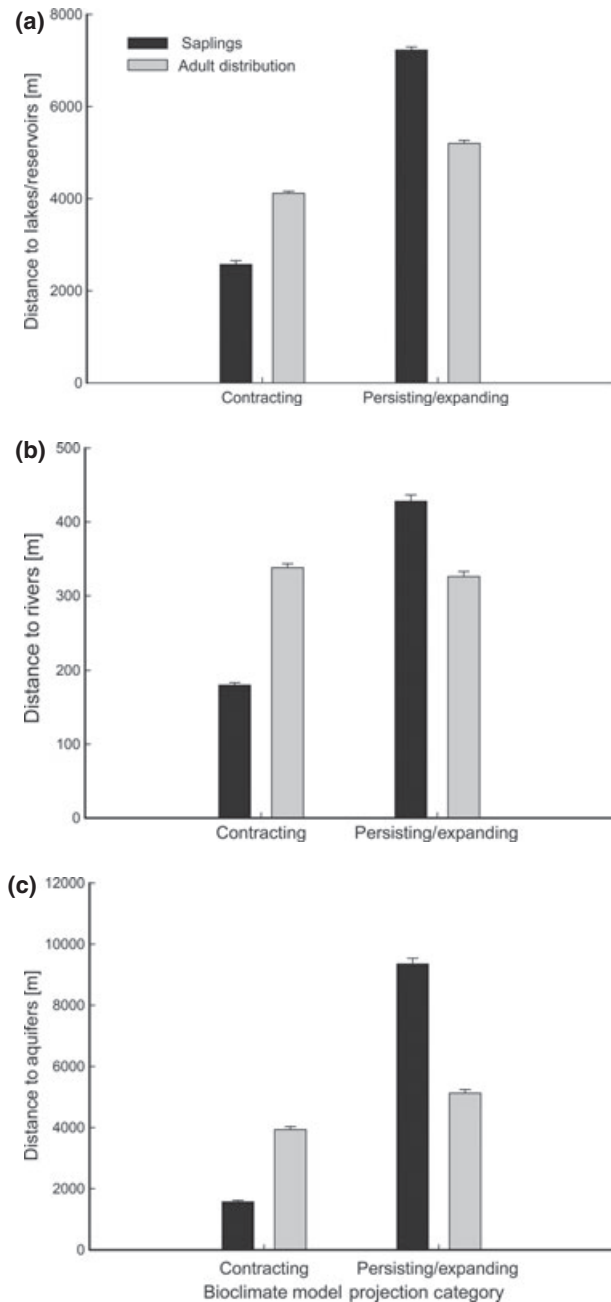


Fig. 4 Distance to (a) lakes/reservoirs, (b) rivers, and (c) groundwater aquifers for valley oak saplings and randomly generated points throughout the valley oak adult distribution in the projected persisting/expanding and contracting areas, as identified by the valley oak bioclimate model. Bars represent \pm standard error.

tation values below the minimum value associated with saplings, and 1.9% of the adult data points occurred above the maximum value associated with saplings (Fig. 6b). Based on a threshold of 34.6 °C maximum August temperature (the highest value at which we

found recruitment), the regional bioclimate model inputs overpredicted areas climatically associated with saplings by 15% (Fig. 7).

Discussion

Based on recorded ongoing regional warming (Ladochy *et al.*, 2007), directional species movement in multiple California systems (Kelly & Goulden, 2008; Moritz *et al.*, 2008) and the valley oak bioclimate model (Kueppers *et al.*, 2005), we expected to see evidence of a warming-based shift having already begun to occur in valley oak woodlands. We expected that recruitment patterns today would be consistent with projections of the future species distribution, demonstrating an early signal of distributional shifts. Our first hypothesis was that recruiting sites would be concentrated in the model-projected expanding and persisting areas and reduced in the projected contracting area. This would imply a correspondence between the bioclimate model projections and observed field data. The lack of significant difference between the null expected distribution and the observed distribution of sites with sapling recruitment indicates that the bioclimate model was not consistent with the observed patterns of sapling recruitment (Fig. 2). However, the lack of significant difference may have been due to the chi square test's sensitivity to small sample size (Zar, 2010). Therefore, we also examined the differences between observed and expected numbers of recruiting sites in each model-projected category. In the model-projected expanding area there were more recruiting sites than expected by the null model. This finding was consistent with the first hypothesis that sapling recruitment would be concentrated in model-projected expanding and persisting areas. However, contrary to this hypothesis, in the model-projected persisting area, there were fewer recruiting sites than expected. In the model-projected contracting area, there was no significant difference between the observed and expected numbers of recruiting sites, also inconsistent with the first hypothesis that recruiting sites would be reduced in the projected contracting area. These results indicate that overall, the bioclimate model successfully predicted areas of potential range expansion, evidenced through increased sapling recruitment in the model-projected expanding area. However, observed patterns of sapling recruitment were not consistent with the model-projected persisting or contracting areas, indicating that other factors aside from regional climate are shaping the future species distribution in these places.

Recent efforts to improve bioclimate modeling include incorporating multiple scales (Kueppers *et al.*,

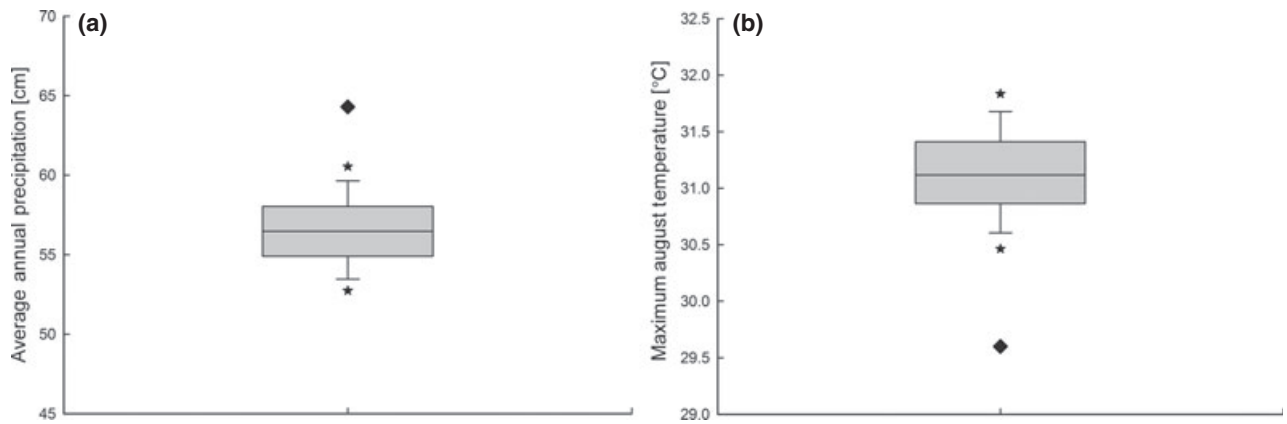


Fig. 5 Box and whiskers represent climate values for the valley oak adult distribution: the box edges mark the first and third quartiles, the whiskers mark the upper and lower ranges of the non-outlier points, and stars represent outlier points. Black diamonds represent the mean value in sites with valley oak sapling recruitment. (a) Mean maximum August temperature for the 52 climate grid cells in recruiting sites and the mean maximum August temperature of 1000 random draws of 52 cells from across the adult distribution. (b) Mean annual precipitation for the 52 cells in recruiting sites and the mean annual precipitation of 1000 random draws of 52 cells from across the adult distribution.

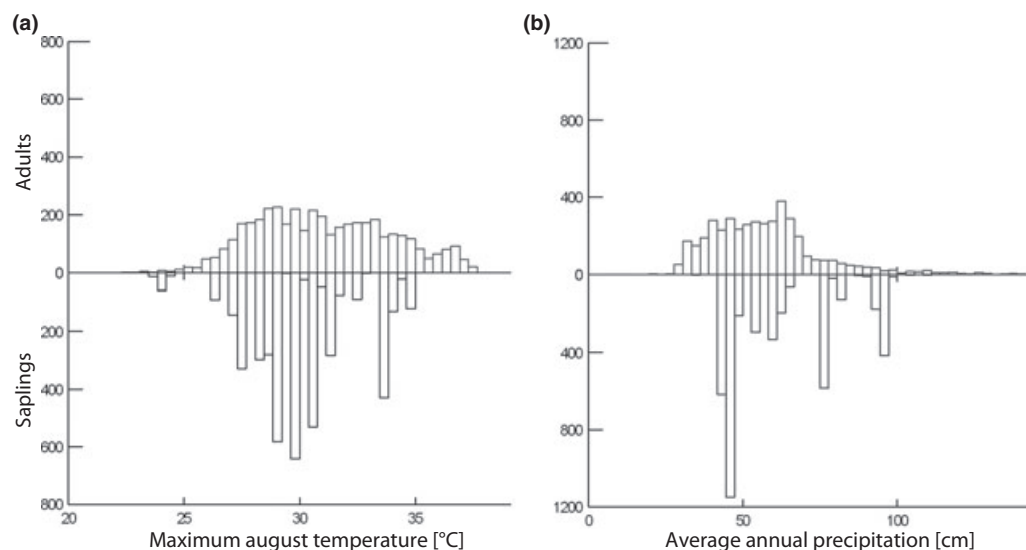


Fig. 6 The range of (a) August maximum temperatures and (b) average annual precipitation associated with valley oak saplings ($N = 4219$) and randomly generated points throughout the adult distribution ($N = 4219$).

2005; Seo *et al.*, 2009) and sample sizes (Stockwell & Peterson, 2002), and different types of abundance data (Brotons *et al.*, 2004; Chefaoui & Lobo, 2008), biotic interactions (Davis *et al.*, 1998; Leathwick, 2002; Araújo & Luoto, 2007), and demography and dispersal (Iverson & Prasad, 2002; Peterson *et al.*, 2002; Keith *et al.*, 2008). The incorporation of spatial demographic data, with a focus on climate-vulnerable life stages and the identification of potential microrefugia, can further refine these efforts and improve predictions of species response to climate change. Instead of overall recruit-

ment patterns consistent with the regional-scale distributional shift projected by the species bioclimate model, our findings support our second hypothesis, suggesting (i) that microrefugia in the form of higher groundwater availability is facilitating valley oak persistence through constricted pockets of sapling recruitment in model-projected contracting areas; and (ii) that saplings have a narrower climate envelope than adults, likely restricting the potential for the species to remain in model-projected persisting areas, where these areas exceed sapling-specific climate thresholds.

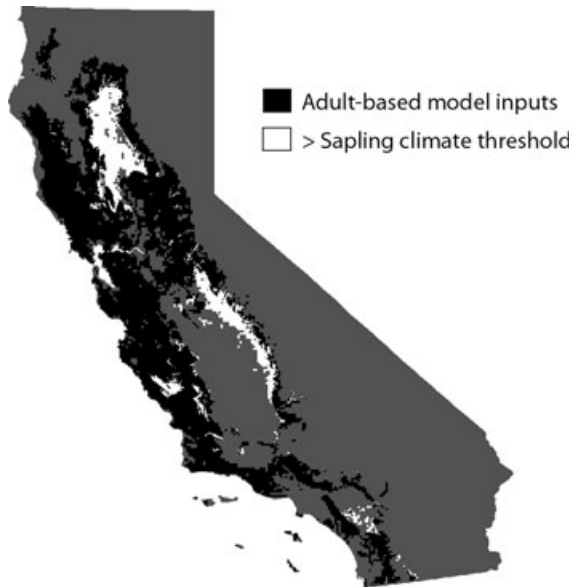


Fig. 7 Valley oak bioclimate model area inputs based on the area of the current potential adult distribution (black) (Kueppers *et al.*, 2005), and areas inputs that would be excluded in a model based on the sapling climate threshold (white). Map credit: A. Cole.

Constriction to microrefugia

Evidence, mainly from Quaternary phylogeographic studies (Keppel *et al.*, 2011), suggests that regional-scale climate refugia were important for species persistence through rapid climate fluctuations during the last glacial maximum and later allowed for postglacial recolonization (reviewed in Dobrowski, 2010; Keppel *et al.*, 2011). In a current extension of this concept, Loarie *et al.* (2008) map predictions of future regional-scale climate refugia for endemic species in California and suggest that areas that harbor species with shrinking ranges, such as scattered mountainous areas, may provide good conservation targets. While much historical work focused on large-scale climate refugia there is also some evidence for species' use of local scale or microrefugia (also referred to as cryptic refugia), microclimates that supported small populations of species beyond the climatic limits of their main distributions (Rull, 2009; Dobrowski, 2010). Recently, restriction to favorable microclimates has been shown to occur near the climatic edges of species distributions (Hennenberg & Bruelheide, 2003) and it has been proposed, in theory, that a spatial shift to particular topographic conditions may act as an early indicator of climate change impacts on a species' distribution (Korner, 1999; Thomas *et al.*, 2001). Protecting microrefugia has been suggested as a potential *in situ* conservation option for

species threatened by climate change (Dobrowski, 2010), however, actual patterns of climate change-related constriction into microrefugia had yet to be demonstrated with current field data.

Work on microrefugia has focused mainly on topographic microclimates (Stewart & Lister, 2001; Dobrowski, 2010), yet other forms of drought stress microrefugia also may exist. Because of valley oaks' direct use of groundwater (Jepson, 1910; Lewis & Burgy, 1964; Griffin, 1973), we expected that drought stress microrefugia might exist for this species in areas of high groundwater availability, and that these areas would be important for recruitment within model-projected contracting areas. Our finding of different distribution patterns of saplings around surface water between the projected expanding/persisting and contracting areas supported this hypothesis. In the projected contracting areas saplings were more restricted to water bodies, indicating that a climate-based shift in local distribution of valley oaks may be already underway, and that microrefugia, in the form of higher groundwater availability, may play a role in mediating the effects of regional climate change. We saw evidence for this both at the local scale with streams and springs (Fig. 3), and at the landscape scale with rivers, lakes and reservoirs, and groundwater basins (Fig. 4a–c).

Our finding that valley oak saplings grow closer to water bodies in the projected contracting areas, at two scales, likely indicates a higher dependence on groundwater availability during the drought stress-vulnerable seedling-to sapling transition phase (Matzner *et al.*, 2003; Tyler *et al.*, 2006). Because of higher temperatures and lower precipitation in projected contracting areas, seedlings there likely experience higher overall drought stress than seedlings in the projected persisting/expanding areas. With warming, seedlings in these contracting areas may be the first to encounter drought stress thresholds that cause them to require quicker access to the water table, restricting recruitment to areas where the water table is relatively high.

We also found that at the landscape scale (but not at the local scale) saplings grow in areas further from water bodies than adults in the persisting/expanding areas. Reasons for this finding are not entirely clear. It may indicate that saplings in these areas are less restricted to higher groundwater availability, as temperatures are lower and precipitation is higher, relatively reducing the overall impacts of drought stress and increasing the importance of other environmental stressors such as herbivory (Tyler *et al.*, 2006; McLaughlin and Zavaleta, in preparation). In persisting/expanding areas, saplings are still within the distribution of adults and our data do not demonstrate an expansion of the distribution.

There were more grazed than ungrazed sites in the projected contracting areas, and more ungrazed than grazed sites in the projected persisting and expanding areas. One hypothesis on oak recruitment failure is that grazing reduces recruitment (Tyler *et al.*, 2006). A potential issue with an uneven distribution of grazing across model-projected categories could exist if grazing impacted distribution of recruitment within a site based on the concentration of cattle around riparian areas (Baily, 1996). However, we see the opposite trend in our data: more recruitment around riparian areas in projected contracting sites (more of which were grazed) than projected persisting/expanding sites. There may be interactions between grazing, climate and recruitment, but our study was not designed to test these, and grazing does not appear to account for the main effects we report.

Sapling vs. adult-based inputs in bioclimate modeling

Our finding that key climate parameters associated with saplings are different from those associated with adults suggests that for species with complex life histories, the choice of life stage in parameterizing bioclimate models can be critical and that the valley oak bioclimate model, which is based on climate parameters associated with adults, may overestimate the area in which valley oak will be able to persist with climate change. The association of recruiting sites with higher rainfall and lower temperatures (Fig. 5a and b) indicates that sites with saplings may be restricted to cooler and wetter portions of the species distribution. While both mean annual precipitation and maximum August temperature were significant predictors of recruitment, the latter was a stronger predictor. These results suggest a narrowing of the climatic niche for saplings. However, short-range dispersal in this species may limit recruitment into areas of newly suitable climate at the cooler and wetter ends of the distribution. Thus, what appears in our data as a niche narrowing or contraction may instead be a geographic niche shift, currently undetectable due to dispersal limitation.

The maximum value of maximum August temperatures associated with saplings was lower than that associated with adults, and the minimum value of average annual precipitation associated with saplings was higher than that associated with adults (Fig. 6a and b), suggesting that there are potential climate thresholds outside of which adults may still persist but recruitment is unlikely to occur. We were unable to randomly select or stratify study sites according to climate conditions, due to the rarity of sites with sapling recruitment, therefore it is possible that unsampled locations with

recruitment at higher temperatures and lower precipitation exist. However, our interviews included land stewards with knowledge of these areas, and recruiting stands were not reported. While our analysis of the range of climate parameters associated with recruitment and the full adult distribution necessarily compared areas of unequal size, we argue that our results indicate a true difference in climate tolerances between saplings and adults. Since larger data sets tend to capture more extreme values, we might expect to see an overall narrower range of climate values associated with recruitment, constrained at both the lower and upper ends relative to the adult values. Instead, the range of sapling values is skewed in the direction we would predict based on our other results (toward lower maximum August temperatures and higher average annual rainfall). This trend is strongest with maximum August temperatures, with 13.2% of the adult distribution occurring above the maximum temperature value associated with saplings and only 0.001% occurring below the minimum value associated with saplings. The trend is weaker but still present for average annual precipitation, with 7% of the adult distribution occurring above the maximum temperature value associated with saplings but only 1.9% occurring below the minimum value associated with saplings (Fig. 6a and b). If the difference were due to more extreme values being captured by the larger sample size, we would expect to see the effects at both the high and low ends of the climatic ranges. That the differences are more pronounced at the dryer and warmer ends of the spectrum suggests that there are different climatic thresholds for saplings and adults.

Difference in the climate envelope between saplings and adults could be explained by both different vulnerability to drought stress between life stages and by changes in the environment over time. Seedlings are less drought stress tolerant than adults (Matzner *et al.*, 2003; Tyler *et al.*, 2006), and have less direct access to the water table (Lewis & Burgy, 1964). Additionally, in a system that has undergone a suite of anthropogenic changes over the past century, climate parameters associated with the current distribution of adults in a long-lived species may be a relict, reflecting recruitment limitation associated with a previous era. Changing environmental conditions in valley oak woodlands likely have increased drought stress in oak seedlings through new stresses including ongoing regional warming (Ladochy *et al.*, 2007), groundwater reductions (Howard *et al.*, 2010), tropospheric ozone exposure (Grulke *et al.*, 2007), and increased herb competition for water from invasive annual grasses (Gordon *et al.*, 1989; Danielsen, 1990; Danielsen and Halvorson 1991). Thus, ambient climate conditions that were tolerable to

current adults when they were saplings may no longer be tolerable by today's recruits.

The use of adult-based bioclimate model inputs may cause the model to overestimate the climate conditions currently necessary for successful recruitment and migration. To explore the extent to which the adult-based valley oak model may overpredict the potential for the species to persist with climate change, we limited inputs to areas within the sapling climate envelope. This reduced model inputs by 15%, indicating that future valley oak distributions will be more restricted with climate change than the current adult-based model predicts. Our basic description of a revised climate envelope map based on saplings is intended to illustrate the potential extent of the difference in model inputs based on adults vs. saplings. Future work should expand on this basic analysis and involve modeling with a range of multiple sapling-based climate parameters to compare model outputs between sapling- and adult-based inputs.

Future valley oak distribution

Our findings indicate that the valley oak bioclimate model, parameterized by adult-based inputs, overestimates the areas in which the species is likely to persist, by not taking into account sapling-specific climate sensitivities; and also underestimates the potential for small populations of valley oaks to remain within much of the projected contracting area around drought stress-mediating microrefugia. Climate change is predicted to increase drought stress and evapotranspiration (IPCC, 2007). If constriction of sapling recruitment around water bodies is due to drought stress, then we would expect this pattern to increase and intensify in the future, ultimately restricting entire populations of valley oak in the projected-contracting zones in pockets of suitable microhabitats. Additionally, we would expect valley oaks to experience complete losses in areas outside the climate envelope associated with sapling recruitment. Our results suggest that a key factor in creating microrefugia is groundwater availability, and that an important factor in differentiating sapling vs. adult climate envelopes is maximum summer temperature. These factors are linked in that higher temperatures likely create dryer soil conditions, making high groundwater availability more important to species persistence. Climate change in California may interact with both, increasing temperatures, reducing snowpack and groundwater recharge, and potential increasing the extent of groundwater withdrawal for human use (Hayhoe *et al.*, 2004).

Bioclimate model predictions involving whole-distribution shifts are useful at large scales, but a focus on changes in local species occurrence may be more relevant and actionable for natural resource managers interested in *in situ* conservation at the level of individually managed landscapes. Our findings support the concern that projections of complete losses of tree species in large parts of their range may be overstated (Pearson, 2006), and molecular studies suggest that migration rates for trees may not be fast enough to keep pace with projected rapid warming (McLachlan *et al.*, 2005). Therefore, identifying and protecting microrefugia where species may persist would be a critical component of conserving species, populations and genetic diversity within areas projected to lose species with climate change (Dobrowski, 2010). Specifically, our results suggest that in Mediterranean systems, where important terrestrial species often depend on access to groundwater (Howard *et al.*, 2010), maintaining groundwater levels and wisely managing riparian areas should be a priority to buffer the system against climate change. More generally, our findings underscore the importance of a focus on life stage-specific climate vulnerability in understanding and predicting climate-related species movement. Fortunately, relevant spatial demographic data often are available on the ground and do not represent prohibitive ecological complexity. Their integration into climate change modeling presents an opportunity for collaboration between field ecologists and modelers that could yield significant improvements in model performance, better anticipate potential species movement, and help guide conservation in a warming world.

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