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## Shrinking windows of opportunity for oak seedling establishment in southern California mountains

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**Abstract.** Seedling establishment is a critical step that may ultimately govern tree species' distribution shifts under environmental change. Annual variation in the location of seed rain and microclimates results in transient "windows of opportunity" for tree seedling establishment across the landscape. These establishment windows vary at fine spatiotemporal scales that are not considered in most assessments of climate change impacts on tree species range dynamics and habitat displacement. We integrate field seedling establishment trials conducted in the southern Sierra Nevada and western Tehachapi Mountains of southern California with spatially downscaled grids of modeled water-year climatic water deficit ( $CWD_{wy}$ ) and mean August maximum daily temperature ( $T_{max}$ ) to map historical and projected future microclimates suitable for establishment windows of opportunity for *Quercus douglasii*, a dominant tree species of warm, dry foothill woodlands, and *Q. kelloggii*, a dominant of cooler, more mesic montane woodlands and forests. Based on quasi-binomial regression models, *Q. douglasii* seedling establishment is significantly associated with modeled  $CWD_{wy}$  and to a lesser degree with modeled  $T_{max}$ . *Q. kelloggii* seedling establishment is most strongly associated with  $T_{max}$  and best predicted by a two-factor model including  $CWD_{wy}$  and  $T_{max}$ . Establishment niche models are applied to explore recruitment window dynamics in the western Tehachapi Mountains, where these species are currently widespread canopy dominants. Establishment windows are projected to decrease by 50–95%, shrinking locally to higher elevations and north-facing slopes by the end of this century depending on the species and climate scenario. These decreases in establishment windows suggest the potential for longer-term regional population declines of the species. While many additional processes regulate seedling establishment and growth, this study highlights the need to account for topoclimatic controls and interannual climatic variation when assessing how seedling establishment and colonization processes could be affected by climate change.

**Key words:** California; climate change; climatic water deficit; microclimate; *Quercus*.

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## INTRODUCTION

Seedling establishment can ultimately govern tree species' regional range shifts under climate change (Jackson et al. 2009, Zhu et al. 2012). Establishment includes seed germination and seedling survival, both of which are highly sensitive to climatic controls (Grubb 1977, Harper 1977, Clark et al. 1999). Projecting seedling establishment under future climates is challenging because site quality for tree seedlings varies at length scales of <1–10 m and can change dramatically from year to year (Clark et al. 1999, Lloret et al. 2009, Kroiss and HilleRisLambers 2015). In contrast, plant species re-distribution under climate change is typically modeled with 1- to 10-km climate grids and multi-decadal climate averages (Franklin et al. 2013). Important establishment dynamics affecting species persistence and colonization may be masked with such spatial and temporal aggregation (Serra-Diaz et al. 2016b). The onus is on ecologists to develop cross-scale approaches that account for the fine-scale spatiotemporal processes that govern seedling establishment when projecting tree species range shifts over decades or centuries at landscape to regional scales.

Here, we model the seedling establishment niche using the general approach of species distribution modeling that has been widely applied to evaluate potential species exposure to climate change (Pearson and Dawson 2003, Thuiller et al. 2006). Such modeling is based on the statistical association of observed species distributions with mapped climatic and other environmental factors (Franklin 2010, Dawson et al. 2011). The major difference in the approach used here is that we model the establishment niche at fine spatial scale (30-m grids) and at an annual time step. The resulting annual maps of site quality capture the dynamic opportunities for seedling establishment under climate change and can be integrated to show the frequency of establishment opportunities over multiple decades. They provide essential information for parameterizing next-generation models of biotic response to climate change, such as spatially explicit population models (e.g., Keith et al. 2008, Midgley et al. 2010).

Tree species distribution models are typically parameterized using observation data from plot

samples and herbarium records without regard to the age of the individuals. Some recent studies have modeled smaller size classes separate from larger adult trees to test for potential ongoing range shifts in response to climate change (Zhu et al. 2012, Bell et al. 2014, Dobrowski et al. 2015, Monleon and Lintz 2015, Serra-Diaz et al. 2016a). Extending this approach to modeling annual seedling establishment processes requires precise aging of individuals, which is not always possible for species that do not leave reliable annual rings in early life stages or that re-sprout following disturbance.

Monitoring interannual seedling establishment dynamics along environmental gradients is one approach that can overcome these difficulties while allowing the effects of specific environmental factors to be isolated (Van Mantgem et al. 2006, Gomez-Aparicio et al. 2008, Michalet et al. 2014). We have employed this approach here, monitoring seedling establishment from seeds sown in experimental gardens arrayed across temperature and moisture gradients to evaluate the statistical association between seedling establishment and spatially downscaled climate factors (Dingman et al. 2013, Serra-Diaz et al. 2016b).

In this study, we parameterize establishment niche models with data from field experiments for two widespread and ecologically important oak species of Mediterranean-climate California, *Quercus douglasii* (blue oak) and *Quercus kelloggii* (California black oak). We selected these species so as to compare establishment niche models and climate change exposure for tree species that share similar life histories and occur in close proximity, but are currently distributed in different climate zones in the mountains of California. *Q. douglasii* dominates hot, dry foothill woodlands, whereas *Q. kelloggii* occupies cooler more mesic montane woodlands and forests (Davis et al. 2016).

We focus on measuring and modeling the seedling microclimatic niche without considering seed supply under the assumption that physical site conditions set fundamental limits on where seedlings can establish across the landscape. Mediterranean-type climates pose extreme physiological challenges for tree seedling establishment because small, shallow-rooted seedlings that emerge in winter or spring must survive extended summer drought and high

summer temperatures near the soil surface (Kolb and Robberecht 1996, Zavala et al. 2000, Mahall et al. 2009, Dingman et al. 2013). Episodes of widespread woody plant establishment may be confined to occasional years when ample seed supply coincides with climatic conditions favoring high rates of seed germination followed with first-year seedling survival (Brown and Wu 2005, Holmgren et al. 2006). Large interannual spatial variation in suitable soil moisture, heat, and light conditions may provide transient “windows of opportunity” (Eriksson and Fröborg 1996) for seedling establishment across the landscape.

A major challenge in modeling the climate for seedling establishment is capturing the integrative nature of relevant climatic predictors. Net solar radiation, soil moisture and thermal conductivity, wind, and humidity all interact to produce dynamic surface energy balance and associated seedling thermal and soil moisture regimes (Gates 2003). Integrated measures that capture interactions related to heat and soil water balance may better predict seedling establishment than standard bioclimatic factors such as annual or seasonal temperatures and precipitation (Bullied et al. 2012). Climatic water deficit (CWD) is one such integrative measure that is strongly associated with tree species distributions in California and elsewhere (Stephenson 1998, Lutz et al. 2010, Anderegg et al. 2015). CWD is the difference between calculated potential evapotranspiration and actual evapotranspiration, and thus integrates solar radiation, air temperature, humidity, and available soil water to provide a measure of time-variant drought stress seedlings are likely to experience during establishment.

Based on current understanding (see *Methods*), we posited that seedling establishment rates for *Q. douglasii* and *Q. kelloggii* should be strongly negatively related to summer drought stress as indicated by CWD and by high air temperatures near the ground surface, the latter especially in canopy gaps. In the foothills and montane environments occupied by these species in California, we would expect both CWD and maximum summer temperatures to be under strong topographic control, decreasing from lower to higher elevations, and from south-to-southwest-facing to north-to-northeast-facing slopes at a given elevation (Ashcroft et al. 2008).

### Research objectives

Our main objective in this study was to demonstrate an approach for mapping and modeling the tree seedling establishment niche over large areas undergoing regional climate change. We illustrate the approach for two ecologically important oak species in Mediterranean-climate California. Controls on seedling establishment for these species are broadly similar to those for other oaks in California as well as oaks of the Mediterranean Basin (e.g., Tyler et al. 2006, Gomez-Aparicio et al. 2008, Maranon et al. 2009). We analyze seedling establishment as a function of modeled CWD and maximum summer temperatures and apply the resulting establishment niche models to historical and projected future climates. Our primary research questions are: (1) How is oak seedling establishment related to modeled gradients in CWD and modeled summer maximum temperature in California’s Mediterranean-type climate? (2) How do the CWD and temperature conditions that favor foothill and montane oak seedling establishment vary interannually across complex mountain topography? (3) How might projected climate change alter the distribution and frequency of microclimate-limited oak establishment windows across these mountain landscapes?

## METHODS

### Study species

*Quercus douglasii* and *Q. kelloggii* both flower in the spring, but acorns of *Q. douglasii* (section *Quercus*) mature by fall season of the same year, whereas *Q. kelloggii* acorns (section *Lobatae*) ripen in 18 months and drop during the fall season of the following year. Acorns on the surface can overheat under direct sun, and acorns buried by scatter-hoarding jays or other processes exhibit higher germination and survival (Borchert et al. 1989). With adequate moisture, germination occurs without delay in *Q. douglasii* and seedlings emerge over the ensuing winter and spring (Matsuda and McBride 1989). Germination and initial development in *Q. kelloggii* may be delayed by weeks or months as it is dependent upon cold stratification (McDonald 1978, Matsuda and McBride 1989). Acorns of both species generally do not survive more than 1 year, and there is essentially no refractory seed bank.

Seedling establishment of both species is strongly dependent on the rate and severity of summer soil water depletion (McDonald 1978, Gordon et al. 1989, Momen et al. 1994, Gordon and Rice 2000, Matzner et al. 2003, Grünzweig et al. 2008). Numerous studies in California foothill oak woodlands have documented increased rates of oak seedling establishment in wetter years (Griffin 1971, Borchert et al. 1989, Tyler et al. 2006, 2008). The role of high temperature in controlling seedling establishment is not as well documented. In California oak woodlands and forest clearings, maximum summer air temperatures next to the soil surface can exceed 55°C, a threshold where tissue damage and seedling mortality have been observed for some Mediterranean-climate tree species (Kolb and Robberecht 1996). Dingman et al. (2013) observed no *Q. kelloggii* seedling establishment in experimental plots in which July average daily maximum surface temperatures exceeded 45°C.

Seedlings of *Q. douglasii* and *Q. kelloggii* are moderately shade-tolerant (McDonald 1990a, Callaway 1992a), and first-year seedling survival for both species may be highest under partial shading (McDonald 1978, Callaway 1992b). In the case of *Q. douglasii*, observed shading effects may be more associated with sheltering of seedlings from herbivory than with amelioration of light damage or heat stress (Callaway 1992b). Once established, both species grow best under high-light conditions, and as a result, both are generally considered shade-intolerant species (McDonald 1990b, Gray et al. 2005, Cocking et al. 2012).

### Study area

Twenty-four experimental gardens were distributed across four landscapes in the southern Sierra Nevada and western Tehachapi Mountains of southern California (Fig. 1). These landscapes included two foothill landscapes where rain is the dominant form of precipitation (San Joaquin Experimental Range (Sierra Foothill; SF), N 37°05', W 119°01', garden elevations 300–400 m; mean annual precipitation (MAP) ~480 mm; Tejon Ranch foothills (Tejon Foothill; TF), N 34°59', W 118°43', garden elevations 725–900 m, MAP ~400 mm) and two montane landscapes where a significant portion of total annual precipitation falls as snow between December

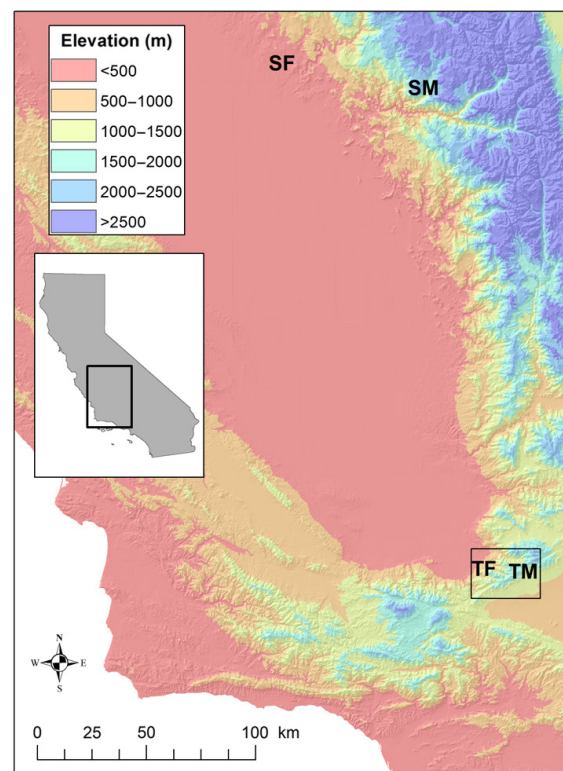


Fig. 1. Location map of Sierra Nevada foothill (SF), Sierra Nevada montane (SM), Tehachapi Mountains foothill (TF), and Tehachapi Mountains montane (TM) study areas. Backdrop is a shaded relief image indicating 500-m-elevation zones. The inset map locates the region in California. The rectangle surrounding the TF and TM study areas demarcates the western Tehachapi Mountains domain for modeling establishment windows of opportunity.

and March (Teakettle Experimental Forest (Sierra Montane; SM), N 36°57', W 119°01', garden elevations 2000–2100 m, MAP ~1000 mm; Tejon Ranch uplands (Tejon Montane; TM), N 34°58', W 118°35', garden elevations 1575–1675 m, MAP ~525 mm).

Oak woodland vegetation at SF is dominated by *Q. douglasii* with scattered *Q. wislizeni* var. *wislizeni* and *Pinus sabiniana*. Soils at this site are coarse-sandy loams derived from granite and classified as thermic mollic Haploxeralfs. Woodland vegetation at TF is dominated by *Q. douglasii* with scattered *Aesculus californica*, and soils are granite-derived, coarse-loamy thermic typic Haploxerolls. SM is dominated by

*Abies concolor* and *Pinus jeffreyi* but also includes *Q. kelloggii*, *Calocedrus decurrens*, *P. ponderosa*, *P. lambertiana*, and *A. magnifica*. Granite-derived coarse-sandy loams at this site are classified as frigid dystric Xeropsamments. Vegetation at TM is a mosaic of *Q. kelloggii* and *P. ponderosa* forest, *Q. kelloggii* and *Q. lobata* woodlands, and annual grasslands; coarse-sandy loams at this site are derived from schist and classified as mesic pachic Haploxerolls.

We modeled the spatial dynamics of establishment niches of *Q. douglasii* and *Q. kelloggii* across all study areas; for brevity, results are illustrated for a 33,000-ha region of the western Tehachapi Mountains that spans a 2000-m elevation gradient and encompasses two of our study landscapes (TF, TM). Vegetation of the western Tehachapi Mountains ranges from desert grasslands at the lowest elevations to oak woodland and chaparral at mid-elevations to conifer forests dominated by *P. jeffreyi* and *A. concolor* at highest elevations. MAP during the 20th century varied across the region from around 250 mm in the driest, low-elevation portions of the area to over 500 mm at the highest elevations (McCullough et al. 2016). Illustrative results for model regions centered on our SF and SM sites are provided in Appendix S1: Fig. S1.

#### Overview of data sources and modeling strategy

Modeling the seedling establishment niche entailed integrating five primary spatial data sets: (1) seedling survival data from experimental gardens, (2) historical 800-m monthly PRISM (Parameter-elevation Relationships on Independent Slopes Model; Daly et al. 2008) grids for monthly average maximum daily temperature ( $T_{\max}$ ) and precipitation (PPT) for the period 1950–2013, (3) projected  $T_{\max}$  and PPT for the period 2010–2099 from three different global climate models (GCMs) produced for CMIP5 (Coupled Model Intercomparison Project; <http://www-pcmdi.llnl.gov/projects/cmip/>) and down-scaled to 800 m by Thrasher et al. (2013), (4) 30-m digital elevation data for climate downscaling and modeling of CWD, and (5) U.S. Department of Agriculture SSURGO digital soils data for modeling of CWD (NRCS [Natural Resources Conservation Service] 2006).

Historical and projected monthly 30-m  $T_{\max}$  and PPT grids were produced by statistical

and spatial downscaling, as described below. These grids were used to create monthly 30-m grids of CWD, which were then summed across the months within each water year (October to September) to produce annual estimates of total water-year CWD ( $CWD_{wy}$ ). Grid values of August  $T_{\max}$  and  $CWD_{wy}$  for 2012 and 2013 were extracted for the 30-m cells at experimental garden locations and used to predict 2012 and 2013 seedling establishment. The resulting statistical models relating seedling establishment to modeled  $T_{\max}$  and  $CWD_{wy}$  were then applied to historical and projected future climate grids to map the seedling establishment niche on an annual time step for the period 1950–2099.

#### Experimental gardens

We monitored and modeled microclimate conditions in relation to oak seedling survival from sown acorns through the first year (“seedling establishment”) in 24 experimental gardens, six in each of four landscapes (Fig. 1). At each site, two gardens were situated on relatively cool north-to-northeast-facing slopes, two on hotter, drier south-to-southwest-facing slopes, and two on level valley or ridge sites. Gardens were deliberately located in canopy gaps in foothill oak woodlands, montane oak woodlands, and mixed conifer forests across the range of local topoclimates. Our experimental design did not systematically test for overstory effects on microclimate and seedling establishment. Gap sizes were smaller in our montane forest sites, and tree cover surrounding the gardens, as estimated with spherical densitometer readings from the center of each garden, varied from <1% to 30% in the foothill sites and from <1% to 77% in montane forests.

Experimental gardens were 5 × 5 m and fenced to exclude both rodents and ungulates. Rodent fencing was extended 48–60 cm underground to exclude pocket gophers (*Thomomys bottae*) and ground squirrels (*Spermophilus beecheyi*), but was only partially effective at excluding pocket gophers, which undoubtedly reduced seedling survivorship in some gardens.

Although the sites were spatially separated, the topoclimates across sites collectively encompassed a relatively wide range of microclimates from warmest and driest conditions on level and south-facing slopes at SF and TF to the coolest,

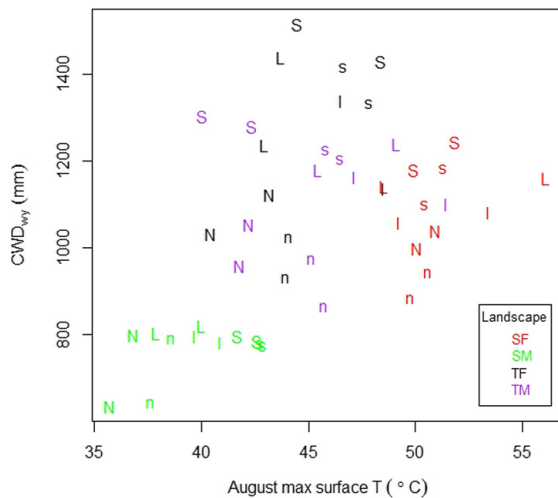


Fig. 2. Average measured maximum daily temperatures at 5 cm above the soil surface during August and modeled total water-year climatic water deficit ( $CWD_{wy}$ ) for 24 experiment gardens located in the Sierra Nevada foothill (SF, red symbols), Sierra Nevada montane (SM, green symbols), Tehachapi Mountains foothill (TF, blue symbols), and Tehachapi Mountains montane (TM, purple symbols) study areas. Symbols for 2012 and 2013 are plotted with lowercase and uppercase letters, respectively. Gardens are situated on north-to-northeast-facing slopes (n,N), south-to-southwest-facing slopes (s,S), or level sites (L,L).

most mesic conditions on north-facing slopes at SM (Fig. 2).

Gardens were sown in October–November 2011 and October–November 2012 with sound acorns of *Q. douglasii* and *Q. kelloggii* collected that year from at least 10 trees of each species within the study landscapes. In both 2011 and 2012, we sowed 100 acorns of *Q. douglasii* in every garden (50 each from TF and SF). Similarly, we planted 100 *Q. kelloggii* acorns in every garden in 2012, 50 from TM and 50 from SM. Because of a poor acorn crop in the southern Sierra Nevada in 2011, we planted only 50 *Q. kelloggii* acorns from the TM landscape in every garden that year, and none from SM. For the analyses reported here, we pooled data from the two seed zones within each garden, as the effects of seed provenance on first-year seedling establishment were weak (L. Sweet, *in preparation*). For *Q. kelloggii*, we analyzed establishment of seedlings from seeds

collected from the TM landscape to maintain consistency in seed provenance between years. First-year seedling survival was recorded from late August to early November in 2012 and from mid-October to early November in 2013.

#### Modeled $T_{max}$ and CWD

Historical monthly PRISM grids for temperature and precipitation were downscaled from 800 m to 30 m using Gradient-Inverse-Distance-Squared (GIDS) downscaling. The GIDS approach develops a spatial multiple regression to predict values of each fine-resolution cell based on values in the coarser grid cells overlapping and surrounding the finer cell. To determine whether the climatic data in the downscaled grids matched the actual conditions that the seedlings were experiencing within the same grid cells, climate downscaling to 30 m was compared to temperature data logger and weather station data collected at our experimental gardens in those locations (see Dingman et al. 2013 for details regarding field temperature monitoring).

Climatic water deficit was modeled at 30 m with the Basin Characterization Model (BCM), which mechanistically models the fate of precipitation as snowpack, sublimation, evapotranspiration, soil storage, runoff, or groundwater recharge in every grid cell (Flint et al. 2013, Thorne et al. 2015). Potential evapotranspiration (PET) is calculated based on the Priestley-Taylor method (Priestley and Taylor 1972) using hourly energy balance calculations for solar radiation and air temperature. The solar radiation model incorporates seasonal atmospheric transmissivity with site parameters of slope, aspect, and topographic shading (Flint and Childs 1987). Actual evapotranspiration (AET) is modeled as the rate of PET until available soil water reaches the soil wilting point, at which point AET is set to zero. CWD is calculated as the difference between PET and AET, and the model balances the hydrologic cycle for each grid cell on a monthly time step. Soil available water storage was obtained from USDA SSURGO county soil survey maps (Flint and Flint 2012).

Global climate model temperature and precipitation projections were downscaled to 800-m scale by Thrasher et al. (2013) using the Bias-Correction Spatial Disaggregation algorithm

Table 1. Coupled Model Intercomparison Project Phase 5 (CMIP5) models used for analysis of climate change effects on seedling establishment.

GCM	RCP	$\Delta$ July $T_{\max}$ ( $^{\circ}\text{C}$ )	$\Delta$ January $T_{\min}$ ( $^{\circ}\text{C}$ )	$\Delta$ PPT <sub>wy</sub> (mm)	$\Delta$ CWD <sub>wy</sub> (mm)
Max Planck Institute Earth System Model (MPI-ESM)	4.5	1.94	1.98	24.38	92.58
Model for Interdisciplinary Research on Climate (MIROC5)	4.5	2.6	1.94	-67.64	156.54
NCAR Community Climate System Model (CCSM4)	8.5	4.07	4.02	14.87	148.82
MIROC5	8.5	4.63	4.61	-111.2	244.79

Notes: Table entries are the differences in 30-year mean values for modeled end-of-century (2070–2099) vs. historical (1951–1980) mean minimum and maximum daily temperatures ( $T_{\min}$  and  $T_{\max}$ ), water-year precipitation (PPT<sub>wy</sub>), and climatic water deficit (CWD) in the western Tehachapi Mountains study area (see Fig. 1). GCM, global climate model; RCP, representative concentration pathway.

Source: Table 1 in McCullough et al. (2016).

(Wood et al. 2004). We used GIDS to further spatially downscale the 800-m products to 30 m for  $T_{\max}$  and PPT to obtain CWD<sub>wy</sub> using the BCM.

#### Projected future climates

We examined four different climate scenarios, summarized in Table 1, that represented hot-dry, warm-dry, hot-wet, and warm-wet projections for our study region (see McCullough et al. 2016 for details) based on downscaled outputs from three different GCMs (MPI-ESM, CCSM4, MIROC5) and two representative concentration pathways (RCPs) from CMIP5 (Stocker et al. 2014). We compared RCPs of 4.5 and 8.5W/m<sup>2</sup>, which represent medium-low- and high-anthropogenic-emission scenarios (Stocker et al. 2014).

#### Statistical analysis of seedling establishment

All statistical analyses were conducted using the R statistical environment (R Core Team 2012). We initially analyzed the proportion of planted seeds that produced 1-year seedlings (“establishment rate”) at each garden using a linear model with logit transform (Warton and Hui 2011). Because the binomial regression models yielded over-dispersed residuals, we opted instead to model establishment rate as a function of environmental factors using quasi-binomial regression (generalized linear model (glm), family = quasi-binomial). We evaluated a large number of microclimate factors and models (L. Sweet et al., *in preparation*), but here we show only results for modeled CWD<sub>wy</sub> and modeled  $T_{\max}$ , as these factors proved to be most strongly associated with seedling establishment among

downscaled climate variables available for spatial prediction.

We fitted separate models for the 2012 and 2013 planting cohorts as well as models based on data pooled across both years. We tested for an effect of cohort year in pooled data by entering year as a fixed effect in the quasi-binomial regression model. Model skill was measured using adjusted squared deviance (adj.  $D^2$ ; Guisan and Zimmermann 2000).

#### Establishment niche mapping

Grid operations were performed using the *raster* package in R (R Core Team 2012). For each species, we applied the fitted quasi-binomial regression models to grids of historical and projected future climate factors to calculate the predicted annual proportion of seeds producing 1-year seedlings for every 30-m grid cell for each model year from 1950 to 2099. We then converted the annual continuous probability grids to 0,1 binary grids (non-establishment site vs. establishment site) using a threshold that maximized training sensitivity plus specificity for the quasi-binomial model (Fielding and Bell 1997). This approach is widely used in species distribution modeling to create binary range maps from probability maps generated by empirical statistical models (Liu et al. 2013); conversion to annual binary maps allowed us to frame our modeling results in terms of the frequency of windows of recruitment opportunity within 30-year climate periods.

Annual binary (0,1 = non-establishment site, establishment site) maps were stacked and summed for 30-year periods to evaluate, for



Table 2. Quasi-binomial regression models relating oak seedling first-year survival to accumulated water-year climatic water deficit ( $CWD_{wy}$ ) and August maximum daily temperature ( $T_{max}$ ) for *Quercus douglasii* (QUDO) and *Quercus kelloggii* (QUKE) for 2012 (sown Fall 2011) and 2013 (sown Fall 2012) cohorts.

Species	Water year	Model	Adj. $D^2$	Intercept	SE	Factor	Est.	SE	
QUDO	2012	$CWD_{wy}$	0.39	<b>2.70</b>	1.37	$CWD_{wy}$	<b>-0.0052</b>	0.0015	
		$T_{max}$	0.44	5.76	2.01	$T_{max}$	<b>-0.25</b>	0.07	
		$CWD_{wy} + T_{max}$	0.47	<b>5.13</b>	1.76	$CWD_{wy}$	-0.0025	0.0017	
	2013	$CWD_{wy}$	0.48	3.38	1.35	$T_{max}$	-0.16	0.080	
		$T_{max}$	0.19	3.44	3.17	$CWD_{wy}$	<b>-0.0058</b>	0.0015	
		$CWD_{wy} + T_{max}$	0.44	<b>2.14</b>	1.65	$T_{max}$	-0.20	0.11	
	2012 and 2013	$CWD_{wy}$	0.41	<b>2.81</b>	0.93	$CWD_{wy}$	-0.0070	0.0025	
		$T_{max}$	0.17	2.52	1.59	$T_{max}$	-0.079	0.010	
		$CWD_{wy} + T_{max}$	0.43	<b>3.45</b>	1.21	$CWD_{wy}$	<b>-0.005</b>	0.0010	
	QUKE	2012	$CWD_{wy}$	0.53	5.21	1.92	$T_{max}$	-0.046	0.055
			$T_{max}$	0.69	<b>11.43</b>	2.38	$CWD_{wy}$	<b>-0.0077</b>	0.0022
			$CWD_{wy} + T_{max}$	0.69	<b>10.06</b>	2.38	$CWD_{wy}$	-0.0022	0.0019
2013		$CWD_{wy}$	0.63	<b>5.33</b>	1.84	$T_{max}$	-0.33	0.12	
		$T_{max}$	0.75	<b>14.97</b>	3.54	$CWD_{wy}$	<b>-0.0079</b>	0.0021	
		$CWD_{wy} + T_{max}$	0.75	<b>12.65</b>	4.39	$T_{max}$	-0.0017	0.0025	
2012 and 2013		$CWD_{wy}$	0.59	<b>5.27</b>	1.30	$CWD_{wy}$	-0.49	0.24	
		$T_{max}$	0.58	<b>9.16</b>	1.70	$T_{max}$	<b>-0.0078</b>	0.0015	
		$CWD_{wy} + T_{max}$	0.68	<b>8.14</b>	1.46	$CWD_{wy}$	<b>-0.39</b>	0.06	
							$T_{max}$	<b>-0.0043</b>	0.0014
							$T_{max}$	-0.21	0.069

Notes: Models include simple models and multiple predictor models testing for the additive effects of  $CWD_{wy}$  and  $T_{max}$  ( $CWD_{wy} + T_{max}$ ). Estimated model coefficients (Est.), standard error of the coefficients (SE), and adjusted squared deviance (adj.  $D^2$ ) are tabulated. Significant model intercepts and coefficients are in bold font ( $P < 0.01$ ) or italicized ( $P < 0.05$ ).

every grid cell, the frequency of potential establishment windows of opportunity under historical and projected future climates. This step placed seedling establishment in the same multi-decadal time frame generally used for analyzing climate means and for parameterizing species distribution models.

Here, we compare the recent historical period 1981–2010 to the end of century, 2070–2099, for the western Tehachapi Mountains, where the steep environmental gradients make it easier to visualize the changing patterns of establishment windows across foothill and montane settings. We composited end-of-century results by taking the average of predicted establishment window frequencies for each of the four climate scenarios at each grid cell. We also analyzed the changing proportion of the western Tehachapi Mountains classified as suitable for each species for each year from 1950 to 2099 and applied a robust 30-year moving median filter to show the general

regional trend in establishment windows over historical and projected future climates.

## RESULTS

### Climate downscaling

Correlation ( $r$ ) of observed with modeled monthly averages of daily maximum air temperatures in 2013 ranged from 0.99 (mean absolute error (MAE) = 1.73°C) at TF to 0.95 at SM (MAE = 4.0°C). Correlation between predicted and observed monthly precipitation (3–4 precipitation gauges per site) ranged from 0.94 (MAE = 6.6 mm) at TM to 0.71 (MAE = 39 mm) at SM.

### Oak seedling establishment in experimental gardens

For *Q. douglasii*, seedling establishment was negligible in gardens where modeled  $CWD_{wy}$  exceeded 1200 mm (Fig. 3A). Establishment increased non-linearly with decreasing  $CWD_{wy}$

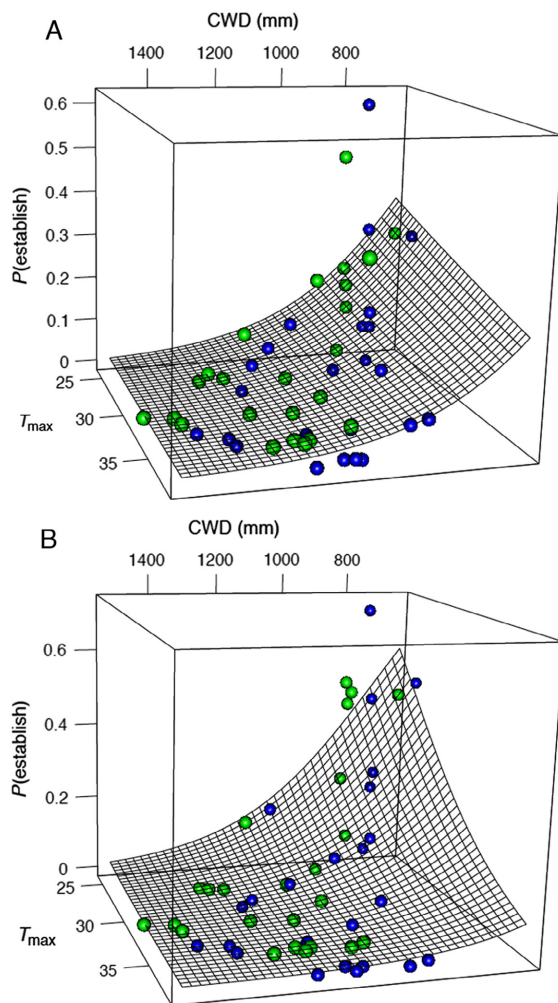


Fig. 3. Proportion of seedlings surviving 1 yr from (A) *Quercus douglasii* and (B) *Q. kelloggii* acorns sown in 24 experimental gardens for the 2012 (blue) and 2013 (green) water years as a function of modeled water-year climatic water deficit ( $CWD_{wy}$ ) and modeled August mean maximum daily air temperature ( $T_{max}$ ). The curved surfaces are the fitted quasi-binomial regression models based on additive effects of  $CWD_{wy}$  and  $T_{max}$ .

and highest establishment was observed in montane sites where  $CWD_{wy}$  remained below 1000 mm. *Q. douglasii* was also significantly negatively related to  $T_{max}$ , although much more so in 2012 than 2013 (Table 2). Some *Q. douglasii* establishment was recorded even in the hottest gardens where modeled  $T_{max}$  exceeded  $38^{\circ}\text{C}$  (Fig. 3A). There was considerable unexplained

variation in establishment rates among gardens with low  $CWD_{wy}$  and low  $T_{max}$  values (Fig. 3A). Multiple regression models combining  $CWD_{wy}$  and  $T_{max}$  were comparable in skill to models based solely on  $CWD_{wy}$ , and the regression coefficients for  $T_{max}$  in the two-predictor model were not significant ( $P > 0.05$ ) for either 2012 or 2013. Univariate models based on  $CWD_{wy}$  did not vary between years ( $P = 0.90$ ), so we elected to use the simple regression model based on pooled 2012 and 2013 data to model the establishment niche for *Q. douglasii*. The larger sample size presumably yielded a more robust establishment niche model and was less cumbersome than applying separate year models to project future establishment conditions.

Establishment of *Q. kelloggii* seedlings decreased sharply with increasing  $CWD_{wy}$  and  $T_{max}$  (Table 2, Fig. 3B). With the exception of one outlying garden at TM, establishment was negligible in gardens where modeled  $CWD_{wy}$  exceeded 1000 mm (Fig. 3B). No seedlings established in gardens where modeled  $T_{max}$  exceeded  $35.5^{\circ}\text{C}$ , and less than 1% of seedlings survived in the set of gardens where modeled  $T_{max}$  exceeded  $32^{\circ}\text{C}$  (Fig. 3B). For individual years, the simple regression model based on modeled  $T_{max}$  was comparable to or outperformed the multiple regression model that included  $T_{max}$  and  $CWD_{wy}$  (Table 2). Using pooled 2012 and 2013 data, the multiple regression model outperformed the simple models, and year effect was significant ( $P < 0.05$ ). For establishment niche modeling, we used the two-predictor model with data pooled across years rather than the best performing model (2013) under the assumption that the model based on two different climate years was more likely to represent the establishment niche for *Q. kelloggii*. In practice, the best two-predictor model (2013) yielded similar results for modeling establishment results as the model based on pooling data for 2012 and 2013 (0.96 correlation between grids of frequency of establishment years for the period 1981–2010).

#### Modeled establishment windows of opportunity in the Tehachapi Mountains, 1981–2010

High interannual variation in  $CWD_{wy}$  produced large year-to-year expansion and contraction of areas predicted to be suitable for oak seedling establishment. These dynamics are

illustrated by comparing model outputs for *Q. douglasii* for the 1998 water year, an El Niño year with very high spring precipitation, to the very dry 2013 water year (Fig. 4). Sixty-three percent of the western Tehachapi Mountains was classified as suitable for *Q. douglasii* establishment during the 1998 water year compared to 6% in 2013.

For the 30-year period 1981–2010, north-facing slopes above ~750 m elevation were classified as suitable for *Q. douglasii* seedling establishment in every year (Fig. 5A). In extreme wet years, modeled *Q. douglasii* establishment sites extended to elevations below 400 m. By comparison, *Q. kelloggii* recruitment sites were generally restricted to north-facing slopes above ~1000 m elevations (Fig. 5B), although in extreme wet years establishment sites extended as low as 600 m on steep north-facing slopes.

The median proportion of the region classified as suitable for *Q. douglasii* seedling establishment within a moving 30-year window was roughly 25% between 1951 and 2010, declining slightly after 1980 due to increasing modeled  $CWD_{wy}$  (Appendix S2: Fig. S1). Over the same period, the frequency of establishment windows for *Q. kelloggii* across the western Tehachapi Mountains is predicted to have decreased from over 20% to less than 15% as a result of increasing  $CWD_{wy}$  and maximum August temperatures (Appendix S2: Fig. S1).

#### Projected 21st-century trends in establishment windows

By the end of the century, the 30-year median extent of *Q. douglasii* seedling establishment sites in the western Tehachapi Mountains is projected to decline from 25% of the region to roughly 17% for the scenario with the least drying (MPI-ESM, RCP 4.5) to less than 10% for the driest scenario (MIROC5, RCP 8.5; Fig. 5C; Appendix S2: Fig. S1 and Appendix S3: Fig. S1). The modeled year-to-year variation in the extent of establishment sites declines between 2070 and 2099 so that even the wettest years produce establishment windows across less than 25% of the region (Appendix S2: Fig. S1). However, steep north-facing slopes above 900 m elevations are modeled as suitable for establishment in most or all years, even under the warmest and driest scenario (Fig. 5C; Appendix S3: Fig. S1).

Establishment windows of opportunity are predicted to shrink more dramatically with 21st-century climate change for *Q. kelloggii* (Fig. 5D). The warm, relatively wet scenario (MPI-ESM, RCP 4.5) projects moderate decline, with a median of 5% of the region modeled as suitable during the 2070–2099 interval (Appendix S2: Fig. S1). Under the hottest, driest scenario (MIROC5, RCP 8.5), only isolated north slopes above 2000 m elevations, comprising less than 0.5% of the region, are modeled as frequently suitable sites for seedling establishment (Appendix S4: Fig. S1).

## DISCUSSION

### Seedling establishment along elevation, $CWD_{wy}$ , and $T_{max}$ gradients

Despite their ecological segregation in California's landscapes, both *Q. douglasii* and *Q. kelloggii* established best above 2000 m in our Sierra Nevada montane gardens, in gaps in forest currently dominated by *A. concolor* and *P. jeffreyi*. Yet, in the southern Sierra Nevada, *Q. douglasii* woodlands are mainly restricted to elevations below 800 m, extending to as high as 1500 m only in small stands on relatively dry ridgelines with moderately deep soils (Baker et al. 1981, Vankat 1982). In the western Tehachapi Mountains, *Q. douglasii* woodlands occur at elevations below 1050 m (Hoagland et al. 2011; D. Gwenzi, unpublished data). We are not aware of any reports of *Q. douglasii* acorn germination, seedling overwintering, or establishment at elevations above 1280 m (Matsuda and McBride 1989, Standiford et al. 1997). Our results provide evidence that microclimate is not preventing at least initial *Q. douglasii* seedling establishment in montane mixed conifer forests. Although this pattern seems contradictory to the distribution of adult trees, it is consistent with niche theory that predicts an increasing role of competition in the favorable part of an environmental gradient (Austin 1990), which is the cool, wet end of our Mediterranean-climate landscapes (Michalet et al. 2014). At the other end of the gradient in our SF gardens, where this species dominates the open woodland overstory, we observed ample *Q. douglasii* germination and emergence, but only rare establishment that was confined to gardens on north-facing slopes. This echoes results of an

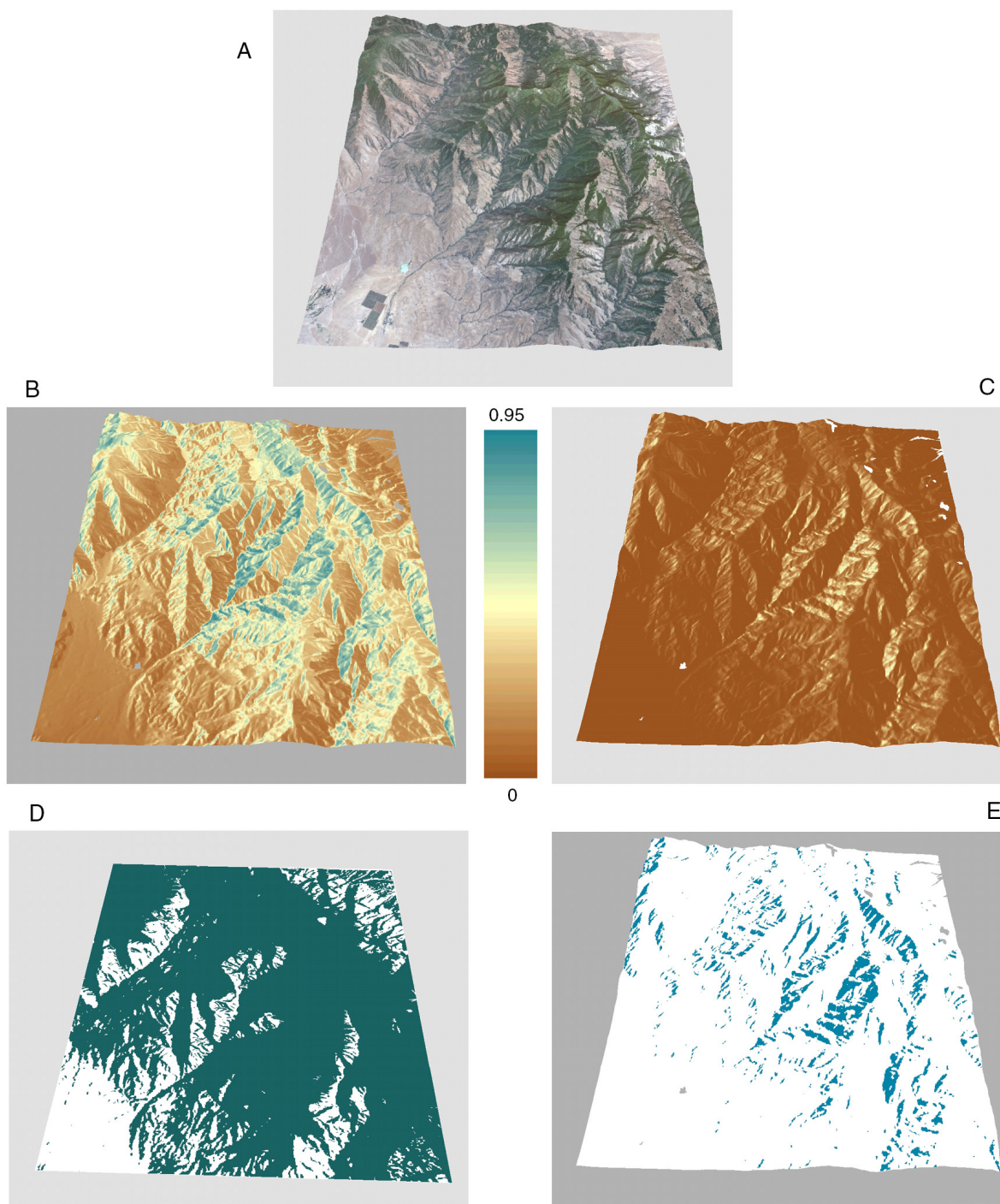


Fig. 4. Example of modeled *Quercus douglasii* seedling establishment sites in the western Tehachapi Mountains, viewed obliquely from west to east to highlight contrasting north-facing vs. south-facing slopes: (A) An aerial photograph of the region in summer 2012 shows the association of vegetation pattern with topography. Predicted establishment rates from sown acorns are displayed for (B) 1998, an extremely wet year, and (C) 2013, an extremely dry year. Values range from 0 (brown) to 0.95 (green) in accordance with the color ramp separating the figures. Resulting binary maps of modeled non-establishment (white) and establishment sites (dark green) are also shown for (D) 1998 and (E) 2013.

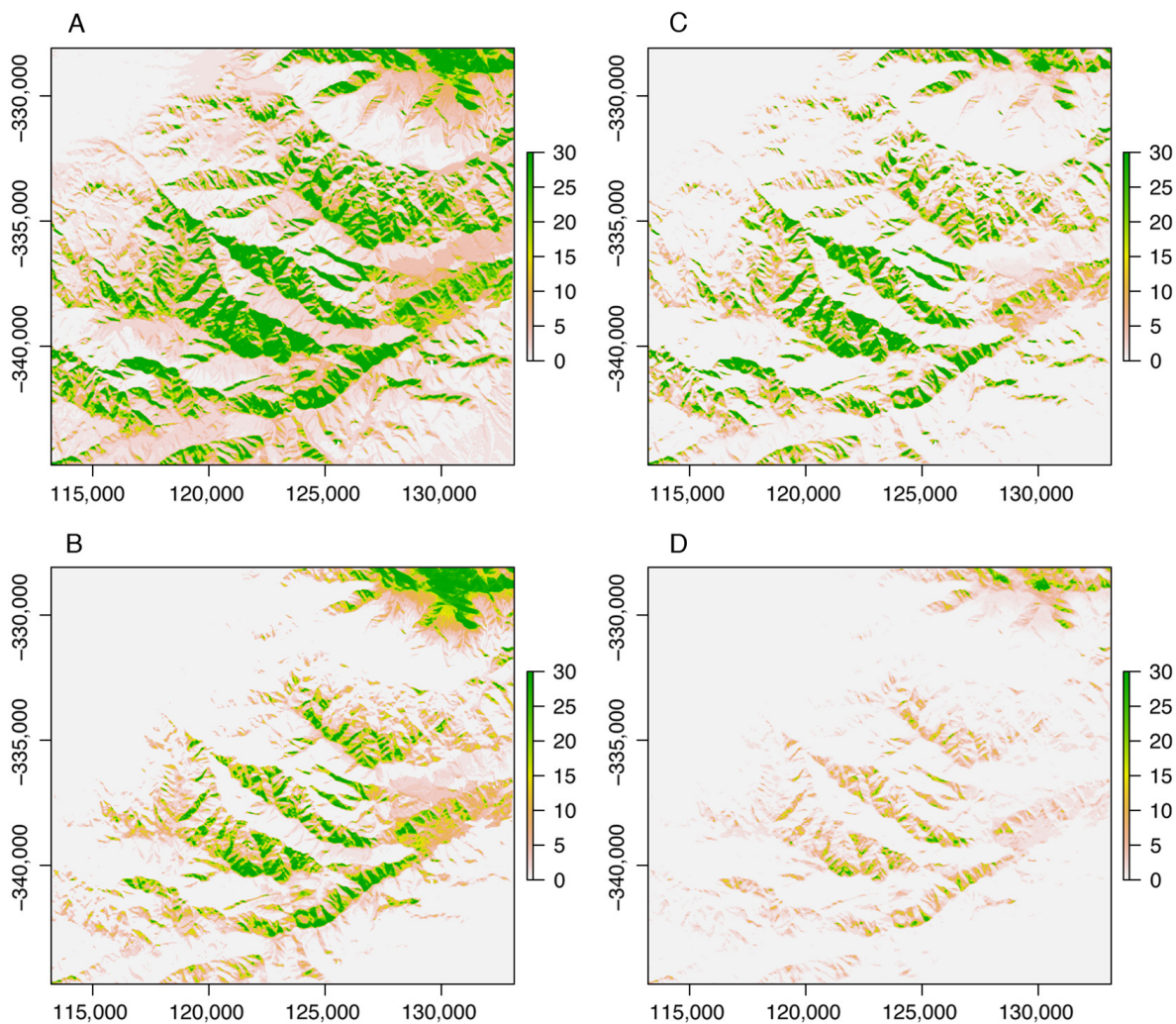


Fig. 5. Maps of the western Tehachapi Mountains displaying the number of years (0–30) when the site was classified as suitable for (A) *Quercus douglasii* and (B) *Q. douglasii* seedling establishment for the period 1981–2010. Panels (C) and (D) display the number of establishment years for the period 2070–2099 based on averaging results obtained with four different climate scenarios for *Q. douglasii* and *Q. kelloggii*, respectively. See Table 1 for information regarding the climate scenarios. Grid resolution is 30 m, and maps are oriented north. Northing and Easting coordinates are in meters.

earlier study at this location that documented moderate rates of *Q. douglasii* seedling emergence on a level site but no seedling establishment, which was attributed to low summer soil moisture (Adams et al. 1992).

The pattern of *Q. kelloggii* seedling establishment is consistent with the current distribution of the species in the southern Sierra Nevada and Tehachapi Mountains. Plot data from Yosemite and Sequoia National Parks in the southern Sierra

Nevada indicate a mean elevation of roughly 1700 m for the species and a lower elevation limit of around 900–1000 m (Urban et al. 2000, Lutz et al. 2010). Further south in the western Tehachapi Mountains, the species is largely restricted to elevations above 1300 m (Hoagland et al. 2011; D. Gwenzi, *unpublished data*). The species extends above 2200 m in the vicinity of our SM gardens as a minor component of the understory, increasing in abundance on unusually xeric sites such

as ridges and areas with shallow soils (North et al. 2002). Canopy-opening disturbance such as fire is required to promote *Q. kelloggii* on more mesic sites in mixed conifer forests in this region (McDonald and Tappeiner 1996). We observed *Q. kelloggii* emerging in some foothill experimental gardens in the spring, but seedlings did not survive the first summer in foothill gardens of either the southern Sierra Nevada or western Tehachapi Mountains, regardless of topographic position. Clearly foothill environments rarely, if ever, meet basic physiological requirements for establishment of seedlings of this species.

Overall, our results suggest that summer drought and heat limit establishment of *Q. douglasii* and *Q. kelloggii* at lower elevations. Overstory vegetation and nurse plants could potentially expand the availability of establishment sites by reducing summer sunlight and heat stress, an effect not accounted for in our experimental design or establishment niche models but documented for oak establishment in both California and Mediterranean regions (Callaway 1992a, Gomez-Aparicio et al. 2006).

Our experimental gardens did not extend high enough in the southern Sierra Nevada or western Tehachapi Mountains to detect upper elevation limits to either *Q. douglasii* or *Q. kelloggii* seedling establishment. However, as noted above, 2012 and 2013 conditions were unusually warm and dry in southern California (Diffenbaugh et al. 2015, Robeson 2015, Copeland et al. 2016). For example, at Friant Government Camp (36°59', 119°43', elev. 125 m) near SF, precipitation for the 2012 and 2013 water years was 259 and 256 mm, respectively, compared to the mean and standard deviation of 363 ± 133 mm for the period 1951–2010. Summer (JJA) daily maximum temperatures averaged 35.4.0°C in 2012 and 36.4°C in 2013, compared to 36.2 ± 1.0°C for the period 1951–2010. At Grant Grove (36°44', 118°58', elev. 2005 m) near SM, precipitation for the 2012 and 2013 water years was 633 and 639 mm, respectively, compared to the mean of 1068 ± 356 mm for the period 1951–2010. Summer (JJA) daily maximum temperatures at Grant Grove averaged 25.0°C in 2012 and 25.4°C in 2013, compared to 22.5 ± 1.2°C for the period 1951–2010.

The warm and dry conditions during 2012 and 2013 may be harbingers of “climate change type drought” (Allen et al. 2010), and establishment

patterns of both oak species in this study are consistent with observed upward elevation shifts in California tree and shrub species in response to warming and drying (Kelly and Goulden 2008). Patterns in growth, however, could differ from initial survival. For example, in a survey of nine mountain ranges in Spain, Benavides et al. (2015) found highest abundance of 1- to 5-year-old juveniles of *Quercus ilex* at elevations several hundred meters above elevations where growth of recruits was highest. They suggested that the contrasting trends in seedling establishment vs. sapling growth could represent a potential stabilizing population process in relation to climatic warming.

Unfortunately, we lack seedling physiological data to causally relate seedling establishment with either  $CWD_{wy}$  or  $T_{max}$ . Thus, our establishment niche models, like SDMs in general, must be viewed as correlative. Also, we have not been able to repeat sowing trials during cooler and wetter years to disentangle the influence of soil moisture or temperature variation from other biophysical factors tied to site location. Bearing these caveats in mind, when establishment niche models are applied to historical and projected future climates, they offer insights into interannual variability in establishment windows and how those might change under projected future climate. Such insights will be important in evaluating vulnerability of oak and other tree species to rapid climate change not only in California but in Mediterranean climates more generally (Grünzweig et al. 2008, Walck et al. 2011).

#### *Regional dynamics of seedling establishment windows of opportunity*

Although on average only 15–25% of the western Tehachapi Mountains were predicted as physically suitable for establishment of either species in recent decades, suitable area extended to over 60% of the region during extreme wet years, notably the El Niño winters of 1982–1983 and 1997–1998. First-year survival is clearly a minimum requirement and no assurance of long-term establishment success, but our results suggest that some portions of the landscape may manifest climate-limited, episodic seedling recruitment, whereas other parts of the landscape are always climatically suitable. In the latter, establishment dynamics are probably more

regulated by biotic factors such as rodent and ungulate consumers and longer-term growth by disturbance-mediated competition for light (Gomez-Aparicio et al. 2008, Cocking et al. 2012). In mountainous regions with such extreme spatial as well as temporal heterogeneity in  $CWD_{wy}$ , establishment dynamics likely vary dramatically over short distances.

There have been a few attempts to predictively map the tree seedling environmental niche based on the statistical association of seedling occurrence or seedling density with mapped environmental variables such as elevation, potential solar radiation, geomorphic factors, and overstory characteristics (Baker and Weisberg 1997, Wimberly and Spies 2001). Our modeling of the seedling establishment niche on an annual time step has required extreme spatial downscaling of PRISM historical climate data and GCM outputs to the scale of local topoclimate. The moderate-to-good skill of modeled  $CWD_{wy}$  and  $T_{max}$  in predicting spatial variation in oak seedling establishment is encouraging, demonstrating that these important biophysical variables can be modeled with available terrain data and downscaled climate data to support distribution modeling of the seedling establishment niche over large areas at ecologically relevant spatio-temporal resolution. We encourage comparative studies for oaks and other dominant tree species in Mediterranean-climate regions to test the generality of these results.

One factor contributing to the predictive skill of modeled  $CWD_{wy}$  is the strong influence of solar radiation on surface temperature regime, evapotranspiration, and vegetation in rugged Mediterranean-climate landscapes (Dobrowski 2011). Solar radiation is reliably modeled at high spatial and temporal resolution in the BCM (Flint and Childs 1987, Flint et al. 2013) and, along with elevation controls on temperature and precipitation, accounts for much of the local spatial variation in  $CWD_{wy}$  across our southern California study regions.

#### *Shrinking windows of opportunity under projected climate change*

Our interpolated recent historical climate data and downscaled climate models under medium- and high-emissions scenarios all suggest declining frequency of establishment windows for both

*Q. douglasii* and *Q. kelloggii*. These projections generally agree with both recent historical trends and dynamic vegetation models projecting upslope migration of drought-tolerant oak species (Kelly and Goulden 2008, Lenihan et al. 2008, McIntyre et al. 2015). The projected declines are more dramatic for *Q. kelloggii* than for *Q. douglasii*, partly because of the combined influence of projected higher summer maximum temperatures and  $CWD_{wy}$ , and partly because of the association of the former with higher elevations that show relatively large changes in  $CWD_{wy}$  as an increasing fraction of modeled precipitation falls as rain rather than snow (McCullough et al. 2016).

Nevertheless, even under the hottest and driest climate scenario (MIROC5, RCP 8.5), conditions for *Q. kelloggii* establishment are projected to occur at least occasionally at the highest elevations and on steep north-facing slopes (Fig. 5). These results are subject to the large uncertainties associated with downscaled climate models (Hall 2014), but suggest the potential for some topoclimatic buffering of regional climate change exposure for the species.

In summary, tree seedling establishment is the necessary first step to colonization of new suitable sites and associated species' range adjustments under rapid climate change. We have demonstrated an approach to modeling the seedling establishment niche that integrates field observation data, in this case from experimental gardens, spatially downscaled climate data, and methods commonly used for species distribution modeling. We have observed relatively strong, non-linear negative association between oak seedling establishment and modeled mean daily August maximum air temperature and annual CWD. Applying those relationships across a mountainous region has revealed high inter-annual spatial variation in the climatically defined seedling establishment niche for both study species, and shrinking windows of opportunity for oak seedling establishment under projected regional climate change. While many other processes also regulate seedling establishment and growth, this study highlights the critical need to consider fine-grained establishment dynamics and topoclimatic controls on seedling establishment when assessing tree species vulnerability to climate change.

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