

1 Weather underground: subsurface hydrologic processes mediate 2 tree vulnerability to extreme climatic drought

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5 Blair C. McLaughlin¹, Rachel Blakey², Andrew P. Weitz³, Xue Feng⁴, Brittini J. Brown⁵, David
6 D. Ackerly³, Todd E. Dawson³, and Sally E. Thompson^{6,7}

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9 1. Hampshire College, Amherst, 01002, Massachusetts.

10 2. La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability,
11 University of California Los Angeles, Los Angeles, 90095, California.

12 3. Department of Integrative Biology, University of California, Berkeley, Berkeley, 94720, California

13 4. Department of Civil, and Environmental, and Geo-Engineering, University of Minnesota, Minneapolis,
14 55455, Minnesota

15 5. Department of Natural Resources and Society, University of Idaho, Moscow 83843, Idaho

16 6. Department of Civil, Environmental and Mining Engineering, University of Western Australia, Crawley,
17 Western Australia, 6009

18 7. Department of Civil and Environmental Engineering, University of California, Berkeley, Berkeley,
19 94720, California

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21 *Corresponding author: Blair McLaughlin, bmclaughlin@hampshire.edu
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23 Abstract

24 Drought extent and severity have increased and are predicted to continue to increase in many
25 parts of the world. Understanding tree vulnerability to drought at both individual and species
26 levels is key to ongoing forest management and preparation for future transitions in community
27 composition. The influence of subsurface hydrologic processes is particularly important in water-
28 limited ecosystems, and is an under-studied aspect of tree drought vulnerability. With
29 California's 2013-2016 extraordinary drought as a natural experiment, we studied four co-
30 occurring woodland tree species, blue oak (*Quercus douglasii*), valley oak (*Quercus lobata*), grey
31 pine (*Pinus sabiniana*), and California juniper (*Juniperus californica*), examining drought
32 vulnerability as a function of climate, lithology and hydrology using regional aerial dieback
33 surveys and site scale field surveys. We found that in addition to climatic drought severity (i.e.
34 rainfall), subsurface processes explained variation in drought vulnerability within and across
35 species at both scales. Regionally for blue oak, severity of dieback was related to the bedrock
36 lithology, with higher mortality on igneous and metamorphic substrates, and to regional
37 reductions in groundwater. At the site scale, access to deep subsurface water, evidenced by
38 stemwater stable isotope composition, was related to canopy condition across all species. Along
39 hillslope gradients, channel locations supported similar environments in terms of water stress
40 across a wide climatic gradient, indicating that subsurface hydrology mediates species'
41 experience of drought, and that areas associated with persistent access to subsurface hydrologic
42 resources may provide important refugia at species' xeric range edges. Despite this persistent
43 overall influence of the subsurface environment, individual species showed markedly different
44 response patterns. We argue that hydrologic niche segregation can be a useful lens through which
45 to interpret these differences in vulnerability to climatic drought and climate change.

46 **Keywords**

47 Water, subsurface, hydrology, lithology, drought, oak woodlands, hydrologic niche, climate
48 change, *Quercus douglasii*

49

50 **Weather underground: subsurface hydrologic processes mediate** 51 **tree vulnerability to extreme climatic drought**

52 **1. Introduction**

53

54 Climate change is anticipated to increase and exacerbate drying in water-limited ecosystems
55 (Gosling & Arnell, 2016), and to increase the frequency and severity of extreme drought
56 (Diffenbaugh *et al.*, 2015, Stocker *et al.*, 2013). Recent global increases in tree mortality related
57 to climatic extremes (Anderegg *et al.*, 2013, Breshears *et al.*, 2009, Van Mantgem *et al.*, 2009,
58 Vicente-Serrano *et al.*, 2013, Williams *et al.*, 2013), point to a likely increase in future drought-
59 related tree mortality (Allen *et al.*, 2010).

60

61 Plants employ a range of strategies to cope with seasonal drought (Vico *et al.*, 2014), including
62 annual life history strategies (Mulroy & Rundel, 1977), deep rootedness (Ehleringer *et al.* 1991),
63 dry season dormancy (Borchert & Rivera, 2001, Vegis, 1964), or drought deciduousness
64 (Manzoni *et al.*, 2015, Vico *et al.*, 2017). An individual's size, canopy position, stand density and
65 associations with invasive species (Bennett *et al.*, 2015, Clark *et al.*, 2014, Gitlin *et al.*, 2006,
66 Nepstad *et al.*, 2007, Young *et al.*, 2017) can impact drought vulnerability. Across species, traits
67 including mean species height, stomatal response, leaf area, stem and/or leaf hydraulic traits, and
68 water potential at the leaf turgor loss point or the zero carbon assimilation point have been
69 associated with variation in drought vulnerability (Anderegg *et al.*, 2016, Bartlett *et al.*, 2012,
70 Breshears *et al.*, 2009, McDowell & Allen, 2015). Biotic (e.g. herbivores, pathogens) and abiotic
71 (e.g. fire) stressors are also important drivers of drought vulnerability (Kolb *et al.*, 2016, Liang *et*
72 *al.*, 2016). These traits and stressors interact with the quantity of water available for plant use

73 during a drought period to determine plant outcomes, including mortality (Feng *et al.*, 2018, Feng
74 *et al.*, 2017).

75

76 In seasonally dry ecosystems, such as woodlands and savannas, the water available to plant
77 species growing in the dry season is largely drawn from that which is stored within the root zone
78 by the end of the wet season in late winter or spring (Dralle & Thompson, 2016, Feng *et al.*,
79 2015). Thus the translation of meteorological or climatic drought (i.e. precipitation deficits,
80 Dracup *et al.*, 1980) into the drought conditions experienced by these plants is determined not
81 only by wet-season precipitation, but by how that precipitation enters, and is stored, transmitted
82 and lost from various subsurface layers, and how plants access those subsurface layers in space
83 and time. Thus, surface hydrological processes such as rainfall redistribution by overland flow
84 (Thompson *et al.*, 2010, Thompson *et al.*, 2011) and subsurface characteristics, such as the
85 infiltration capacity, depth, porosity distribution and permeability of the subsurface environment
86 (Brooks *et al.*, 2015, Guo & Lin, 2016), together with rooting depth, and how plant locations are
87 situated with respect to the hillslope catena (i.e. the lateral soil and topographic variation along a
88 hillslope) or local or regional groundwater, all place controls on water availability, and plants'
89 experience of drought (Dawson *et al.*, 2020). The broad implication of these hydrological
90 processes is that individuals or populations of plants with varying functional traits exposed to a
91 common meteorological drought, can experience different anomalies in water availability,
92 complicating both understanding and predictions of drought vulnerability (Feng *et al.*, 2019, Feng
93 *et al.*, 2018, Feng *et al.*, 2017).

94

95 Several studies suggest that the responses of vegetation growing in seasonally-dry climates to
96 meteorological drought depend on the interactions between climate, subsurface hydrology and
97 landscape features. Hahm *et al.* (2019a), for example, demonstrate that in a subset of locations
98 across California, limited subsurface water storage capacity, rather than variations in seasonal

99 precipitation, appears to constrain plant productivity, such that variability in annual vegetation
100 growth is independent of variations in annual precipitation. In Australian savannas, plant drought
101 mortality varied by parent rock lithology (with mortality ranging from greatest to least across
102 igneous metamorphic to sedimentary rock types to alluvium, Fensham & Holman, 1999),
103 presumably reflecting differences in vadose zone porosity and permeability profiles. Some
104 studies have considered how landscape positioning along site-scale topographic, climatic and soil
105 moisture gradients influence water stress and mortality outcomes (Anderegg *et al.*, 2013, Gitlin *et*
106 *al.*, 2006, Young *et al.*, 2017), but few address processes in the subsurface (Brown *et al.*, 2018,
107 Fensham & Holman, 1999).

108

109 Our ability to address this influence of subsurface processes is facilitated by the fact that plants
110 are not located randomly on the landscape (Dawson, 1990). Instead, species tend to grow in
111 locations where their physiological needs with respect to water supply are matched by the
112 dynamics of plant available water (Shantz, 1927, Solbrig & Orians, 1977), and such variations in
113 water availability can explain up to 60% of species' spatial distributions at landscape scales
114 (García-Baquero *et al.*, 2016). As such, plant species exhibit contrasting hydrologic niches
115 (Silvertown *et al.*, 2015, West *et al.*, 2012, Dawson, 1990) – differences in their physiological
116 requirements for growth, survival and reproduction with respect to water supply. These
117 differences are reflected in different species distributions across spatial hydrologic gradients
118 defined by climate, topography, and subsurface properties (Ackerly *et al.*, In press, Dawson *et al.*,
119 2020, Araya *et al.*, 2011, Silvertown, 2004, Silvertown *et al.*, 2001, Silvertown *et al.*, 1999,
120 Pockman and Sperry 2000).

121

122 In this study, we use the unprecedented 2013-2016 California drought (which included the
123 hottest, driest 3-year period since instrumental records commenced in 1895 (Mann & Gleick,

124 2015)) as a case study to explore how subsurface processes and variation in species' hydrologic
125 niches (which influence their regional and site-scale distributions) led to different drought
126 responses of species and individuals. In a previous study (Brown et al. 2018), our group explored
127 regional patterns of blue oak dieback and climate with a focus on response thresholds, predicting
128 future areas of the species' persistence using climate futures and the influence of regional
129 groundwater loss. In this paper, we expand on that work with a cross-species and multi-scale
130 analysis of the variations in species' drought response and vulnerability and the importance of the
131 subsurface environment more broadly. We considered four broadly distributed, co-occurring
132 species—blue oak (*Quercus douglasii*), valley oak (*Quercus lobata*), grey pine (*Pinus sabiniana*),
133 and California juniper (*Juniperus californica*)—representing a range of hydrologic niches and
134 contrasting dependence on subsurface water resources. We compared dieback patterns across the
135 species' ranges using summer 2015 USDA Forest Service flyover survey data (Fettig *et al.*, 2019,
136 USDA Forest Service, 2017), and, where sufficient data existed for blue oak and grey pine, we
137 examined these dieback patterns as a function of precipitation, temperature, underlying lithology
138 (as a proxy for subsurface characteristics) and groundwater gravitational anomalies (measured by
139 satellite). “Dieback probability” refers to the percent of trees that have visible and significant
140 canopy leaf loss, based on the aerial surveys, in a particular location at the end of the drought
141 period. We complemented these regional analyses with three years of data collected from a field
142 site where all four species occurred at the xeric edge of the blue and valley oak and grey pine
143 distributions, and from two additional sites within the more mesic parts of the blue and valley oak
144 distributions.

145

146 We asked the following:

- 147 1) What was the influence of climate on tree dieback and mortality? Was spatial
148 variation in these factors more strongly predicted by absolute levels of 2013-15
149 precipitation and temperature, or by drought anomalies, relative to historical means?

150 2) What was the influence of subsurface conditions (physiography, hydrology,
151 lithology) on tree dieback and mortality? Do subsurface features and processes
152 mediate how trees experience climatic drought?

153

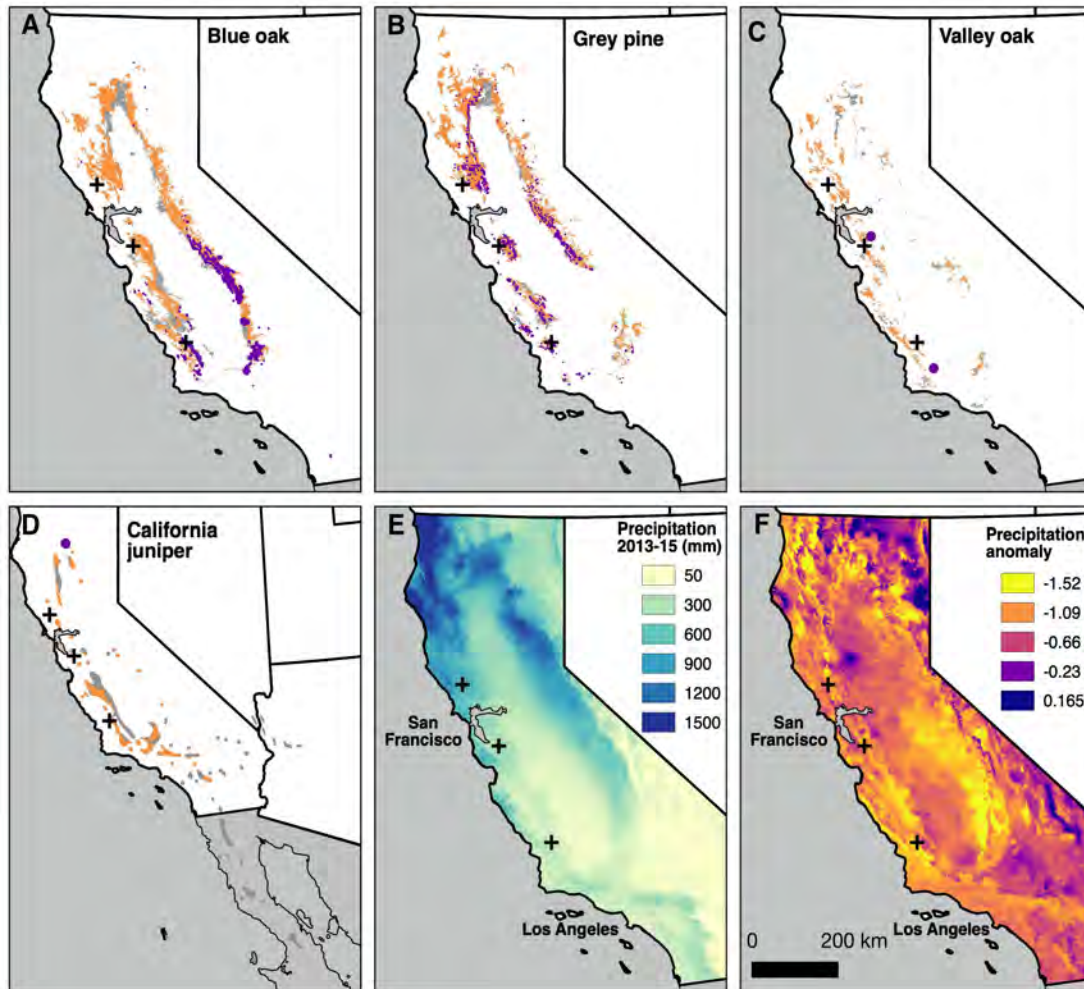
154 We suggest that the hydrologic niche concept can provide a useful lens through which to
155 interpret species-level differences in drought vulnerability in co-occurring species with
156 overlapping distributional climatic associations.

157

158 **2. Methods**

159 **2.1 Study sites**

160 The California Sierra Nevada and Coast Range water-limited foothill woodlands form a unique
161 ecosystem, situated in a Mediterranean-type climate between higher altitude conifer forests and
162 lower elevation grasslands (Pavlik, 1991). They are primarily characterized by endemic blue and
163 valley oak and grey pine, with an annual grass understory, and are often grazed by cattle (Pavlik,
164 1991). Our regional-scale analyses encompassed the majority of the range of the three endemic
165 study species and part of the California juniper distribution, which extends further east and south
166 (Figure 1).



167

168 **Figure 1:** California distributions of the four study species (A) blue oak (B) grey pine (C) valley oak and (D) California
 169 juniper. Orange / grey in A-D indicate areas covered /not covered by Forest Service aerial mortality surveys and areas
 170 of observed dieback are shown in purple (including outlines for blue oak and gray pine and shown as a point for valley
 171 oak and California juniper to increase visibility). Panel E shows average water year precipitation (2013-2015) and (F)
 172 shows drought precipitation anomaly. A positive anomaly shows a wetter-than average year. Study sites are shown as
 173 crosses (north to south: Pepperwood, Blue Oak Ranch Reserve and Private Ranch). Panel A is redrawn from Brown et
 174 al. (2018).

175

176 We also worked at three field sites on the western margin of the ecosystem, spanning most of its
 177 north-south extent: two research reserves, Pepperwood Preserve (Pepperwood) and Blue Oak
 178 Ranch Reserve (BORR), and a private property, referred to here as “Private Ranch” (Figure 1,
 179 panel F). Cattle currently graze at Pepperwood and Private Ranch, while BORR has not been
 180 grazed for approximately 20 years. The three sites span a gradient in aridity, with a historical
 181 average annual precipitation (AAP, 1980-2010) of 1000 mm at Pepperwood, 600 mm at BORR

182 and 300 mm at Private Ranch (Flint and Flint 2013). The sites vary in geology and topography,
183 with deeper incised canyons and minimal riparian zones at BORR and Pepperwood, and broad
184 alluvial floodplain valleys flanked by shallow hills at Private Ranch.

185

186 **2.2 Study species**

187 The four study species were the dominant trees at Private Ranch, and the two oaks are dominant
188 at BORR and fairly common at Pepperwood (the pine and juniper are absent or rare at these
189 sites). The species reflect contrasting deciduous/evergreen life history strategies and rooting
190 depth. Previous studies report a range of deep and shallow roots for blue oak (Griffin, 1973,
191 Miller *et al.*, 2010) and grey pine (Powers, 1990), a deep rooted morphology for valley oak
192 (Lewis & Burgy, 1964, Lewis & Burgy, 1966), and potentially mid-level roots in California
193 juniper based on its relatively small stature, slow growth and extreme drought tolerance (Willson
194 *et al.*, 2008). Distributional climate associations and size characteristics of the study species are
195 shown in Section S1 and Table S1 of the SI.

196 **2.3 Regional datasets**

197 We analyzed the occurrence of tree crown dieback during the drought for blue oak and grey pine
198 within its regional distribution, as a function of climate, lithology and groundwater depth
199 anomalies. Water year (October 1-September 31) climate data were obtained from a 270 x 270 m
200 downscaling of PRISM (Daly *et al.*, 1994) produced by Flint and Flint (2012, regularly updated),
201 from which we calculated historical averages (for 1980-2010), drought year averages (for 2013-
202 2015), and the drought year anomalies ([mean drought year (2013-15) – historical baseline]/
203 interannual standard deviation of historical baseline) of three climate variables: annual
204 precipitation [mm], summer/fall temperatures [°C], and climatic water deficit (CWD) [mm]
205 (Basin Characterization Model (Flint & Flint, 2012)). See Figure 1 E-F for state-wide
206 precipitation averages and drought anomalies. We explored, but did not include, SSURGO data

207 on soil water holding capacity (visual assessment of analyses indicated no influence on canopy
208 condition, see Figure S1).

209

210 We obtained species distributions from the California GAP Analysis database (maps of existing
211 vegetation at the species level for dominant, overstory species) (Davis et al., 1998), and dieback
212 data from the 2015 USDA Forest Service Aerial Detection Monitoring campaign (US Forest
213 Service, 2015), collected in the summer of 2015 (sampling details in SI Section S2.2). The aerial
214 surveys cover 44% of California, and 40%-88% of the ranges of the study species (Figure 1 A-D,
215 Table 1). Dieback of California juniper and valley oak was recorded in only one and two
216 locations respectively (Figure 1, C and D). Dieback of blue oak and grey pine was more
217 extensive, covering 5.57 and 0.73% of these trees' distributions, enabling further analyses of
218 dieback in relation to climate and landscape variables. To facilitate such comparison, dieback
219 data were converted from polygons to points using a 270 x 270 m resolution grid matching BCM
220 climate layers. Dieback points were assigned if the overlapping dieback polygon covered >25%
221 of the grid cell, non-dieback points were assigned throughout the remaining study area. Points
222 falling within water bodies were removed from the dataset.

223

224 Lithological data were obtained from the USGS Californian Geology map (Ludington *et al.*,
225 2007). These data contain over 100 separate lithological types (SI, Table S2), which influence
226 but do not directly correspond to different subsurface hydraulic properties (Hahm *et al.*, 2019a,
227 Hahm *et al.*, 2019b). Exploratory analyses indicated that the study species were broadly
228 distributed in their location across sedimentary and granitic parent materials. Although both
229 lithologies can weather into deep, water-storing subsurface environments that supply plants with
230 water (Dawson *et al.*, 2020, Hahm *et al.*, 2019a, Hahm *et al.*, 2019b, Holbrook *et al.*, 2014, Klos
231 *et al.*, 2018, Rempe & Dietrich, 2018) it is reasonable to expect that the resulting porosities,
232 conductivities and their distributions, as well as the depth of soil and weathering – or at least the

233 distribution of such factors through space -- would differ between these broad parent rock types
 234 (Jenny, 1961). For this reason, we analyzed parent rock type as a factor contributing to
 235 subsurface characteristics, using the highest-level lithology categories: igneous/metamorphic vs.
 236 sedimentary/unconsolidated (SI, Table S2).

237

238 Changes in subsurface water storage were computed using data obtained from NASA's GRACE
 239 satellite (Famiglietti *et al.*, 2011, Swenson, 2012) at a 55 km resolution, comparing storage during
 240 August 2015 to a baseline period prior to the drought (mean August values from 2004-2009).

241 Attribution of groundwater changes to natural and anthropogenic causes at regional scales is not
 242 straightforward as recharge declined and anthropogenic abstraction increased markedly during the
 243 drought (Xiao *et al.*, 2017). Since the majority of the study area is rangeland, we assumed that
 244 most deep water abstraction would be associated with groundwater pumping for stock watering,
 245 which typically has lower water demands than crop agriculture (Hanak *et al.*, 2019). A

246 comparison of the GRACE groundwater anomaly between the heavily irrigated croplands of the
 247 California Central Valley and the rangeland-dominated Tulare, San Joaquin and Sacramento
 248 basins, suggested that rangeland groundwater declines were approximate a third (-2.9 km³/yr) of
 249 those in the Central Valley (-10.0 km³/yr) (Xiao *et al.*, 2017), despite the rangelands covering
 250 over twice the area of the Central Valley. These findings suggest that our interpretation of the
 251 GRACE signal as a proxy for changes in plant available subsurface soil moisture are reasonable,
 252 if necessarily imprecise. Additional information about regional datasets used is provided in the
 253 SI, Section S2.

254

255 **Table 1:** Distribution and dieback metrics for *Q. douglasii*, *Q. lobata*, *P. sabiniana*, and *J. Californica*. Area sampled
 256 refers to the 2015 Aerial Detection Survey undertaken by the USDS Forest Service to identify areas of forest dieback
 257 across California. California state area taken from US census data.

	<i>Q. douglasii</i>	<i>Q. lobata</i>	<i>P. sabiniana</i>	<i>J. californica</i>
Total distribution area (ha)	3,468,996	818,586	2,496,599	480,225

Percentage of California covered by distribution	8.2	1.9	5.9	1.1
Total area sampled (ha)	2,725,221	586,317	2,207,613	189,719
Percentage of total distribution sampled	78.6	71.6	88.4	39.5
Total area of dieback detected (ha)	151,819	699	16,222	47
Percentage of sampled distribution recorded as dieback	5.6	0.1	0.7	<0.1

258
259

260 2.4 Field data

261

262 A total of 877 trees across the three study sites were studied during late summer in 2014 and
263 2015. We used a targeted sampling design to ensure that we captured the phenomenon of interest
264 – poor tree canopy health. At all sites, we visually searched the site and consulted with land
265 managers to find areas of poor canopy condition around which we had access to the full hillslope
266 catena. At the most xeric site, Private Ranch, we located three subsites around areas with poor
267 canopy condition. We extended the subsites uphill and downhill to span the full hillslope catena.
268 Subsites were approximately 200x200 m. At the other two sites, Pepperwood and BORR, we
269 looked for, but did not find areas with similarly high levels of canopy stress, so we selected three
270 otherwise similar subsites where blue and valley oak occurred. (See SI Fig S3 for schematic
271 diagram of subsites). The subsites appeared to be generally representative of where our species
272 occurred across the site in terms of characteristics like slope, aspect and land use.

273

274 Within each subsite, we established four quadrats of approximately 60 x60 m, two in the channel
275 area and two in the hill area (SI Fig S3). We identified species and visually assessed the canopy
276 condition of all adult trees (over 10 cm DBH) in each quadrat, termed hereafter “full surveys.”

277 Canopy condition was assessed as the percent of a tree’s canopy that was bare, binned in interval

278 categories of 10%, including 100% bareness for canopies that appeared to be devoid of leaves.
279 Canopy condition measurements were calibrated between data collectors. Not all species were
280 present in all subsites or quadrats (SI Tables S3 and S4). Three hill valley oaks at the Pepperwood
281 site and two channel grey pines at the Private Ranch site were added to the full survey *post-hoc*
282 given their inclusion in the survey subset described below. Full surveys were conducted in
283 August/September of 2014.

284

285 Within each subsite, we established a transect that extended from the channel to the hilltop
286 crossing the area of poor canopy condition, if present. Along this transect we selected a subset of
287 adult trees for more intensive sampling that had at least a few leaves, and were at least three m
288 distance from one other and from roads, termed hereafter “survey subset.” Where possible, we
289 located three trees in the upper and three in the lower part of the transect. Where multiple trees
290 met these criteria, we sampled randomly. For each tree in the survey subset we visually assessed
291 canopy condition as described above, and also collected stems for stemwater isotope analysis and
292 measured diameter at breast height (DBH). Trees were also geolocated with a 0.5 m resolution
293 Trimble GPS unit. We mapped channels and calculated the height above the nearest drainage for
294 each individual (‘elevation above channel’). Survey subset data were collected during
295 August/September 2015. Mortality confirmation surveys were conducted in spring 2017, the
296 growing season after the end of the drought.

297

298 Xylem water isotope analysis followed Dawson and Ehleringer (1993) and is detailed in the SI
299 (Section S3.1). From these xylem water isotope data, the extent of evaporative enrichment of tree
300 water isotope composition was quantified by calculating the Euclidean distance(s) of the xylem
301 water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ isotope values from each site’s local meteoric water line (LMWL) and plotted
302 in dual isotope space ($\delta^2\text{H}$ as a function of $\delta^{18}\text{O}$, ‰ VSMOW), where the LMWL represents the
303 isotopic composition of local precipitation (Weitz 2018). These plant isotope departures from

304 their LMWL are unitless measures, as they are derived in dual isotope space (‰ / ‰ VSMOW).
305 However, the “LMWL departure” distances reflect, in relative terms, how much of the water
306 available to each tree has undergone post-precipitation isotopic modification; effectively the
307 amount of source water fractionation has occurred because of evaporative processes that lead to
308 isotope enrichment of the residual water that trees might take up. This metric therefore measures
309 how much trees rely on water stored in shallow layers, largely soils (which is influenced to a
310 greater extent by evaporative processes that cause enrichment, rendering these shallow waters
311 less similar to the original precipitation inputs), relative to water stored at greater depths (less
312 exposed to evaporative enrichment and thus more similar to precipitation) (Benettin *et al.*, 2018,
313 Oshun *et al.*, 2016, Simonin *et al.*, 2009). The smaller the LMWL departure, the greater the tree’s
314 use of deeper subsurface water.

315

316 **2.5 Statistical analysis**

317 We used a variety of regression approaches to explore variation in observed drought vulnerability
318 (dieback at regional scales, canopy condition at site scales) using the R project for statistical
319 computing for all analyses (R Development Core Team 2016). Spatial processing and mapping
320 were conducted in Arc GIS v10 and QGIS v2.14. The *spsurvey* R package was used for the GRTS
321 method (Kincaid *et al.*, 2015) and the *lme4* R package was used for linear mixed-effects models
322 (Bates *et al.*, 2015). Model residuals were checked for normality and homogeneity of variance,
323 and data were transformed as necessary.

324 **2.5.1 Regional analyses**

325

326 We used a model selection approach with logistic regression to attribute the drivers of variation in
327 canopy dieback for blue oak and grey pine (the two species that experienced substantial dieback
328 at regional scales in our dataset), with respect to climatic and subsurface drivers of water
329 availability. We thinned the datasets using the generalized random tessellation stratified (GRTS)

330 method to avoid spatial autocorrelation (Stevens & Olsen, 2004), which can increase the risk of
331 Type I errors in statistical analysis (Dormann *et al.*, 2007). We used GRTS to select spatially
332 balanced samples for dieback and non-dieback points equal to the number of discrete dieback
333 patches (continuous areas of dieback) recorded (blue oak: 490, grey pine: 1105). Therefore, our
334 response variable consisted of equal numbers of dieback and non-dieback points. All continuous
335 predictor variables were scaled and centered prior to analysis.

336

337 We modeled the relationship between the probability of dieback of blue oak and grey pine as a
338 function of climate variables, using absolute drought year (2013-15) values and drought
339 anomalies (CWD, annual precipitation, summer and fall temperatures). We found that CWD and
340 annual precipitation were highly correlated ($r = -0.88$ for blue oak and -0.89 for grey pine). We
341 retained precipitation in the regression models rather than CWD because of its more
342 straightforward interpretation as a direct climate variable (models run with CWD instead of
343 annual precipitation were highly similar and are shown in SI table S5). This left six climate
344 metrics (historical values, absolute drought year values, or drought anomalies associated with
345 annual precipitation, and summer/fall temperature), which we evaluated one at a time using an
346 information theoretic approach (Anderson & Burnham, 2002) (SI table S6). For each climate
347 measure (annual precipitation and summer/fall temperature), we retained the model containing
348 the variable (historical, absolute drought year, or anomaly) with the lowest BIC, and tested for
349 significance using the Wald test. We next added the subsurface variables (change in GRACE
350 storage and lithology) to the model, checking whether they improved model fit by comparing the
351 BICs (a change in BIC of more than 2 indicates a significant improvement (Raftery, 1995)).
352 Finally, because no climate anomalies were retained in the model after the first round of selection
353 (described above) given the stronger effects of absolute drought year values, we additionally
354 tested the hypotheses that precipitation anomaly would secondarily influence dieback probability
355 and that its effect might change with absolute drought year precipitation by adding precipitation

356 anomaly and an interaction between precipitation anomaly and absolute drought year
357 precipitation to the model and checking whether these terms improved model fit by comparing
358 the BICs.

359

360 2.5.2 Field data analysis

361

362 **Survey subset:** For the *survey subset* data collected at Private Ranch, across all species (N=49)
363 we applied a linear mixed effects model, with canopy condition as the response variable,
364 stemwater LMWL departure, species, and DBH as fixed predictor variables, and sub-site as a
365 random predictor variable. To test whether the relationship between canopy condition and
366 stemwater LMWL departure held for individual species, we ran linear regressions with canopy
367 condition as the response variable and stemwater LMWL departure as the predictor variable
368 individually for blue oak (N=19), grey pine (N=12), valley oak (N=9), and California juniper
369 (N=9). Stemwater LMWL departure was related to an individual's distance from the channel;
370 therefore, we conducted an exploratory analysis of each parameter's relationship to canopy
371 condition. We did not include elevation above channel in the model: stemwater LMWL
372 departure was a stronger predictor of canopy condition than elevation above channel, and we
373 hypothesized that groundwater availability was the mechanistic driver of variation in canopy
374 health.

375

376 Across the three study sites within the *survey subset*, for blue oak (N=55) and valley oak (N=32)
377 separately, we ran general linear models to assess the influence of stemwater LMWL departure,
378 DBH and site (a proxy for climate) on canopy condition. To explore the range of the hydrologic
379 niche for each species, we compared the variance in stemwater stable isotope LMWL departure
380 for blue and valley oaks across all three sites using a Bartlett's test of homogeneity of variances.

381

382 **Full surveys:** Because the *full survey* data were not fully factorial and were frequently
383 heteroscedastic, we ran individual tests of differences of group means on various parts of the data
384 set based on *a priori* hypotheses. The family-wise error rate for multiple tests was accounted for
385 with a Bonferroni correction. Because of the spatial structure in the full survey data, statistical
386 inferences from these data are limited to the study sites. However they provide valuable
387 ecological inferences for interpreting species' drought response at each site. Because there was
388 only one hill valley oak individual at the Private Ranch site, it was removed from analyses.

389

390 At the Private Ranch site, to evaluate whether there were differences in canopy condition across
391 species in channel and hill environments, we ran one-way ANOVAs with unequal variance across
392 all species in the hills, and across all species in the channels. To explore pairwise *post-hoc*
393 comparisons, we used a Games-Howell *post-hoc* test. To evaluate differences between
394 channel/hill environments within species, we ran individual t-tests with unequal variance
395 separately for each species.

396

397 For the *full survey* data across all three study sites, to evaluate differences in canopy condition
398 across sites for oaks in the channels and for oaks on the hills we ran one-way t-tests with unequal
399 variance and a Games-Howell *post-hoc* test across sites for hillslope and channel locations
400 separately. To evaluate overall differences between blue and valley oak canopy health, we ran a
401 t-test with unequal variance using data from all sites, and tested for difference in variance using a
402 Bartlett's test. To explore the influence of landscape position on canopy condition, we ran
403 individual t-tests (accounting for variance as needed), on channel versus hillslope locations for
404 blue and valley oaks separately at each site.

405 **3. Results**

406 **3.1. Regional scale**

407

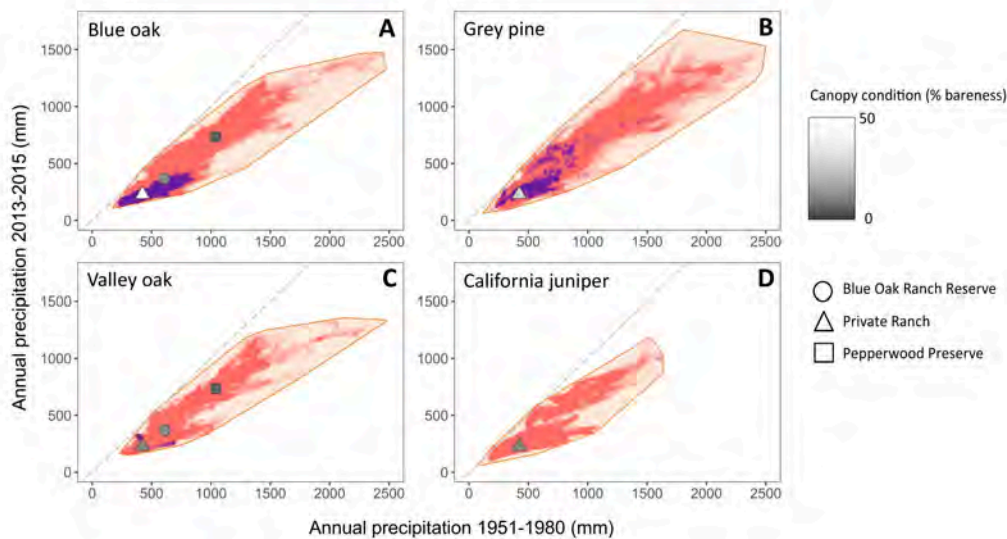
408 As reported in Table 1, regional drought dieback amongst the study species varied from minimal
409 (valley oak and juniper), to approximately 1% and 6% of the surveyed area (grey pine and blue
410 oak, respectively). These differences emerged despite many similarities in the exposure of the
411 different species to climatic drought (Figure 2). For all species, across each species' distribution,
412 drought-averaged annual precipitation (2013-2015) was lower than historical means, with the
413 greatest anomalies occurring in typically wet parts of the range of blue oak, grey pine and valley
414 oak (Figure 2 A-C). In these three species, dieback was centered on regions where both historical
415 and drought year precipitation were low. Conversely, California juniper experienced (very
416 limited) dieback in areas of typically higher rainfall (Figure 2) (we do not have direct ground
417 observation to determine whether drought is the apparent cause of mortality in these locations).
418 Climate conditions at the three study sites are shown in Figure 2 panels A and C, which also
419 demonstrate the worsening canopy condition (increasing bareness) for blue oak along the aridity
420 gradient from Pepperwood Preserve, to Blue Oak Ranch Reserve, to the poorest canopy
421 conditions at Private Ranch.

422

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426
 427 **Figure 2:** Annual precipitation (AP) versus drought year precipitation for all sites within the range of A) blue oak, B)
 428 grey pine, C) valley oak and D) California juniper. The one-to-one line is shown on all plots (blue dashes), points
 429 below the 1:1 line indicate areas drier than average conditions. Locations where USFS aerial surveys identified
 430 dieback are plotted in orange, blue points are areas where no dieback was observed, and the surrounding blue polygons
 431 represent the full distribution of the species. The study sites are indicated with over-sized shapes, shaded to indicate
 432 the canopy condition at each site. Panel A is based on Brown et al. (2018).

433 Table 2 and Figure 3 show the results of the logistic regressions that evaluated the relationships
 434 between canopy dieback, and climate and subsurface characteristics for blue oak and grey pine.
 435 Table 2 shows effect sizes for significant predictor variables, and Figure 3 shows the fitted
 436 relationships of dieback probability to these regressors individually. The associations between
 437 climate and dieback for all tested variables are shown in the SI, Table S4. As illustrated in Figure
 438 3 panels A and B, the relationship between dieback probability and 2013-15 precipitation was
 439 more threshold-like for blue oak than grey pine --- blue oak dieback probabilities became
 440 negligible (<10% in the mean) once 2013-15 precipitation exceeded 400mm. Conversely for
 441 grey pine, dieback probability declined near linearly with increasing 2013-15 precipitation until it
 442 was approximately 800 mm, after which dieback probability was also <10% on average.
 443
 444 Figure 3 panels A and B show how dieback probabilities varied with 2013-15 precipitation and
 445 summer/fall temperatures. For both species, increasing temperature increased the probability of

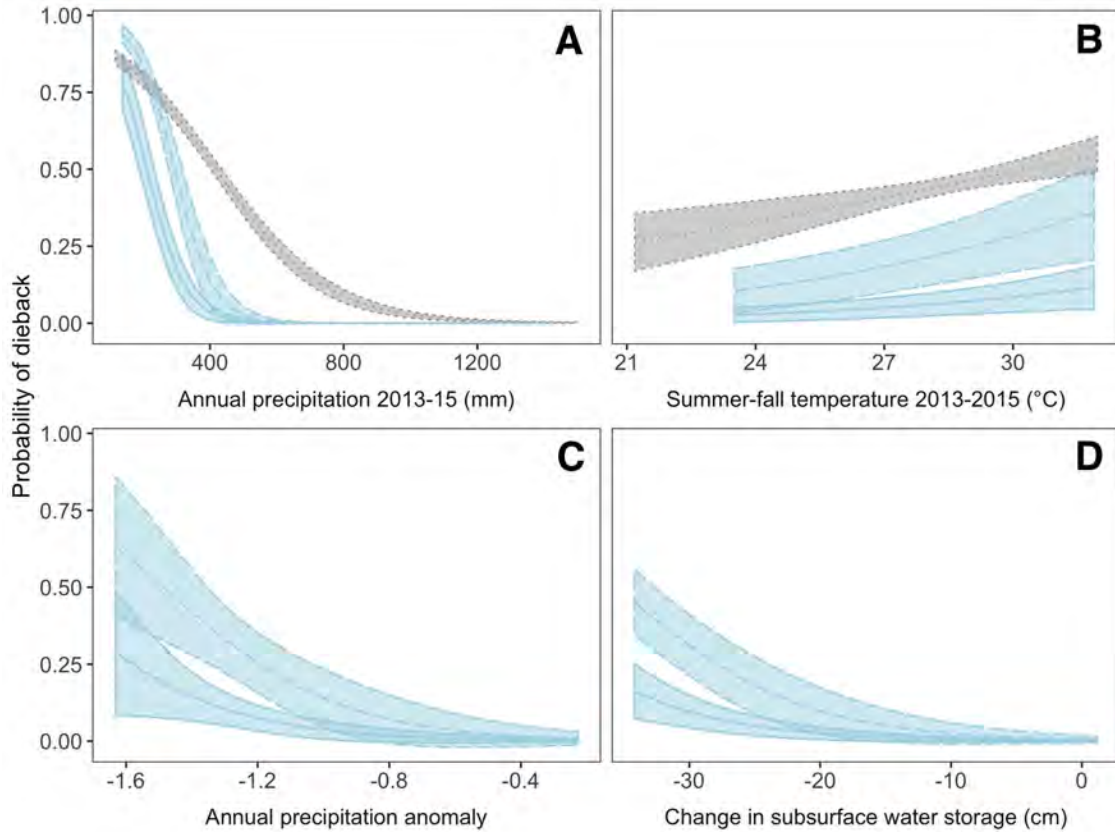
446 dieback, although the effect was weaker than that of precipitation. These results were robust to
 447 exchanging precipitation for CWD in the models (SI Table S5). Figure 3 panels C and D show
 448 that for blue oak only, precipitation anomaly and change in subsurface water storage
 449 (groundwater anomaly) were significant predictors of dieback.

450 For blue oak, lithology had a significant effect on canopy dieback, with greater dieback
 451 on granitic compared to sedimentary lithologies. At any particular level of climatic variables,
 452 presence on granitic rock more than doubled the probability of dieback.

453
 454 **Table 2:** Summary of logistic regression models predicting probability of dieback for blue oak and grey pine using
 455 2013-15 average precipitation, summer/fall temperature, standardized annual precipitation anomaly, interaction
 456 between 2013-15 average precipitation and precipitation anomaly, change in subsurface water storage (GRACE), and
 457 lithology (igneous/metamorphic was the intercept). Only significant terms are included in presented models.

Tree	Variable	Estimate	z	p
<i>Q. douglasii</i>	Intercept	-1.20 ± 0.28	-4.32	<0.001
	2013-15 Precipitation	-3.58 ± 0.40	-8.86	<0.001
	2013-15 Summer/Fall Temperature	0.32 ± 0.10	3.35	<0.001
	Precipitation anomaly	-0.97 ± 0.30	-3.20	0.001
	Precipitation anomaly: 2013-15			
	Precipitation interaction	-1.40 ± 0.45	-3.09	0.002
	Change in subsurface water storage	-0.97 ± 0.19	-4.94	<0.001
	Lithology	-1.45 ± 0.25	-5.77	<0.001
<i>P. sabiniana</i>	Intercept	0.21 ± 0.05	-3.90	<0.001
	2013-15 Precipitation	-1.55 ± 0.08	-19.75	<0.001
	2013-15 Summer/Fall Temperature	0.20 ± 0.06	3.50	<0.001

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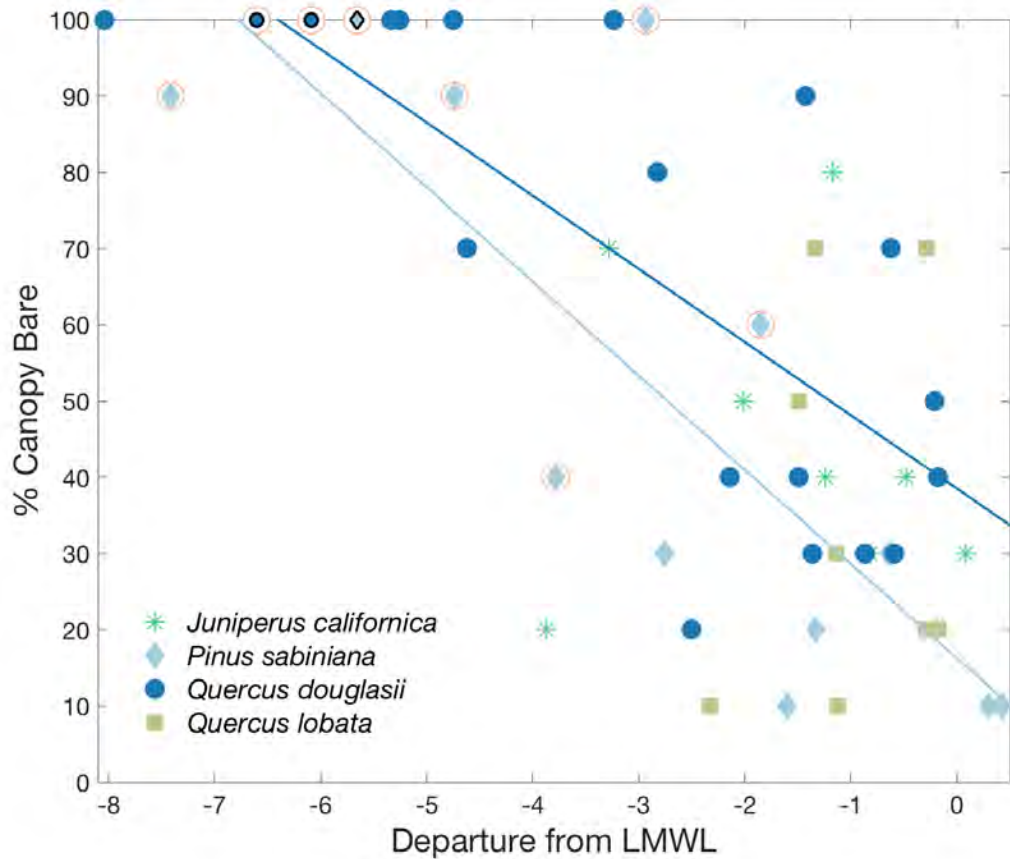


463
 464 **Figure 3:** Logistic regression showing fitted relationships between probability of dieback and environmental variables
 465 for blue oak (blue) and grey pine (grey). Environmental variables included average annual precipitation in drought
 466 years 2013-2015 (mm) (A), average summer/fall temperature in drought years 2013-2015 (°C) (B), standardized annual
 467 precipitation anomaly (mm) (mean drought year – historical baseline/standard deviation of historical baseline) (C), and
 468 change in subsurface water storage between 2015 and pre-drought baseline (cm thickness) (D). Fitted relationships
 469 were calculated with other variables equal to their means: Annual precipitation 2013-15 (364 mm blue oak / 453 mm
 470 grey pine); Summer-Fall temperature 2013-2015 (28.6 °C blue oak / 28.4 °C grey pine); Annual precipitation anomaly
 471 (-1.2); Change in subsurface water storage (- 27 cm). The best model for blue oak contained geology type, therefore
 472 relationships were fit for lithology type separately for blue oak: igneous/metamorphic (dashed line) and
 473 sedimentary/unconsolidated (solid line). Grey pine shows no effect of lithology (dotted line). Fitted relationships show
 474 means and 95% confidence intervals.

475
 476

3.2. Field scale: survey subset

477
478
479 Amongst the *survey subset* at Private Ranch (where all four species co-occurred), stemwater
480 LMWL departure was the strongest predictor of canopy condition across all 4 species (Figure 4,
481 SI Table S7a), with a smaller LMWL departure value (i.e. use of deeper water) associated with
482 better canopy condition. For individual species, stemwater LMWL departure predicted species
483 canopy condition for blue oak and grey pine but not valley oak or California juniper (Figure 4, SI
484 Table S7b). When considering stemwater LMWL departure values within species individually,
485 we found the highest variability in blue oak (var = 6.25, range = 7.9) and grey pine (var = 5.76,
486 range = 7.8) with much lower variability in valley oak (var = 1.0, range = 3.4) and California
487 juniper (var = 1.9, range 2.7). All trees with LMWL departure values less than -5 had 90-100%
488 canopy bareness; that is, if trees sourced water that deviated by more than 5 units (essentially a
489 5‰ departure) from local precipitation inputs, this reflected a significant impact of evaporation,
490 and thus the trees' dependence upon shallow water, which was in very low abundance. This
491 caused tree crowns to lose essentially all of their leaves. Mortality was only observed in blue oak
492 and grey pine at the Private Ranch site. Of the *survey subset* individuals, 11% of blue oaks and
493 38% of grey pines died (SI Table S8).



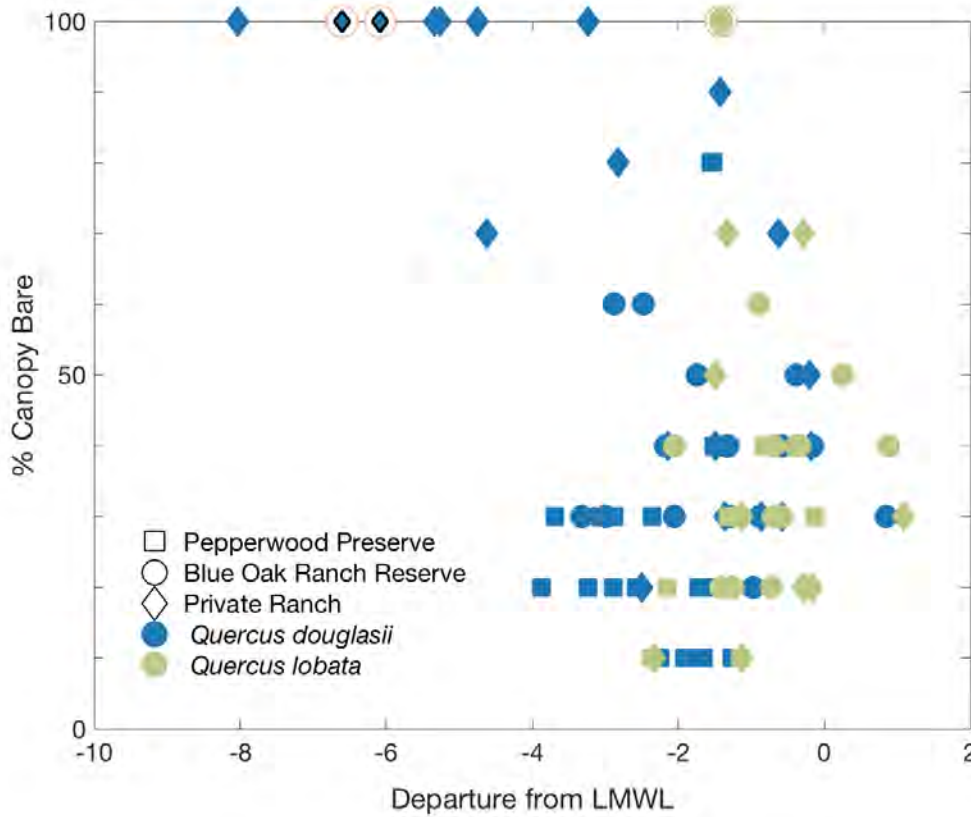
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495

496 **Figure 4:** Tree canopy condition (% bare, high values indicate poor canopy condition) and stemwater departure from
 497 LMWL at the Private Ranch site in September 2015 for all study species, plotted separately as indicated. Black
 498 outlines around symbols indicate that the individual was unable to be measured due to mortality or completely bare
 499 canopy, in which case the departure value from September 2014 was used. Red circles indicate confirmation of
 500 mortality in 2016. More negative departure values indicate the use of shallower water sources and less negative values
 501 indicate use of deeper water sources. The relationship between LMWL departure and canopy condition was significant
 502 for all species together and for *Q. douglasii* and *P. sabiniana* individually, lines represent regression lines for
 503 corresponding colored points.

504

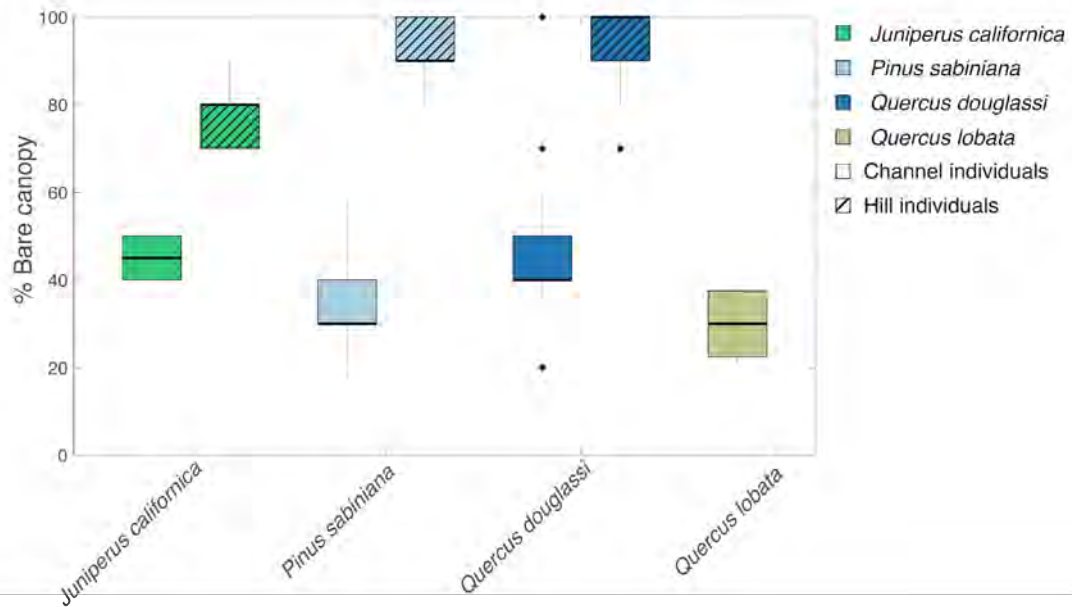
505 In the *survey subset*, across all three field sites, blue oak canopy condition was related to
 506 stemwater LMWL departure and site (a proxy for climate) with the poorest canopy condition
 507 observed at the most xeric site, Private Ranch (Figure 5, SI Table S9). Valley oak canopy
 508 condition was not predicted by LMWL departure or by site, and all valley oak stemwater LMWL
 509 departures were above -2.5 ‰, with little variability. Variability in valley oak stemwater LMWL
 510 departure over all sites was significantly less than that of blue oaks ($p < 0.0001$) (blue oak mean =
 511 -2.3, var = 3.2; valley oak mean = -0.9, var = 0.6).



513 **Figure 5:** Tree canopy condition (% canopy bare, high values indicate poor canopy condition) and stemwater departure
 514 from LMWL for *Q. douglasii* and *Q. lobata* across all 3 study sites in September 2015, with site and species plotted as
 515 indicated. Black outlines around symbols indicate that the individual was unable to be measured due to mortality or
 516 completely bare canopy, in which case the departure value from September 2014 was used. Red circles indicate
 517 confirmation of mortality in 2016. More negative departure values indicate the use of shallower water sources and less
 518 negative values indicate use of deeper water sources. Raw data shown. LMWL departure was a significant predictor
 519 of canopy condition for *Q. douglasii* (SI Table S9).
 520

521 **3.3. Field scale: full surveys**

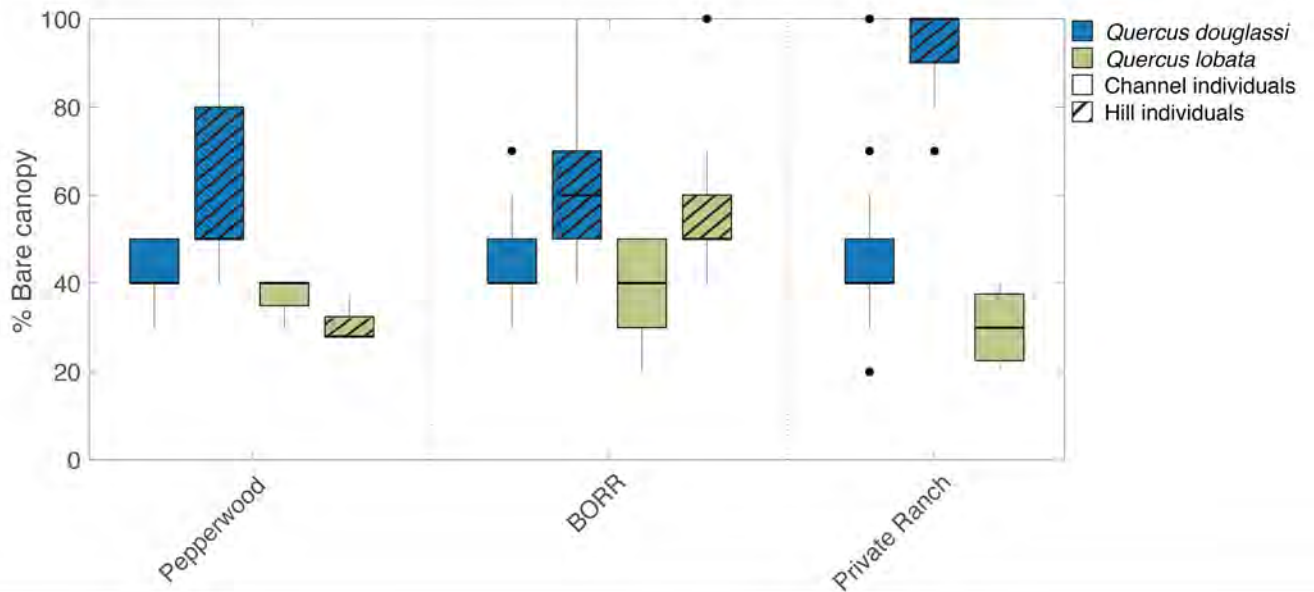
522 At the Private Ranch the full surveys found no significant differences in canopy condition across
 523 species in channel locations, but did find differences across species in hillslope locations ($F_{2,23} =$
 524 31, $p < 0.001$) with California juniper faring better than blue oak or grey pine, and blue oak and
 525 grey pine similar to each other (Figure 6). Within each species, the individuals in the channels
 526 had significantly better canopy condition than those on hillslopes (Figure 6, SI Table S10, S11).



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Figure 6: Canopy condition from *full survey* data at Private Ranch site (% bare canopy, high values indicate poor canopy condition) by species plotted as indicated, showing channel (solid colors) and hillslope (hash marks) landscape position. Figure shows boxplots of data for all individual trees at all subsites combined, dots represent outlier points.

533 At all three sites, the full survey found significant differences in blue oak canopy condition
534 between channel and hillslope locations. There was a significant difference in valley oak canopy
535 condition between channel and hillslope locations at BORR, but not at Pepperwood (Figure 7,
536 Table S12). Across all three sites, we did not detect significant differences among any of the
537 oaks growing in the channels, but did detect differences among the oaks growing on hills ($F(4,$
538 $14.9) = 365.3, p < 0.001$), with hillslope blue oaks at the Private Ranch site in poorer condition
539 than at BORR and Pepperwood (which were similar to each other) (Figure 7, Table S13). We
540 also found that canopy condition was overall poorer ($F(1, 83.9) = 53.1, p < 0.001$, mean: blue
541 oak=60%, valley oak=44%) and more variable ($p < 0.001$, var: blue oak=529, valley oak=196) in
542 blue oaks than in valley oaks.



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Figure 7: Canopy condition (% bare canopy, high values indicate poor canopy condition) for *Q. douglasii* (blue) and *Q. lobata* (green) across all study sites, showing channel (solid colors) and hill (hash marks) landscape positions. Figure shows boxplots of data for all individual trees at all subsites combined, dots represent outlier points.

547 4. Discussion

548 4.1 Regional mortality patterns

549

550 Statewide aerial surveys indicated that dieback during the drought was most substantial for grey

551 pine and blue oak, with little valley oak dieback and no drought-related dieback in California

552 juniper (Figure 1 and 2). The absence of dieback in California juniper is likely attributable to its

553 relatively dry climatic distribution and its high resistance to water stress (e.g., within its generally

554 drought-tolerant genus, it is the species with the greatest resistance to xylem cavitation (Willson

555 *et al.*, 2008)). The three other study species, however, have similar geographic and climatic

556 distributions (Figure 1), suggesting that in interpreting the differences in observed species-level

557 drought responses, consideration should be given to the role that local subsurface conditions and

558 hydrologic niche play in decoupling the effects of climatic drought from what plants may

559 experience in terms of water availability.

560

561 For blue oak, in addition to an expected relationship between dieback and climate (Brown *et al.*,
562 2018, Kueppers *et al.*, 2005) we also saw an effect of precipitation anomaly on drought
563 vulnerability and an interaction between drought year precipitation and precipitation anomaly on
564 drought vulnerability, with the negative effect of anomaly on dieback probability more
565 pronounced as absolute drought year precipitation values increased (i.e. anomaly increased
566 dieback more in wetter sites). That blue oaks in different areas responded differently to the same
567 absolute drought year precipitation, depending on the extent to which drought year values
568 departed from average, suggests that blue oaks are locally adapted and/or acclimated to climatic
569 conditions of their growing sites. However, the stronger impact of absolute climate variables
570 over climate anomalies on dieback suggests that there is likely a dry-edge vulnerability threshold
571 for this species. While higher anomalies occurred in wetter sites, higher dieback occurred at the
572 driest sites indicating that while local adaptation to climate may be important, there also likely
573 exists an absolute dry climate threshold response. At xeric edge sites approaching this threshold,
574 local drivers of water availability (as explored in the field scale patterns below) may become
575 more important to tree survival during drought.

576

577 In addition to the effects of climate, we saw greater dieback on sites with higher GRACE
578 groundwater anomalies (Brown *et al.*, 2018), and less dieback occurring on sedimentary rather
579 than granitic lithologies. The effect of lithology on blue oak dieback was particularly striking in
580 areas that experienced substantial loss of subsurface water – in these places, the probability of
581 dieback on granitic rock types was more than double that seen on sedimentary lithologies (Figure
582 3B). Sensitivity of plant outcomes to subsurface characteristics is in line with ecohydrological
583 expectations, which emphasize the importance of subsurface water storage capacity in
584 constraining plant water use (Porporato *et al.*, 2004, Porporato *et al.*, 2001). It also parallels the
585 previous findings of Fensham and Holman (1999), who similarly found that drought mortality
586 was highest on igneous rock types. Although identifying mechanisms for the geological

587 moderation of drought impacts on blue oak at regional scales is impossible, both storage capacity
588 (Hahm *et al.*, 2019a) and specific yield (i.e. water yield per change in water table depth) would be
589 expected to be higher, in general, on sedimentary substrates (Dawson *et al.*, 2020), consistent
590 with these findings. The two species that showed very little dieback, valley oak and California
591 juniper, had less overlap with igneous rock types in their statewide distribution (38% and 39%
592 respectively) compared to the trees that experienced dieback (blue oak: 49%, grey pine: 51%) (SI
593 Fig. S2), potentially contributing to their lower drought vulnerability.

594
595
596

597 **4.2 Canopy condition patterns at the field scale**

598
599 Land owners with century-long family connections to the Private Ranch site reported that the
600 extent of the local tree die-off in 2015 was unprecedented. Located near the xeric edge of the
601 blue oak, valley oak and grey pine distributions, Private Ranch was the only one of our study sites
602 where we observed substantial drought mortality (in blue oak and grey pine). Differences in
603 canopy condition between species were overlaid on a persistent contrast between canopy
604 condition in hillslope versus channel areas for all species, with relatively good canopy condition
605 and no mortality in alluvial channels, and poorer, more variable canopy condition as well as
606 mortality on adjacent hillslopes (Figure 6). A consequence of our targeted sampling design was
607 that we were limited in our ability to pick up other potential site-scale drivers of drought
608 resilience unrelated to the topographic/hydrologic gradients on which we focused.

609

610 Stemwater LMWL departure was a strong predictor of canopy condition when considering all
611 species together, and for blue oak and grey pine individually, with canopy condition declining
612 with increasing LMWL departure, and mortality generally occurring amongst those individuals
613 with the most negative LMWL departures (Figure 4), corresponding to the use of evaporatively-
614 enriched water sources (Dawson & Simonin, 2011). Such shallow soil water sources are more

615 tied to recent fluctuations in rainfall relative to more stable, deeper subsurface water sources.
616 Thus these deeper pools could sustain plant function and improve performance during periods of
617 climatic drought, creating hydrologic refugia (McLaughlin *et al.*, 2017).

618

619 Private Ranch is located within the Paso Robles subbasin of the Salinas Valley Aquifer. Along
620 the minor stream valleys in this aquifer, alluvial sediments up to 30 m thick form a highly
621 permeable, unconfined aquifer (California Department of Water, 1999, California Department of
622 Water, 2004, Fugro West, 2001). Soils mapping for Private Ranch indicates that the channel
623 areas are located on such alluvial sediments, suggesting that vegetation growing in these areas
624 could have access to large and persistent supplies of subsurface water (National Resource
625 Conservation Service, 2009). Conversely, the hillslope areas comprise rocky and shallow soils,
626 indicating that hillslopes and channels represent distinct subsurface environments at Private
627 Ranch. Channels provide plants access to persistent water resources in the unconfined aquifer,
628 while hillslopes offer limited water storage, such that during the drought vegetation growing on
629 hillslopes was dependent on (minimal) winter rainfall stored in shallow soils.

630

631 The differences in the variability in stemwater LMWL departure values and canopy condition for
632 each species at Private Ranch can be considered in terms of where species grew across the
633 landscape, as a tree's LMWL departure was correlated with its vertical distance from the channel
634 (SI Fig S4). At Private Ranch, valley oak was found in relatively close proximity to the channels,
635 and showed consistently less negative LMWL departure values. Blue oaks and grey pines grew
636 over more of the landscape, occupying both channel and hillslope areas (Figure 4). The high
637 variability in LMWL departure values and canopy condition for blue oaks and grey pines likely
638 reflects the high variation in groundwater availability across their local topographic and
639 lithological range. Individuals that died were located far from the channel and exhibited very
640 negative LMWL departures. It is unclear whether during non-drought conditions grey pine and

641 blue oak growth on the hillslopes is sustained purely by seasonal rainfall or by water in the deep
642 subsurface that was then depleted during the drought period (Hahm *et al.*, 2018, Howitt *et al.*,
643 2014, Oshun *et al.*, 2016). If trees were generally dependent on deep subsurface waters, the high
644 porosity and specific yield of the alluvium near the channel (Fugro West, 2001) would reduce the
645 decline in the water table depth (per unit of water used by plants), helping trees to sustain access
646 to groundwater resources in this area. These observations at the edge of the three endemic study
647 species' ranges suggest that the channel hydrologic environments could become important
648 climate change refugia (McLaughlin *et al.*, 2017), particularly at xeric range edges, given
649 projected regional warming and drying (Flint & Flint, 2012).

650

651

652 Although substantial mortality was only observed at Private Ranch, the direction of relationship
653 between landscape position and canopy condition for blue oak was found at all sites in the full
654 surveys. Because we only had stemwater isotope data from the survey subset, we were not able
655 to directly relate these differences in canopy condition between channel and hill areas to LMWL
656 departures. All individuals at the two more mesic sites maintained relatively low LMWL
657 departure values (indicating high access to groundwater) compared to the Private Ranch site, as
658 well as better canopy condition, with no individuals at the two more mesic sites dropping below
659 the -5 LMWL departure threshold where we began to see more extreme canopy loss. This may
660 have been due to site-specific hydrology or to the lower pressure on groundwater (e.g. higher
661 recharge rates, lower anthropogenic withdrawal) given the lower climatic drought extent at the
662 two more mesic sites.

663

664 Canopy conditions were strikingly similar in channel environments across species and across the
665 study sites (Figure 6 and 7). For example, the canopy condition of channel blue oaks at Private
666 Ranch, which experienced only 174 mm of rainfall in 2014 (less than many desert environments)

667 was very similar that of channel blue oaks at Pepperwood, which experienced over 3 times as
668 much rainfall (590 mm), and to those at BORR which experienced mid-level rainfall. Canopy
669 conditions in channel valley oaks were even better at Private Ranch than at Pepperwood.
670 Consistent with Hahm et al.'s (2019a) observation that annual growth of vegetation in
671 Mediterranean systems was controlled by subsurface hydrology rather than precipitation, and
672 Fan's (2015) review of strong groundwater influences on plant growth relative to precipitation in
673 seasonally dry, arid and semi-arid ecosystems, our findings indicate that landscape position
674 and/or associated sub-surface processes that confer higher groundwater access may regulate the
675 trees' environments during severe drought, decoupling the drought stress they experienced from
676 climate.

677

678 **4.3 Synthesis and interpretation – a role for the hydrologic niche**

679

680 Although blue and valley oak and grey pine share similar broad climatic distributions, their
681 distributions at the landscape-scale and degree of dependence on subsurface water resources vary
682 – variations we interpret as arising from hydrologic niche segregation amongst the species, with
683 valley oaks demonstrating a narrower, more specialized, and blue oak and grey pine
684 demonstrating a broader, more general hydrologic niches. This niche partitioning broadly follows
685 the framework laid out in Fan (2017) in which plant species shift water uptake strategies along a
686 topographic drainage gradient. Valley oaks are associated with valley floors, alluvial terraces and
687 levees and occasional ridgetops, possibly where they access perched water tables (Griffin, 1977,
688 Jepson, 1910). They exhibit consistent water potentials despite seasonal or extreme drought
689 conditions (Weitz, 2018, Griffin, 1973), presumably due to persistent access to deep water
690 sources. Valley oak LMWL departure values measured in this study were consistent and small,
691 also indicating access to deep water sources, even on hilltops. Greenhouse experiments show
692 that valley oak root morphology is independent of moisture availability during development, and
693 always exhibits a primary deep tap root (Callaway, 1990). *In situ* observations indicate that

694 valley oaks support deep root systems that can exceed 23 m in depth (Lewis & Burgy, 1964,
695 Lewis & Burgy, 1966); shallow-rooted individuals are not reported.
696
697 In contrast, blue oaks grow across a range of topographic and hydrologic conditions, from valley
698 bottoms to upper slopes (Griffin, 1977). Blue oaks may tap the water table (Miller *et al.*, 2010),
699 but they also grow on shallow soils and exposed hillsides without likely persistent access to deep
700 subsurface water (Griffin, 1973, Jepson, 1910). Water potentials in blue oaks vary amongst
701 individuals on seasonal scales (Callaway & D'Antonio, 1991, Feng *et al.*, 2019, Griffin, 1973)
702 and under multi-year drought conditions (Weitz, 2018). Experimental studies indicate that
703 whether blue oak seedlings invest in shallow or deep root growth depends on moisture
704 availability (Callaway, 1990). In situ observations show highly variable rooting depths (e.g., 1.5
705 to >23 m; Lewis & Burgy, 1964, Lewis & Burgy, 1966, Millikin & Bledsoe, 1999). Stemwater
706 LMWL departure values measured in blue oaks in this study were also highly variable,
707 suggesting that individuals relied on a range of water storage profiles. The importance of climate
708 anomaly and an interaction between climate anomaly and absolute climate for blue oak dieback,
709 as observed in this study, may be associated with genetic adaptations or plasticity, and thus
710 hydrologic niche parameters that vary by population. It could alternatively be a manifestation of
711 varying hydrologic niche segregation along a climate gradient, such that in drier areas, blue oak
712 populations may rely more on deep water reserves, and consequently be less exposed to climatic
713 drought (although we did not see this pattern in our field data).
714
715 Grey pine is under-studied relative to blue and valley oak (Graves, 1932). It grows on dry
716 hillsides and granite outcrops but also banks of streams and floodplains. Like blue oak it is
717 reported to have a dimorphic rooting habit, producing either a deeper tap root or a shallower root
718 system depending on site conditions (Powers, 1990). At Private Ranch, it was the most drought-
719 vulnerable species with over 50% mortality and its outcomes were strongly impacted by

720 landscape position and access to subsurface water. Regional drivers of grey pine dieback were
721 unclear, which may be related to its likely relatively shallow rooting system (Canadell *et al.*,
722 1996) compared to oaks. Changes in subsurface storage could have occurred at depths
723 inaccessible to grey pine roots, and lithological differences may have been less important in
724 driving mortality than biotic factors such as pine bark beetles (Howard, 1992).

725

726 Taken together, these observations suggest a relatively broad hydrologic niche for blue oak and
727 grey pine, in contrast to a narrower niche exhibited by valley oak. Blue oak is plastic in its
728 utilization of water resources, growing under conditions that range from seasonal dependence on
729 shallow soil water to persistent access to deeper water sources. Valley oak, by contrast, depends
730 on its deep-rooted morphology and grows only where it can access deep water resources, which
731 are presumably important for both sapling recruitment and adult survival (McLaughlin &
732 Zavaleta, 2012, Brown & Davis, 1991). The distinction between the narrow and broad
733 hydrologic niches of valley oak versus blue oak and grey pine helps to explain their variable
734 responses to the 2013-16 drought. Narrow niche segregation by valley oaks into locations with
735 persistent subsurface water resources reduced valley oak drought vulnerability relative to blue
736 oak and grey pine individuals, despite their common climatic drought and resulted in lower and
737 less variable drought vulnerability amongst valley oaks than blue oaks and grey pines at species
738 levels. Thus the differences in hydrologic niche explain both the site-scale and distributional-
739 scale patterns of drought vulnerability we observed in these three species.

740

741 These results demonstrate the importance of hydrologic niche differences when considering
742 species' responses to climate change and to climatic extremes. Although some authors suggest
743 that habitat generalists may be buffered against climate-induced range contractions (Watling *et*
744 *al.*, 2013) our findings suggest that species with broader, or more generalist, hydrologic niches
745 (i.e. blue oak) initially may be more vulnerable to climatic drought than those with a narrower

746 niche, because of their ability to grow in locations with less climatically stable subsurface water
747 sources. This poses an interesting comparison between hydrologic niche and water use
748 strategies: prolific water users have a competitive advantage relative to plants with more
749 conservative water use strategies when water is available at the expense of greater exposure to
750 water stress during droughts (Feng *et al.*, 2017). Similarly, species with a more general, or
751 broader, hydrologic niche can grow in a wider variety of locations than more specialized species,
752 at the risk of experiencing greater water stress during drought.

753

754 In general, changes in local scale distributions may provide an early indicator of range
755 contractions induced by climate drying, as in McLaughlin and Zavaleta's (2012) analysis of
756 *Quercus lobata* sapling recruitment patterns, and Anderegg *et al.*'s (2013) analyses of aspen
757 mortality in the US Southwest. Hydrologic refugia (McLaughlin *et al.*, 2017) may maintain
758 small, and possibly temporary, local populations even in the xeric edges of the current
759 distribution. Prolonged drought, however, will impact both species with narrow hydrologic
760 niches, and broad-niched species with populations remaining in such refugia. For example,
761 following 40-year rainfall declines in Australia, tree species (*Eucalyptus* and *Banksia* sp.) relying
762 on deep water have experienced unprecedented mortality in recent years as water tables (finally)
763 drop below their rooting depth (Challis *et al.*, 2016, Matusick *et al.*, 2018). Similarly, relative
764 differences in vulnerability between blue and valley oak may become less pronounced under
765 conditions of prolonged drought and high groundwater extraction.

766

767 Our study found large differences in climatic drought vulnerability within and across four study
768 species at distributional and site scales. Within species, vulnerability in blue oak and grey pine
769 was strongly related to absolute precipitation and modulated by subsurface characteristics –
770 including changes in subsurface water storage, lithology and local landscape position. These
771 subsurface drivers were superimposed on climatic drought and together determined plant access

772 to subsurface moisture reserves, explaining variations in vulnerability at the regional scale for
773 blue oak and at the site scale for blue oak and grey pine. We interpreted these variations using
774 the hydrologic niche concept, which explains how different species with similar climatic
775 distributions may be exposed to different water deficits due to different subsurface conditions.
776 With the exception of juniper, species-level vulnerability was not due to differences in climatic
777 distributional associations among the three endemic species. We suggest that hydrologic niche
778 segregation can drive differences in species-level drought vulnerability where species co-occur
779 within a community and across the region, and that this vulnerability may shift over time as
780 climate and hydrologic resources change. Using these insights for prediction, however, will
781 require a better understanding of how plant available water storage capacity in the subsurface
782 zone varies across landscapes. Currently available mapping products describe either parent
783 geology, which is only coarsely related to water storage capacity, or describe subsurface
784 hydraulic properties within 2 m of the surface - missing much of the root zone.

785

786 Warmer future climates will intensify the summer dry season and the intensity of future droughts
787 in California and other water-limited regions (Flint & Flint, 2012, Gosling & Arnell, 2016),
788 however environmental gradients of water availability are not fully captured by climate (Fan
789 2015). Our findings suggest that in Mediterranean woodlands, current patterns of climatic
790 drought vulnerability, mediated through sub-surface processes, may lead to long-term changes in
791 plant communities. Understanding likelihood of such changes requires better resolving how
792 hydrologic processes and the structure of the subsurface environment mediate plant water deficits
793 and drought vulnerability (Dawson *et al.*, 2020). Projecting species distributional shifts or
794 attempting to understand drought vulnerability purely based on climatic drought severity or
795 species-level traits risks omitting important variability in outcomes arising from differences in
796 water deficit amongst species with varying hydrologic niches and from the underlying hydrologic
797 and lithological conditions across species' ranges.

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814 Data Accessibility Statement:
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816 The data that support the findings of this study are available from the corresponding
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825 6. References

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