

Age and stand structure of oak woodlands along a gradient of conifer encroachment in northwestern California

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Citation: Schriver, M., R. L. Sherriff, J. M. Varner, L. Quinn-Davidson, and Y. Valachovic. 2018. Age and stand structure of oak woodlands along a gradient of conifer encroachment in northwestern California. *Ecosphere* 9(10):e02446. 10.1002/ecs2.2446

Abstract. Many fire-maintained savannas and woodlands are suffering the effects of fire exclusion and the concomitant invasion of fire-sensitive trees. In the Pacific West, woodlands dominated by either Oregon white oak (*Quercus garryana*) or California black oak (*Quercus kelloggii*) have transitioned from oak-dominated to conifer-dominated (primarily by the native Douglas-fir; *Pseudotsuga menziesii*) forest conditions with corresponding losses of plant and animal biodiversity. In spite of the prevalence of this transition, few studies have documented these temporal shifts and the consequences for oak woodland ecosystems. To better understand this process, we assessed tree species composition and age structure across 10 sites in northwestern California, USA. Species composition varied, but Douglas-fir, Oregon white oak, and California black oak had the greatest proportional dominance within and across sites. Across all ten sites, we cored 1747 trees from 10 different species. The majority (>80%) of oak stems dated between 1850 and 1910 (69% plots dated within a 40-yr period from 1860 to 1900). Less than 1% of the oak stems originated after 1960. Across the gradient of encroachment (i.e., oak to conifer dominance) at each site, the most common encroaching species was Douglas-fir, which primarily established after 1970 (73% across all sites). Douglas-fir structural attributes were not associated with any of the abiotic factors evaluated, although non-significant trends show greater densities of Douglas-fir in oak stands at the northern end of the study region. Oak seedlings were common in all 10 study sites; however, we documented very few oak saplings regardless of the biophysical conditions. This study highlights that (1) the process and severity of encroachment is consistent across the region, resulting in substantial oak habitat loss and a shift toward conifer dominance and vegetative homogeneity in formerly diverse woodlands of northwestern California; and (2) Oregon white oak and California black oak woodlands require concerted management effort to ensure their survival and future persistence.

Key words: California black oak; conifer encroachment; dendroecology; Douglas-fir; fire exclusion; Oregon white oak; *Pseudotsuga menziesii*; *Quercus garryana*; *Quercus kelloggii*.

Received 7 June 2018; revised 7 August 2018; accepted 21 August 2018. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

In many savannas and woodlands worldwide, fire exclusion and land-use history have led to

the establishment of forests (Scholes and Archer 1997, Staver et al. 2011). In North American oak (*Quercus* spp.) woodlands and savannas, the cover and dominance of non-oak trees have

increased dramatically over the last century (Copenheaver et al. 2004, Moore and Huffman 2004, Gedalof et al. 2006, Stam et al. 2008, Gilligan and Muir 2011). While tree encroachment is a successional process in the absence of natural disturbances, the resulting shifts in woodland ecosystem structure and composition are likely outside of the historical range of variability in many locations (Landres et al. 1999, Weins et al. 2012). Fire plays a critical role in moderating the dynamic interplay between trees and herbaceous plants in oak woodlands (Higgins et al. 2000, Engber et al. 2011). When fires are excluded from these ecosystems, changes can be drastic, with woody vegetation invading openings, outcompeting grasses and forbs, and leading to densely wooded and less diverse landscapes (Livingston et al. 2016). Shifts in savanna and woodland ecosystem structure and composition vary greatly in relation to the biophysical environment, land-use history and Euro-American settlement patterns (Thilenius 1968), grazing regimes (Scholes and Archer 1997), and changes in climate (e.g., Bond and Midgley 2000, D'Odorico et al. 2010).

In the Pacific West, oak woodlands dominated by *Quercus garryana* Dougl. ex. Hook and *Quercus kelloggii* Newberry are classic examples of woodlands that visually appear to have widespread conifer encroachment. Individual studies suggest transitioning from oak- to conifer-dominated forest (>50% canopy cover) conditions at some locations (Sugihara and Reed 1987, Engber et al. 2011, Cocking et al. 2012). In northwestern California, where there is a mosaic of rapid transitions between soil types, these two oak species commonly occur near or adjacent to both conifer-dominated stands and grasslands. Both oak species can persist in monodominant and mixed oak woodlands and can also intermingle with other hardwoods and conifers (Sawyer 2007). In northwestern California, the most common encroaching conifer species is coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco).

Consequences of Douglas-fir encroachment in deciduous oak woodlands include oak mortality (Devine and Harrington 2013), the loss of plant and animal biodiversity associated with oak habitats (Thysell and Carey 2001, Livingston et al. 2016), alteration of forest composition and structure, increases in fire-sensitive species, and

reduction in herbaceous fuels (Stam et al. 2008, Engber et al. 2011). Nevertheless, few studies in the Pacific West have documented the temporal shifts in conifer-encroached oak woodland ecosystems (e.g., composition, structure, and establishment dates), or the consequences for native oak trees (i.e., regeneration and mortality), and existing studies have generally been limited in geographic distribution. The goals of this research were to (1) investigate the spatial and temporal patterns of tree encroachment across a large area where Oregon white oak and California black oak co-occur (spanning 2° of latitude); (2) evaluate the regional variability of tree establishment patterns and the biophysical factors that influence stand structure in conifer-encroached oak woodlands; and (3) provide data to inform the increasing policy and management momentum around these issues, both in northwestern California and throughout the ranges of the two oak species (Standiford and Purcell 2015, Valachovic et al. 2015).

Across a northwest-to-southeast (mesic to xeric) transect of northwestern California spanning over 2° of latitude, we studied Oregon white oak and California black oak woodlands in three phases of Douglas-fir encroachment in order to characterize stand structure, composition, and species-level differences in the timing of tree establishment. We asked the following questions: (1) How do stand structure, species composition, and the timing of tree establishment vary within and across a gradient of encroachment? and (2) Do stand structure characteristics vary in relation to biophysical characteristics? We hypothesized that the majority of oak stems established during or following Euro-American settlement (mid-19th century-on) and that the majority of oak trees predate Douglas-fir trees in stands where they co-occur (similar to oak stands in the Pacific Northwest region of the United States; e.g., Devine and Harrington 2006, Gilligan and Muir 2011). We also expected that oak regeneration declined over the last half-century due to changes in disturbance regimes (e.g., fire, grazing, browsing) and associated changes in stand structure and composition. Across the study region, we expected greater densities of Douglas-fir in cooler/more mesic environments, and more dead oak trees (indicators of past encroachment) in stands that have transitioned to Douglas-fir

dominance (cf. Devine and Harrington 2013). We also expected fewer oak seedlings in stands now dominated by Douglas-fir, and greater densities of both oak and conifer seedlings in mesic environments (Devine et al. 2007, Gilligan and Muir 2011). This research has direct implications for oak woodland management and restoration in northwestern California (Valachovic et al. 2015), but also across broad regions in the Pacific West and in other areas where woody encroachment has altered the composition and structure of savannas and woodlands.

METHODS

Study area

The study area was located in the Northern Coast Ranges of California spanning 2° of latitude (41.2°–39.0°) and 0.6° of longitude (123.9°–123.3°; Fig. 1) with a Mediterranean climate with cool, wet winters and warm, dry summers. Average annual precipitation ranges from 1430 to 2780 mm, with dry conditions increasing along a west-to-east gradient (PRISM Climate Group, Oregon State University; <http://prism.oregonstate.edu>). Inland portions of the study area experience cooler winters than the coastal regions. The summer climate varies greatly, with high temperatures ranging from 27° to 37°C depending on the elevation and distance from the moderating effects of the Pacific Ocean.

California's Northern Coast Ranges host a mosaic of forest types, including deciduous oak woodlands and savannas as well as mixed evergreen/conifer forests most commonly dominated by Douglas-fir (Barbour et al. 2007). We focused on mixed Oregon white oak and California black oak woodlands that are currently experiencing a spectrum of Douglas-fir encroachment severities. Other dominant and/or co-dominant tree species in our study sites include white fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.), California buckeye (*Aesculus californica* (Spach) Nutt.), Pacific madrone (*Arbutus menziesii* Pursh), California incense-cedar (*Calocedrus decurrens* (Torr.) Florin), tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh), canyon live oak (*Quercus chrysolepis* Liebm.), California live oak (*Quercus agrifolia* Née), and California laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.).

Site selection and field sampling

Ten sites were selected on both private (8) and public (2) lands across northwestern California (Fig. 1) with relatively similar compositional characteristics (close proximity of oak-, conifer-, and prairie-dominant ecosystems; Fig. 2). Sites ranged in elevation from 375 to 1180 m and all occupied rolling and dissected terrain. Six sites (23 of 90 total plots) had evidence of scattered Douglas-fir harvest (stumps) from approximately 50 yr ago (no oak stumps; Table 1). Harvesting did not include all of the largest Douglas-fir trees, and the variability between sites confirmed that oak levels were consistent across sites with and without fir harvest history (Table 1). Half of the sites were actively grazed by domestic cattle, and most stands had some prior grazing over the last century.

At each of the 10 sites, we used stratified random sampling to locate nine 0.1-ha circular plots across oak stands in three broad encroachment categories: oak-dominant stands where conifers were not present or limited to the sub-canopy (three plots); oak-dominant stands with Douglas-fir in an intermediate or co-dominant canopy position (three plots); and oak stands where Douglas-fir occupied the dominant canopy position or was emergent in the canopy throughout the stand (three plots; Fig. 3; see Schriver 2015 for further classification details). At each plot, we collected environmental data (slope, aspect, slope position, landform type, and elevation) and plot coordinates and recorded obvious disturbances (e.g., windthrow, fire, grazing, harvesting). For all trees ≥ 5 cm diameter at breast height (1.37 m, dbh), we recorded species, dbh, oak stem form (single- or multi-stemmed), status (live/dead), total tree height, and height to live crown (hereafter crown height). Within each plot, we recorded species and diameters of all stumps if present. We visually estimated canopy position for each tree and classified each into open-grown, dominant, co-dominant, intermediate, overtopped, and understory canopy classes using a similar classification scheme to previous mixed oak–conifer stand structure studies (Hunter and Barbour 2001, Cocking et al. 2012). We considered trees to be in the overstory if they occupied open-grown, dominant, co-dominant, or intermediate canopy positions. The 10 closest Oregon white oak and California black oak trees

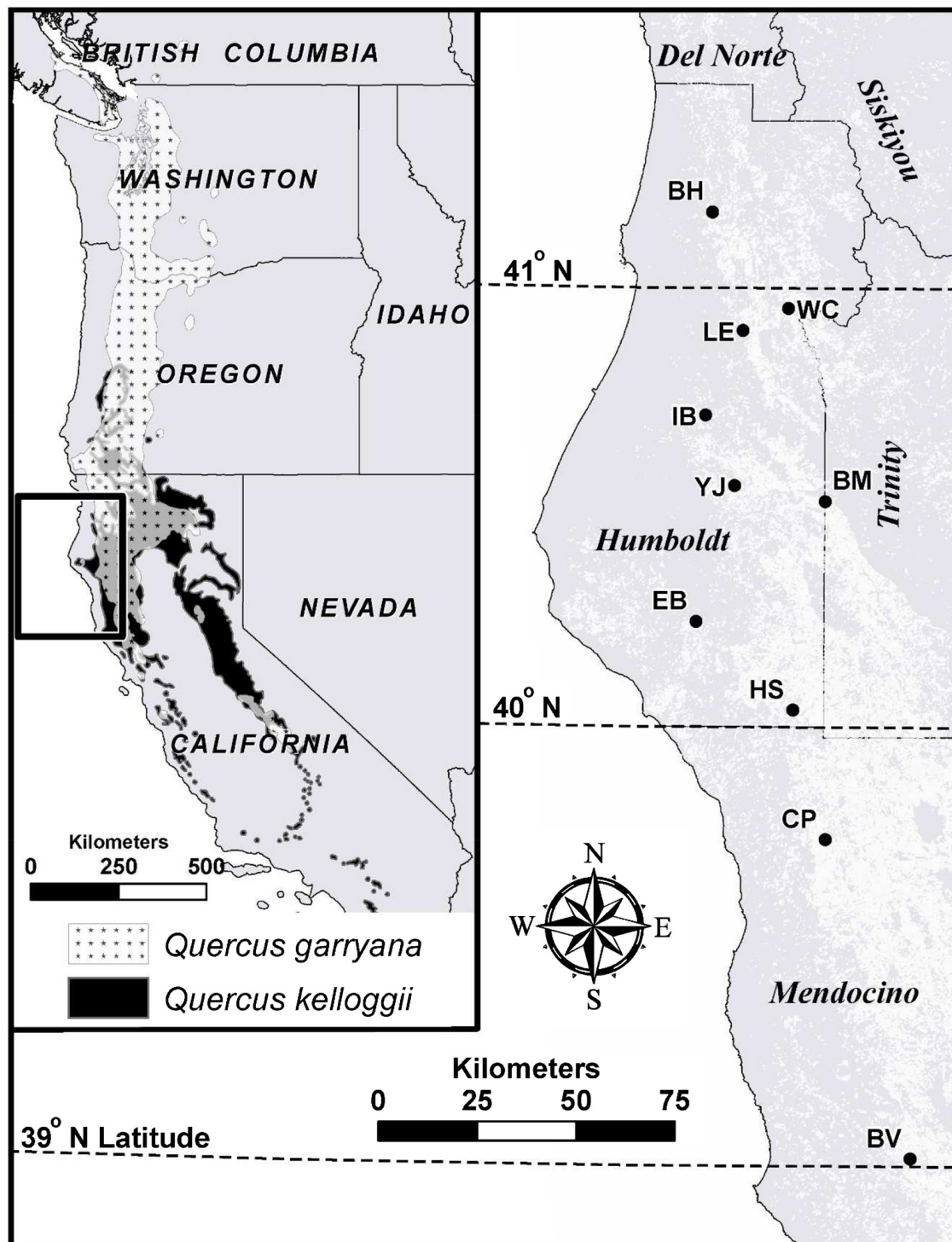


Fig. 1. Study area located in the North Coast region of California with depiction of the range distributions of Oregon white oak (*Quercus garryana*) and California black oak (*Quercus kelloggii*; map credit: B. Twieg; oak distribution from Little 1971). Ten study locations are indicated by site codes that correspond to the 7.5-min USGS quad the sites are located in.



Fig. 2. Representative landscape exhibiting close proximity of oak, conifer, and savanna ecosystems occupying the rolling and dissected terrain of northwestern California. Photo credit: Y. Valachovic.

to plot center were mapped and cored as close to the ground as possible (~ 30 cm height above the ground) in order to estimate dates of stem establishment (Stokes and Smiley 1996). Multi-stemmed oaks were tallied, and when cored, the largest stem was selected to determine individual stem age. Due to our inability to discern the exact origin of oak stems (acorn germination vs. sprouts from pre-existing individual), we defined oak stem establishment as a stem originating from either a seedling or sprout. Additionally, the 10 closest conifers or other hardwood trees to plot center were mapped and cored. Up to five of the largest living trees nearest the 0.1-ha plot were also cored in order to estimate the earliest dates of stem establishment within the sampling area. To characterize tree regeneration, we tallied seedlings (<30 cm tall) and saplings (<5 cm dbh

and >30 cm tall) by species on six randomly located 1×2 m nested quadrats and one randomly located 0.025-ha nested plot, respectively, within each 0.1-ha plot.

Data analysis

Relating stand structure to biophysical environment.—We evaluated whether stand structure varied in relation to the biophysical environment by using all plot-level data (90 plots) and conditional inference trees (Hothorn et al. 2006). Conditional inference trees are binary recursive data-partitioning algorithms that generate dichotomously branching regression trees, available as the function `ctree` in the add-on package `party` in R (R Core Development Team 2015). We selected conditional inference trees from the family of recursive partitioning methods due to the

Table 1. Stand structure attributes of Oregon white oak (*Quercus garryana*; QUGA), California black oak (*Quercus kelloggii*; QUKE), Douglas-fir (*Pseudotsuga menziesii*; PSME), and all species (Total) in 10 oak sites under a gradient of Douglas-fir encroachment conditions (xeric-to-mesic climate from left to right) and across sites (Regional) in northwestern California.

SPECIES	WC	BV	BM	CP	LE	HS	YJ	IB	EB	BH	Regional
QUGA											
SD (trees/ha)	371 (30–840)	164 (0–440)	429 (0–810)	191 (0–540)	236 (0–470)	183 (60–320)	234 (0–830)	302 (170–530)	106 (10–230)	504 (60–1310)	272 (0–1310)
BA (m ² /ha)	14.7 (3.3–23.7)	12.1 (0–26.3)	14.9 (0–29.2)	14.4 (0–35.0)	16.6 (0–33.1)	17.9 (6.3–33.8)	10.9 (0–31.9)	21.6 (13.7–29.7)	14.3 (0.3–43.5)	22.9 (3.5–37.7)	12.1 (0–43.5)
Multi-stem (%)	24 (0–54)	31 (0–74)	29 (0–46)	12 (0–41)	17 (0–45)	41 (0–77)	33 (0–83)	16 (0–38)	22 (0–50)	35 (4–74)	26 (0–83)
Height (m)	13.7 (1.5–43.2)	12.6 (2.5–26.5)	9.7 (2.1–29)	14.6 (3.4–23.5)	11.7 (1.7–29.5)	14.6 (1–25)	12.7 (1.5–21.6)	12.5 (2–25.5)	12.1 (3.9–25.1)	15.3 (0.6–29.9)	13 (0.6–43.2)
Dead stems (%)	12 (0–31)	14 (0–57)	39 (5–100)	5 (0–14)	29 (7–100)	9 (0–32)	29 (0–67)	11 (0–39)	9 (0–20)	36 (14–75)	19 (0–100)
Co-dom (yr)	72 (69–83)	32 (27–40)	58 (57–68)	52 (43–70)	32 (27–36)	44 (34–55)	30 (23–45)	37 (33–40)	49 (43–59)	44 (41–51)	44 (23–83)
Seedlings (ha ⁻¹)	1111 (0–3333)	370 (0–1667)	3518 (0–15000)	5185 (0–10833)	7685 (0–35833)	2315 (0–8333)	3704 (0–19167)	14167 (0–43333)	5278 (0–34167)	11667 (0–49167)	5500 (0–49167)
Saplings (ha ⁻¹)	0 (0–0)	0 (0–0)	4 (0–40)	0 (0–0)	9 (0–80)	0 (0–0)	0 (0–0)	4 (0–40)	0 (0–0)	18 (0–40)	4 (0–80)
No. plots present	9	8	8	8	8	9	8	9	9	9	85
QUKE											
SD (trees/ha)	133 (0–370)	92 (0–170)	84 (10–180)	43 (0–130)	139 (0–430)	36 (0–90)	98 (0–310)	50 (20–130)	20 (0–60)	43 (0–210)	74 (0–430)
BA (m ² /ha)	6.5 (0–17.2)	13.1 (0–37.2)	10.3 (0.3–19.3)	7.8 (0–16.3)	12.5 (0–33.4)	10.2 (0–30.8)	11.9 (0–30.5)	6.0 (2.1–22.6)	5.7 (0–21.6)	3.3 (0–18.7)	8.7 (0–37.2)
Multi-stem (%)	27 (0–67)	36 (0–82)	21 (0–58)	17 (0–100)	8 (0–43)	3 (0–30)	38 (0–100)	18 (0–80)	6 (0–57)	38 (0–100)	21 (0–100)
Height (m)	11.9 (3.4–25)	12.2 (2–28.3)	12.8 (4–31.7)	19.5 (5.7–33.6)	10.6 (2–23.8)	19.8 (5–40.8)	15 (3.4–26.1)	11.7 (3.5–21.3)	17.2 (5.9–29.5)	15.1 (3.8–27.3)	14.3 (2–40.8)
Dead stems (%)	11 (0–25)	16 (0–35)	14 (0–30)	15 (0–50)	13 (0–50)	1 (0–10)	17 (0–43)	4 (0–20)	7 (0–50)	20 (0–50)	12 (0–50)
Co-dom (yr)	71 (68–78)	36 (23–47)	65 (60–84)	60 (39–85)	29 (20–36)	58 (43–79)	36 (28–42)	35 (29–41)	58 (48–84)	47 (34–50)	47 (20–85)
Seedlings (ha ⁻¹)	926 (0–2500)	370 (0–1667)	2037 (0–7500)	3518 (0–7500)	2130 (0–10000)	2500 (833–4167)	463 (0–1667)	278 (0–1667)	2963 (0–9167)	1944 (0–15000)	1713 (0–15000)
Saplings (ha ⁻¹)	0 (0–0)	0 (0–0)	4 (0–40)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–40)
No. plots present	8	8	9	7	8	6	8	9	8	5	76
PSME											
SD (trees/ha)	400 (50–940)	211 (0–500)	294 (0–900)	254 (0–530)	557 (20–1010)	426 (10–2070)	540 (10–1360)	367 (40–650)	207 (0–450)	254 (0–590)	351 (0–2070)
BA (m/ha)	22.3 (0.5–54.1)	17.1 (0–43.2)	28.4 (0–79.0)	14.8 (0–38.5)	28.4 (0.2–75.5)	17.7 (0.2–50.6)	24.4 (0.1–58.1)	17.8 (0.2–36.3)	19.7 (0–56.8)	28.0 (0–66.4)	21.9 (0–79.0)
Height (m)	16.2 (2.4–55.9)	14.8 (4–47.5)	16.3 (2–48.8)	15.3 (4.3–35.3)	12.8 (1.2–47.1)	15.2 (3.8–38.3)	11.8 (3.6–46)	10.5 (2.5–31)	18.4 (4–45.7)	29.4 (3.2–47.5)	15.7 (1.2–55.9)

(Table 1. Continued.)

SPECIES	WC	BV	BM	CP	LE	HS	YJ	IB	EB	BH	Regional
Dead stems (%)	13 (0–47)	1 (0–4)	9 (0–32)	20 (0–100)	9 (0–27)	0 (0–0)	11 (0–24)	5 (0–14)	1 (0–2)	7 (0–16)	7 (0–100)
Seedlings (ha ⁻¹)	370 (0–1667)	1481 (0–5833)	1574 (0–13333)	648 (0–3333)	556 (0–4167)	1296 (0–3333)	1389 (0–8333)	741 (0–5000)	1019 (0–2500)	833 (0–4167)	991 (0–13333)
Saplings (ha ⁻¹)	129 (0–640)	538 (80–1200)	133 (0–960)	129 (0–360)	138 (0–840)	1396 (0–5200)	284 (0–1320)	298 (0–2080)	956 (0–3720)	80 (0–520)	408 (0–5200)
Stumps (ha ⁻¹)	na	40 (40–40)	na	90 (10–130)	33 (10–90)	23 (10–30)	10 (10–10)	na	20 (10–40)	na	41 (10–130)
No. plots present	9	8	6	7	9	9	9	9	7	7	80
Total											
SD (trees/ha)	1043 (670–1490)	548 (240–760)	836 (310–1270)	588 (520–810)	937 (460–1560)	672 (290–2260)	877 (600–1270)	752 (330–1080)	506 (80–950)	802 (520–1310)	756 (80–2260)
BA (m ² /ha)	48.4 (27.9–79.5)	50.6 (35.6–70.2)	53.9 (26.6–98.3)	39.7 (25.4–62.1)	57.5 (29.1–87.0)	46.8 (28.4–76.0)	47.9 (31.9–73.0)	46.8 (22.5–62.6)	47.2 (20.2–83.6)	54.2 (27.9–79.5)	49.5 (20.2–98.3)
Dead stems (%)	11 (5–17)	9 (1–15)	23 (6–33)	10 (1–15)	12 (0–30)	6 (0–19)	19 (8–28)	9 (0–23)	7 (3–13)	24 (11–35)	13 (0–35)
Seedlings (ha ⁻¹)	5278 (0–15000)	3241 (0–9167)	7963 (0–22500)	9352 (1667–12501)	11203 (833–40000)	7500 (1667–16666)	7315 (833–19167)	15463 (0–45000)	108333 (0–42500)	14537 (0–50834)	9268 (0–50834)
Saplings (ha ⁻¹)	591 (0–2080)	551 (80–1200)	916 (0–3880)	324 (0–1000)	293 (0–840)	1564 (0–5200)	316 (0–1480)	311 (0–2120)	1138 (0–3800)	133 (0–600)	614 (0–5200)
No. species present	6 (4–8)	5 (3–7)	3 (2–4)	4 (1–5)	3 (2–4)	3 (2–4)	3 (3–4)	3 (3–5)	5 (2–7)	2 (1–3)	14

Notes: Plot-level mean (ranges) of stem density (SD), basal area (BA), and crown height (Height), seedlings (<30 cm tall), and saplings (<5 cm dbh and >30 cm tall), and number of tree (≥5 cm dbh) species present across plots at each site are reported. Percentage of multi-stem oaks and dead stems was calculated using stem density. Median years until oak–conifer co-dominance at the plot level (range in parentheses) are reported for each site.



Fig. 3. Three representative oak stands currently experiencing a range of Douglas-fir encroachment in north-western California: (left) oak-dominant, (middle) oaks with mid-story conifers, and (right) oaks suppressed by a closed-canopy Douglas-fir. Photo credits: L. Quinn-Davidson (left and right) and Y. Valachovic (center).

algorithm's ability to analyze large, multivariate, non-parametric datasets as well as to create directly interpretable models. Conditional reference trees are based on a global null hypothesis of independence between any of the predictor

variables (abiotic and biotic factors) and a single response variable (stand structure attribute; e.g., Oregon white oak stems/ha). If the null hypothesis cannot be rejected, the calculation stops; otherwise, the algorithm selects the predictor

variable with the strongest association with the response variable (Müller and Hothorn 2004, Hothorn et al. 2006). The strength of this association was evaluated by a P -value that corresponds to a test between the partial null hypothesis of the predictor and response variables. The algorithm continued to partition response variable observations using any of the predictor variables until the univariate P -value exceeded significance ($\alpha = 0.05$), avoiding a selection bias toward predictor variables and a statistically appropriate regression tree with no pruning or cross-validation necessary.

Individual response variables were stand structure attributes of Oregon white oak, California black oak, and Douglas-fir at the plot level. These structural attributes included species-specific live stem density (trees/ha), live basal area (m^2/ha), relative density (i.e., percentage of overstory composition by species), proportion of multi-stem oak trees, proportion of dead stems (based on stem density), and seedling density (seedlings/ha). Due to the low number of oak saplings, sapling density was excluded from analysis.

We analyzed each species-specific stand attribute in order to evaluate the strength of geographic (abiotic, location) variables vs. competition-related (biotic) variables. The first regression used only abiotic factors as predictors, whereas the second regression included both abiotic and biotic factors (theoretically dominant variables). Abiotic factors included slope, elevation, aspect (two indices), slope position and type, location (UTM coordinates), site (categorical), and average climate variables (precipitation, temperature). Aspect was transformed into two indices, solar radiation and heat load, to estimate potential direct incident radiation and temperature from warmer/drier (1; southwestern) to cooler/wetter (0; northeastern) slopes (Roberts and Cooper 1989, McCune and Keon 2002). Climate variables were derived from interpolated site-level 30-yr seasonal averages (1981–2010) using PRISM data (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>). Precipitation variables included fall (September–November), winter (December–February), and spring (March–May) precipitation. Temperature variables were limited to maximum summer (June–August) and minimum winter temperature. Predictive biotic factors included species-specific stem density,

basal area, relative density, proportion of multi-stem oak trees, and proportion of dead stems. Additionally, we created linear regression models predicting age from dbh and total height (separately) for each study species at each site and across sites (see Appendix S2). Total height averages were also calculated for all three tree species per plot (Table 1).

Tree age structure.—Extracted tree cores were mounted, sanded, and dated following standard dendrochronology techniques (Fritts 1976, Speer 2010). Tree rings were counted under a binocular microscope and subsequently measured with a tree-ring scanning system (WinDendro software, Regent Instruments, version 2009b). All annual ring widths were visually and statistically cross-dated using the computer program COFECHA (Holmes 1983). When cores missed the pith, a geometric model of annual tree growth was used to estimate the number of years to pith (Duncan 1989). Cores missing the pith by more than 15 yr (3%) or those with rotten centers (14%) were considered minimum age counts and excluded from temporal analyses of tree establishment, but were included in figures to visualize historical (pre-1850) tree age structure. To address the potential variation in the number of years to coring height, we grouped stem establishment dates into 10-yr bins and calculated 5-yr smoothing averages to illustrate species-specific age structure trends.

To correct for coring height for Douglas-fir age samples, we destructively sampled 10 saplings from oak-dominant stands at each study site then cut, sanded, and aged along 10 cm height intervals to create site-specific age-to-height linear regressions ($n = 97$ total saplings; $R^2 = 0.19\text{--}0.96$ across sites). Across sites, the average rate of juvenile height growth to coring height of Douglas-fir was 10.4 cm/yr (range: 1.2–18.5 cm/yr across sites; not shown). A lack of California black oak and Oregon white oak saplings (we observed nine individuals across 90 plots) prohibited this type of destructive sampling and analysis. Instead, we used existing post-fire California black oak sprout growth data from mixed conifer–oak stands in northeastern California (27 plots; Cocking et al. 2014) to approximate the oak sapling height growth rate. The median maximum sprout height in stands burned at high severity (>75% overstory mortality; 23 plots) and low-to-moderate severity

(0–74% overstory mortality; 4 plots) was divided by years since fire (10) to estimate the rate of height growth for multi-stem (41.6 cm/yr) and single-stem (17.3 cm/yr) oak saplings, respectively (data from Cocking et al. 2014). We used different rates of height growth for single-stem and multi-stem oak trees, assuming that a higher severity disturbance (removal/top-killed oak stem) would promote a greater sprouting response in oaks (cf. Cocking et al. 2014) and result in a greater proportion of multi-stem trees. In contrast, we assumed a lower severity disturbance would be less likely to promote multi-stem trees and would result in a greater proportion of single-stem oaks (as in Copenheaver and Keyser 2016). We believe the estimate of annual single-stem oak growth is a highly conservative approximation for our study area because of climatic differences between our study region and the area studied in Cocking et al. (2014), but reasonable given 10-yr tree age bins.

Tree establishment patterns.—The timing of stem establishment was evaluated for all tree species, but our focus was on Oregon white oak, California black oak, and Douglas-fir because they overwhelmingly dominated all sites (cumulatively >95% total basal area across the 10 sites; Schriver 2015) and previous research on Oregon white oak (Sugihara and Reed 1987, Engber et al. 2011) and California black oak (Stewman 2001, Cocking et al. 2012) stands in northern California consistently identified Douglas-fir as the predominant encroaching species. We evaluated the temporal and spatial patterns of tree establishment by examining intra- and inter-species synchronicity of tree ages within and across sites. The two oak species are prolific sprouters following disturbance, and thus, we use the term oak “stem” establishment instead of tree establishment. Stem ages for Oregon white oak and California black oak were also compared with Douglas-fir ages to examine their relative patterns of stem establishment. For example, co-occurrence of Oregon white oak stem ages across sites would suggest similar timing of stem establishment at multiple locations, which may indicate broad-scale factors that influenced Oregon white oak establishment. K1D software (Gavin 2010) was used to evaluate the timing of tree establishment among event records (in our case, event records were tree ages at the plot level within each site and tree ages

aggregated at the site level for comparison among sites). K1D is a modification of Ripley’s K function (Ripley 1977) for one dimension, time. K1D has been increasingly used for a wide array of comparisons (e.g., Gavin et al. 2006, Schoennagel et al. 2007), including temporal relationships between tree establishment and disturbances (e.g., Amoroso et al. 2011, Tepley and Veblen 2015). We examined the temporal pattern of tree establishment within a window of time (t years), in which the K function was calculated using a multivariate (MEK) bidirectional model (Gavin 2010). The bidirectional approach implies that events (tree ages) at each location (plot or site level) were evaluated irrespective of temporal direction; that is, tree ages at one location (R) occurred prior to, co-occurred with, or followed tree ages of all other aggregated locations (A). The multivariate K function was transformed to an L function for graphical interpretation, and a 95% confidence envelope for the $L_{RA}(t)$ values was calculated (Appendix S1). Values of $L(t)$ above, below, or in between the confidence interval indicate synchrony, asynchrony, or independence (random), respectively, between event records at that timescale. The proportion of single- vs. multi-stem oak trees was also summarized as an additional indicator of stem establishment patterns at each site, in which we interpreted multi-stem trees as indicative of sprout origin (Table 1 and Fig. 4; also see Copenheaver and Keyser 2016). Multi-stem (sprout origin) trees were also an indicator of pre-existing oaks at the site. For plots with conifer stumps, stump diameters were compared with site-level frequency distributions of Douglas-fir dbh and age–dbh regressions to evaluate the proportion of missing large-diameter conifers from stand and age structures (Appendix S2).

RESULTS

Stand composition and structure

In total, 7995 trees and 14 species occurred across 90 plots within the 10 sites. The most common trees were Douglas-fir (3540 trees; 88% plots), Oregon white oak (3061 trees; 94% plots), and California black oak (791 trees; 84% plots). These three species were present at all sites and in most plots within sites (Table 1). The percentage of plots where Oregon white oak, California black oak, and Douglas-fir dominated the overstory (>50%

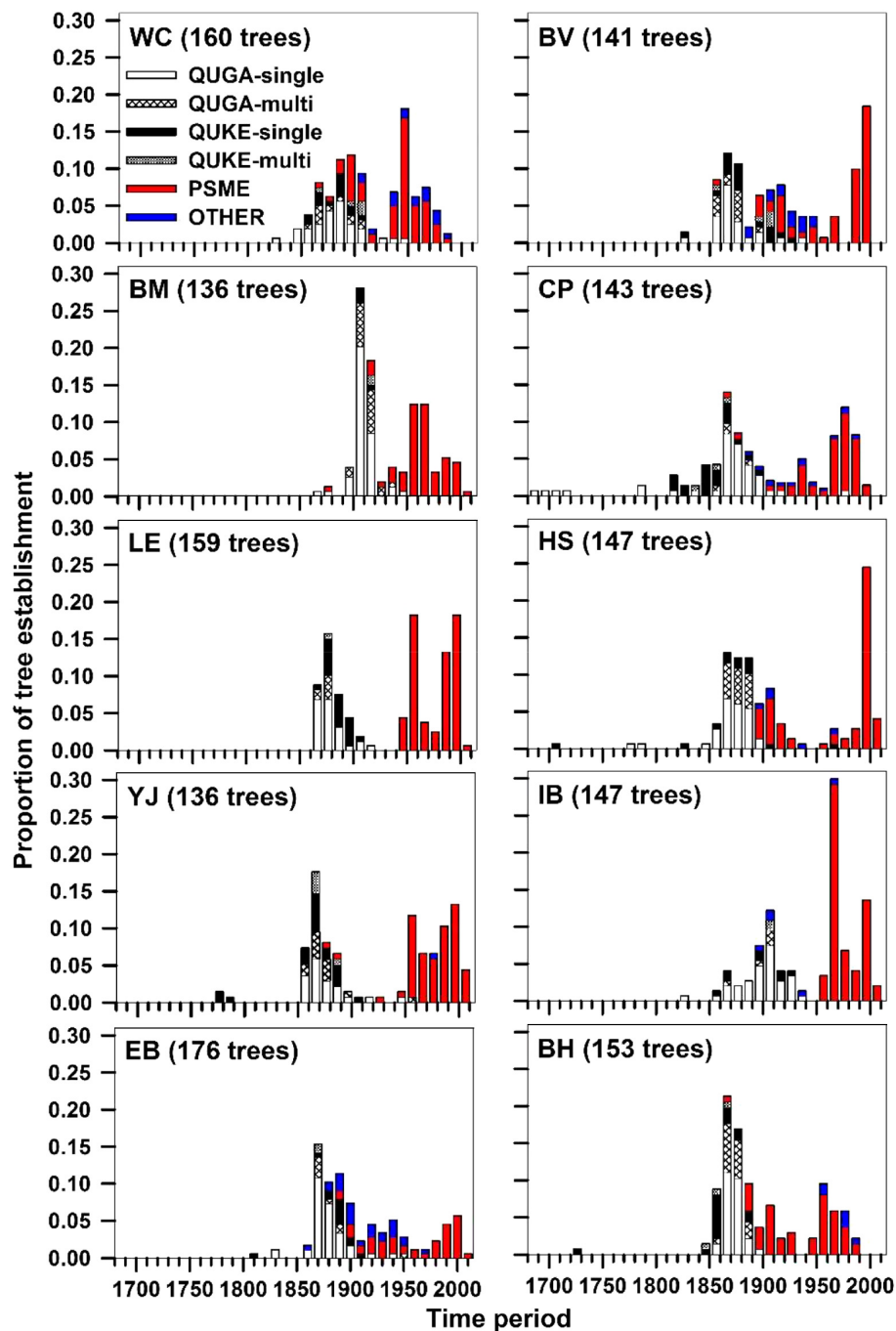


Fig. 4. The proportion of tree ages of Oregon white oak (QUGA; white), California black oak (QUKE; black), Douglas-fir (PSME; red), and other tree species (white fir, bigleaf maple, California buckeye, Pacific madrone, California incense-cedar, tanoak, California live oak, canyon live oak, ponderosa pine, and California laurel; blue) in 10 oak sites under a gradient of Douglas-fir encroachment conditions in northwestern California. Single-stemmed (single) and multi-stemmed (multi) oak trees are represented by solid and patterned colors, respectively.

relative density) was 46.0%, 2.2%, and 29.0%, respectively. Other tree species included Pacific madrone (216 trees), California buckeye (100 trees), California laurel (95 trees), tanoak (61 trees), canyon live oak (42 trees), California live oak (23 trees), California incense-cedar (17 trees), toyon (*Heteromeles arbutifolia* (Lindl.) M. Roem.; 13 tall stem form), ponderosa pine (*Pinus ponderosa* Douglas ex. Lawson & C. Lawson; 7 trees, 6 located at CP), bigleaf maple (*Acer macrophyllum* Pursh; 5 trees), and white fir (2 trees). The mean total live stem density and basal area were 756 trees/ha and 49.5 m²/ha, respectively. Substantial variation existed among sites, with tree density varying by two orders of magnitude (from 80 [EB] to 2260 [HS] stems/ha) and basal area by a factor of 4 (20.2 [EB] to 98.3 [BM] m²/ha; Table 1).

Oregon white oak was the most abundant oak across the study plots, with stem density and basal area averaging 272 trees/ha and 12.1 m²/ha (range of 0–1310 trees/ha and 0–43.5 m²/ha), respectively. Oregon white oak averaged 25.1 cm dbh (range of 5.5–112 cm) with approximately 92% of stems between 10 and 40 cm dbh and fewer than 3% of stems >50 cm dbh (Fig. 5). Oregon white oak had the lowest height of the three dominant species, averaging 13 m (ranging 0.6–43.2 m; Table 1). In all but one site (EB), the oak total heights in oak-dominated stands were lower (on average 1.8 m less) than in oak stands that had become dominated by conifers. Sites included variable proportions of single- and multi-stem Oregon white oak across oak tree ages (Table 1). Thirty-three percent of stems across all size classes had multi-stemmed tree structure (Fig. 4). Oregon white oak had the greatest relative proportion of dead stems, especially at smaller sizes (<15 cm dbh), with half of the sites containing only dead stems in one or more plots. On average, 30% vs. 11% of Oregon white oak stems were dead in the sites that had become dominated by conifers vs. oak-dominant stands, respectively. Oregon white oak also exhibited relatively weak and inconsistent relationships among age, dbh, and total height variables (Appendix S2).

California black oak was less common than Oregon white oak, with stem density and basal area averaging only 74 trees/ha and 8.7 m²/ha (range of 0–430 trees/ha and 0 to 37.2 m²/ha), respectively (Table 1). However, California black oak stems were generally larger than Oregon

white oak, averaging 34.7 cm dbh (range of 6.9–139.5 cm), with 89% of tree stems between 10 and 55 cm dbh. Likewise, California black oak were generally taller than Oregon white oak, averaging 14.3 m across sites (ranging from 2 to 40.8 m; Table 1). Similar to Oregon white oak, California black oak were taller in conifer-dominant stands than in oak-dominant stands (on average 1.7 m taller) at all but two sites (EB and BH). The proportion of multi-stem California black oak was lower than Oregon white oak (26% of trees were multi-stemmed; Table 1) and varied across size classes (Fig. 5). Smaller California black oak dead stems were common (>50% of dead stems were 10 and 15 cm dbh; Fig. 6). On average, 19% vs. 11% of California black oak stems were dead in stands that had become dominant by conifers vs. oak-dominant stands, respectively. California black oak exhibited slightly stronger relationships among age, dbh, and total height than Oregon white oak (Appendix S2).

Across all species and sites, Douglas-fir was the most abundant tree, with stem density and basal area averaging 351 trees/ha and 21.9 m²/ha (range of 0–2070 trees/ha and 0–79 m²/ha), respectively. Douglas-fir trees were the largest diameter trees at seven sites (averaging 21.1 cm dbh; range of 5–180 cm dbh; Fig. 5), although most (88%) stems were ≤40 cm dbh. Douglas-fir trees were also the tallest, averaging 15.7 m (ranging 1.2–55.9 m), and were on average 4.8 and 2.8 m taller than Oregon white oak and California black oak, respectively, in oaks stands that had become dominated by conifers. Douglas-fir exhibited the lowest proportion of dead stems among the three dominant tree species (11% of stems were dead on average; Fig. 5 and Table 1). On average, 11% vs. 8% of Douglas-fir stems were dead in conifer-dominant vs. oak-dominant stands, respectively. Douglas-fir consistently exhibited strong age relationships between dbh and total height at all 10 sites ($P \leq 0.001$; Appendix S2). Previously harvested Douglas-fir (stumps) constituted a relatively small proportion of the stand structure at the six sites that had past conifer harvests (ca. 1960s). Across these sites, Douglas-fir stump density averaged 40 ha⁻¹ (range of 10–130), representing an average of 15% of the present-day total Douglas-fir stem density (range of 11–44%; Table 1). Current Douglas-fir stem density and basal area were not

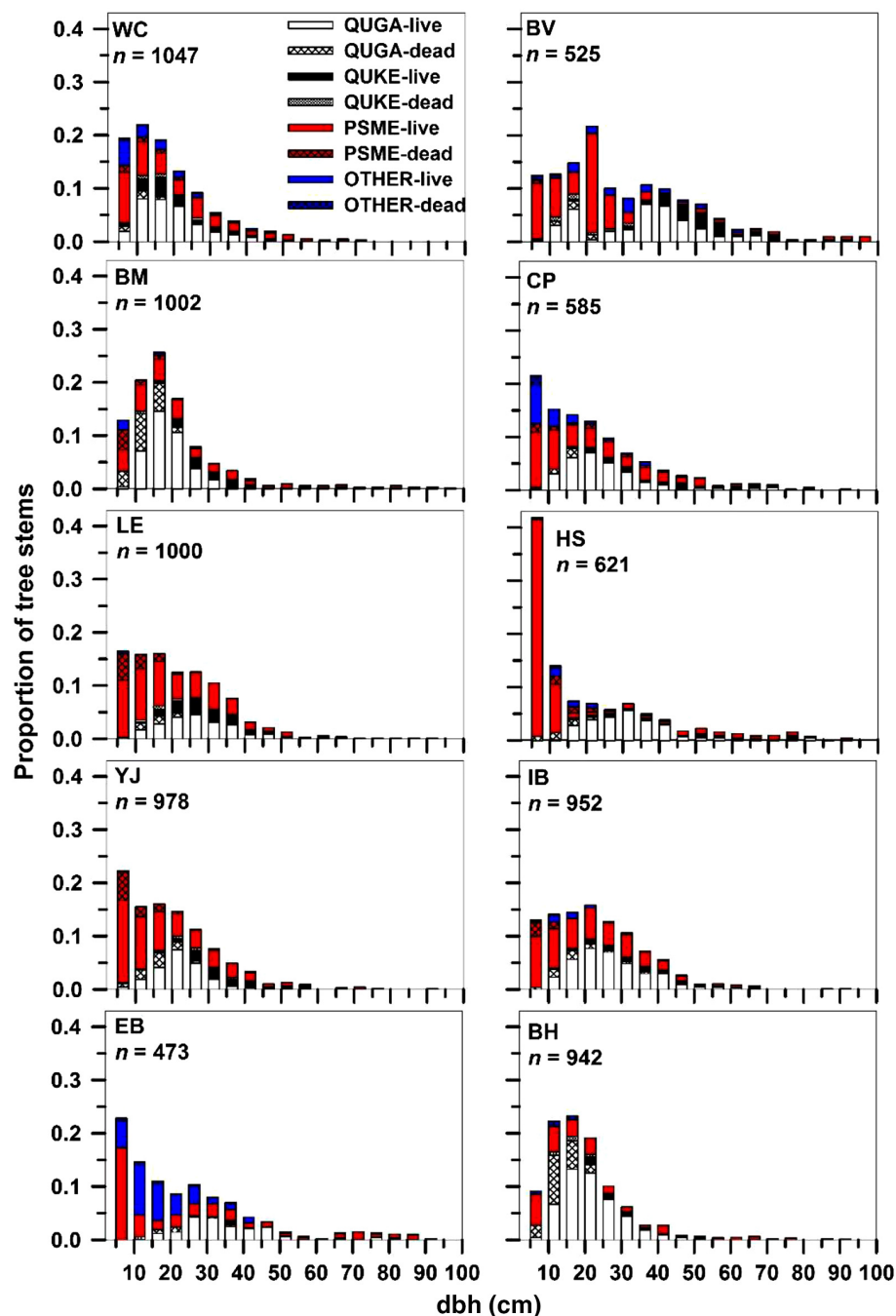


Fig. 5. Proportional size distribution of live and dead tree stems (≥ 5 cm dbh) of Oregon white oak (QUGA; white), California black oak (QUKE; black), Douglas-fir (PSME; red), and other species (white fir, bigleaf maple, California buckeye, Pacific madrone, California incense-cedar, tanoak, California live oak, canyon live oak, ponderosa pine, and California laurel; blue) in 10 oak sites under a gradient of *Pseudotsuga menziesii* encroachment conditions mixed oak–conifer woodland sites in northwestern California. No more than 1.3% of the trees were >100 cm dbh at any site.

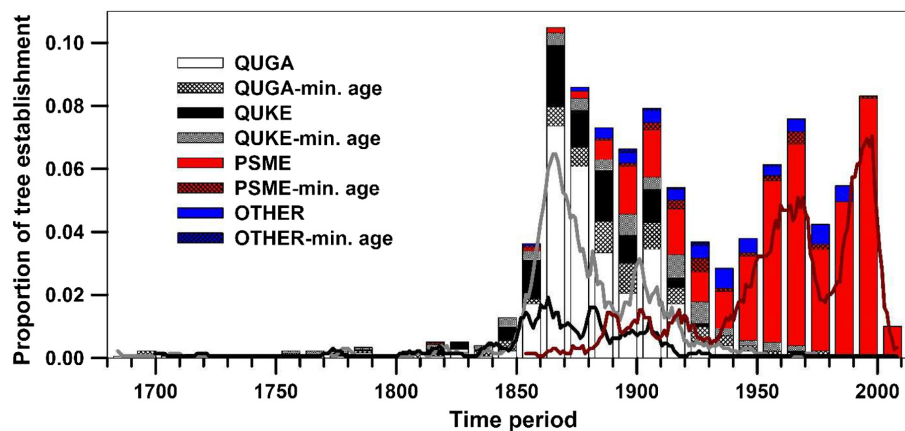


Fig. 6. The proportion of tree ages of Oregon white oak (QUGA; white), California black oak (QUKE; black), Douglas-fir (PSME; red), and other tree species (white fir, bigleaf maple, California buckeye, Pacific madrone, California incense-cedar, tanoak, California live oak, canyon live oak, ponderosa pine, and California laurel; blue) in 10-yr bins with a 5-yr smoothing average (solid horizontal lines) for 10 oak sites under a gradient of Douglas-fir encroachment conditions ($n = 90$ plots; 1742 trees) in northwestern California. Trees with rotten centers or greater than 15 yr to pith are labeled as minimum ages (min. age; hashed bins).

significantly different between harvested and unharvested sites ($P > 0.05$, t test). Other tree species (Pacific madrone, tanoak, canyon live oak, and California laurel) cumulatively represented <7% of the total stem density and basal area (see Table 1). Evidence of other types of disturbance in plots included fire (scarred or charred trees; 13 plots), ungulate grazing (9 plots), and feral pig (*Sus scrofa*) injury (1 plot).

Relating stand structure to biophysical environment

Across all 90 plot locations (10 sites), we assessed whether stand structure (live and dead stems by species) varied in relation to biophysical characteristics. Live stem density of Oregon white oak was greater in plots north of 40.51° latitude (341 trees/ha vs. 163 trees/ha on average; abiotic factors considered alone; $P = 0.026$). Lower proportions of dead Oregon white oak stems occurred in plots at or below 918 m elevation and in plots receiving on average ≤ 391 mm of fall (September–November) precipitation (abiotic factors considered alone; $P = 0.012$ and $P = 0.006$, respectively). However, no other abiotic variables were associated with live Oregon white oak or California black oak stand structure attributes.

As predicted, all live structure attributes (stem density, basal area, and proportion of

multi-stemmed trees) of Oregon white oak were negatively related to Douglas-fir. Oregon white oak stem density was greater in stands with $\leq 12\%$ overstory Douglas-fir ($P = 0.001$) and lower in stands with $> 49\%$ overstory Douglas-fir ($P = 0.002$). Likewise, the proportion of multi-stem Oregon white oak was greater in stands with $\leq 46\%$ overstory Douglas-fir ($P = 0.007$). Oregon white oak basal area was greater in stands with $\leq 25\%$ Douglas-fir and $\leq 23\%$ California black oak in the overstory ($P < 0.001$), and lower in stands with $> 25\%$ overstory Douglas-fir and no multi-stemmed Oregon white oak ($P = 0.016$). The relative density of Oregon white oak was higher in stands with ≤ 14.7 m²/ha Douglas-fir and ≤ 7.7 m²/ha California black oak ($P < 0.001$ and $P = 0.017$, respectively), and lower in stands with > 14.7 m²/ha Douglas-fir and the absence of multi-stem Oregon white oak trees ($P < 0.001$). Oregon white oak seedling densities were greater in stands with > 27.8 m²/ha Oregon white oak ($P < 0.001$), and lower in stands with ≤ 27.8 m²/ha Oregon white oak and $< 55\%$ overstory Oregon white oak ($P = 0.003$). Unlike Oregon white oak, California black oak live attributes (stem density, proportion of multi-stems, or seedling density) were not associated with Douglas-fir or most other biotic variables. The exception to this was that California black oak basal area was highest in

stands with $\leq 19\%$ overstory Oregon white oak ($P = 0.005$) and had a higher relative density with $\leq 8.2 \text{ m}^2/\text{ha}$ Oregon white oak ($P < 0.001$). Greater proportions of Oregon white oak stems were dead in stands with $> 34.5 \text{ m}^2/\text{ha}$ Douglas-fir ($P < 0.001$), while greater proportions of California black oak stems were dead in stands with $> 38.0 \text{ m}^2/\text{ha}$ Douglas-fir ($P < 0.001$).

Douglas-fir-dominant stands had low abundance of living oak trees. Trends show that the relative density of Douglas-fir was higher in stands with $\leq 12.0 \text{ m}^2/\text{ha}$ Oregon white oak ($P < 0.001$), stem density was greater in stands with $\leq 48\%$ overstory Oregon white oak ($P < 0.001$), and basal area was greater in stands with $\leq 51\%$ overstory Oregon white oak ($P < 0.001$). Douglas-fir (live) structural attributes were not associated with any of the abiotic factors evaluated, although non-significant trends show greater densities of Douglas-fir in oak stands at the northern end of the study region. Likewise, the proportion of dead Douglas-fir stems was not associated with any abiotic or biotic factors.

Tree establishment patterns

Across all ten sites, we cored 1747 trees from 10 different species. Forty-two percent of cored trees were Douglas-fir (734 trees; median age 43 yr; range 6–142 yr), 36% were Oregon white oak (629 trees; median age 136 yr; range 41 to > 324 yr), and 16% were California black oak (279 trees; median age 138 yr; range 45–301 yr). Other species collectively accounted for 6% of cored stems and included Pacific madrone (35 trees), California buckeye (26 trees), California laurel (20 trees), canyon live oak (9 trees), California incense-cedar (3 trees), tanoak (3 trees), and California live oak (3 trees), with median ages ranging between 37 and 98 yr. Of the trees cored, 278 (16%) were assigned a minimum age (due to encountering a rotten center or > 15 yr to pith), of which 82% of these trees were Oregon white oak and California black oak. These trees are not included in the age analysis but are shown in Fig. 6.

The majority of Oregon white oak and California black oak stems (86% and 81%, respectively) dated between 1850 and 1910 across the 10 sites, with less than 0.1% of either species dating within the last 70 yr (Figs. 4 and 6). In 69% of plots (across study sites), the majority of oak stems established within a ~20- to 40-yr time

period between 1860 and 1900. One-third of the plots revealed longer intervals of establishment (~60 to 80 yr). Regional tree establishment patterns (aggregated tree ages by site; Fig. 6) and temporal K1D analysis (Appendix S1) illustrate synchronous (simultaneous) establishment from inter-annual to multi-decadal timescales for both oak species across the 10 sites. Within sites (among plots), temporal K1D analysis indicated that Oregon white oak established synchronously (co-occurred) at inter-annual (1–3 yr) to multi-decadal (> 20 yr) scales at each of the 10 sites (Appendix S1). California black oak temporal patterns were more variable than Oregon white oak within sites. At the plot level within sites, four sites (BH, BV, IB, and LE) had independent (random) establishment patterns, three (BM, EB, and YJ) had inter-annual to multi-decadal synchrony, two (CP and WC) had decadal asynchrony, and one (HS) had only multi-decadal synchrony (Appendix S1).

As predicted, most Douglas-fir established more recently than oaks and relatively continuously at each site, with 73% of all conifer establishment after 1950 (Fig. 6). Within sites, Douglas-fir predominantly had inter-annual to multi-decadal scale synchrony in tree establishment, and most establishment occurred a century later than oaks (Figs. 4 and 6 and Appendix S1). Within and across sites, Oregon white oak and Douglas-fir ages exhibited asynchronous (i.e., distinctly separate) establishment (K1D analysis; Appendix S1). Comparisons of California black oak and Douglas-fir within sites also exhibited asynchronous establishment, although with greater variability than Oregon white oak and Douglas-fir comparisons (Fig 4; Appendix S1).

Current regeneration

Across all sites and along the sampled encroachment gradient, total seedling regeneration averaged 9268 ha^{-1} (range of 0–50,834 ha^{-1}). Seedling composition was dominated by Oregon white oak (average of 5500 seedlings/ha) but was significantly lower (on average $1000\times$ less) in plots that had become dominated by conifers (range of 0–3333 ha^{-1}) vs. oaks (range of 0–49,167 ha^{-1}). California black oak was the second most common seedling, with 1,713 seedlings/ha on average (range of 0–15,000 ha^{-1}), although unlike Oregon white oak, seedling densities were not significantly

different in plots dominated by conifers (range of 0–7500 ha⁻¹) vs. oaks (range of 0–15,000 ha⁻¹). Douglas-fir was the third most common seedling, averaging 991 ha⁻¹ (range of 0–13,333 ha⁻¹). Sapling densities for both Oregon white oak and California black oak were low across all stand types and sites (range of 0–80 ha⁻¹ and 0–40 ha⁻¹, respectively; Table 1). The vast majority of saplings were Douglas-fir, averaging 408 ha⁻¹ across sites (range of 0–5200 ha⁻¹; Table 1). Douglas-fir seedling densities were not significantly different between harvested and unharvested sites ($P > 0.05$; t test), although sapling density was significantly greater at harvested sites ($P = 0.01$). Other tree species cumulatively represented <11% of the total regeneration across sites.

DISCUSSION

Oak woodland composition and establishment patterns

Oak woodlands throughout northwestern California that span the range of mesic to xeric environments exhibited substantial changes in composition and structure over the last century. Our findings were consistent with other studies that have demonstrated significant conifer advancement in Oregon white oak ecosystems in Oregon and British Columbia (Thilenius 1968, Gedalof et al. 2006, Gilligan and Muir 2011, Copes-Gerbitz et al. 2018) and the few California black oak-dominated ecosystems sampled in northern California (Stewman 2001, Cocking et al. 2012). Woodland structures in our study sites varied in relation to the biophysical environment (i.e., higher live densities of Oregon white oak in northern sites and plots with low Douglas-fir overstory), but also illustrated a consistent pattern of the majority (>80%) of oak stem establishment during or following Euro-American settlement (1850–1910). Importantly, most of the oak stems predated Douglas-fir trees where they occupied the same stand. Less than 1% of the oaks established after 1960 across all 10 sites regardless of the biophysical site conditions. In contrast, the majority of Douglas-fir established after 1950 (73%), with abundant regeneration at all sites (i.e., not only in more mesic or cooler microsite or geographic locations), indicating a trajectory of oak stands shifting toward conifer dominance. Starting in the 1950s, climatic

conditions were wetter and therefore more favorable for Douglas-fir establishment. Our findings also confirmed our expectation of more dead oak trees in stands that have become dominated by Douglas-fir (cf. Devine and Harrington 2013).

There were also important geographic patterns of encroachment. We found evidence of greater stem densities of Oregon white oak at more northerly latitudes, consistent with a more dominant northern distribution within the species' natural range. We also found evidence of slightly greater stand densities of Douglas-fir in oak stands at the northern end of our study region indicating more rapid encroachment in these areas. Oaks were two to five meters taller in stands that had become dominated by conifers than in open oak stands. We interpret the greater oak height as a product of light competition from Douglas-fir, which leads to prioritization of vertical growth over full canopy development. The height trend was consistent across the gradient (mesic to dry) of sites and we found no relationships of stand structure or composition associated with plot-level environmental variables. We found fewer dead stems and greater heights of California black oak in encroached stands than Oregon white oak indicating a slightly better ability to persist under conifer-dominated canopies.

Mechanisms of establishment

Fire is considered a primary driver in the persistence of open-grown oak woodlands and savannas because fire kills young non-sprouting species (e.g., conifers; Engber and Varner 2012), whereas young oaks are able to resprout and larger, established oaks can withstand the intensity of many (lower-intensity) fires. When a fire-free interval is sufficiently long, conifers increase in size, develop thicker bark, and become more resistant to fire. Although the importance of low-severity fire in maintaining oak woodlands is well recognized, the relationship between oaks and fire remains complex, as oaks can tolerate and take advantage of a wide range of fire severities (e.g., through sprouting after top kill or injury; e.g., Cocking et al. 2014, McDonald 1990). The effects of periodic fire, ignited via lightning or Amerindian cultural burning, historically promoted the persistence of oak savannas and woodlands within broader conifer-dominated landscapes (Sawyer 2007). Additionally, Euro-

American settlers in the late 19th and early 20th centuries also relied on oak woodlands and actively managed for them (e.g., Pinchot 1898).

Considering the spatial synchrony identified in establishment patterns, we believe that the pulse of oak establishment during the 1880–1910 period is attributed to several broad-scale historical legacies. These include changes in the fire regime (less frequent and/or shifts in fire activity), regional climate changes (National Climate Assessment 2014), and the game demand of Euro-American settlers that significantly reduced deer populations and also increased cattle and sheep grazing (with shifts in fine fuels and fire activity; e.g., Savage and Swetnam 1990) during this time period. The sheep and cattle industries in the early 20th century depended heavily on oak woodland and savanna landscapes for browse for livestock and game. The regional sheep industry peaked in the late 1800s (e.g., Connor 1921) and declined until it moved overseas in the late 1960s. By the early 20th century, attitudes toward fire became increasingly negative and use of prescribed fire began to decline in the United States (Pyne 2001), leading to significant funds and resources deployed to suppress wildland fires. The combination of anthropogenic practices converging in time across the region (i.e., major land-use changes, resources to suppress fires and shifts in grazing activity) led to broad-scale changes in stand structures and the ability of Douglas-fir from nearby stands to dramatically increase into open woodlands beginning in the mid-20th century. The ecological consequences of fire suppression and altered grazing patterns likely reduced the competitive advantage of native grasses and initiated ecological succession of native Douglas-fir oak woodlands initiating changes in composition and structure. Our research highlights that shifts in composition and structure are widespread throughout northwestern California, but also that alterations of ecosystem conditions occur rapidly, with conifers becoming co-dominant and causing declines in oak health in as little as 20 yr due to compound interactions of endogenic (e.g., ecological succession) and exogenic (e.g., human impacts) processes.

Another important finding was evidence of single- and multi-stem oak trees of all ages across sites, suggesting that a variety of disturbances

(low- to high-severity) and regeneration pathways led to existing oak stand structures (i.e., through both acorn/seedlings and resprouting) and that oaks have been present at these sites for many centuries. While we did not take a census of all oak trees at each research site, our sampling identified that many individual oak trees in this study were more than 300 yr, and many more than 300 yr were rotten in the center (see Figure 6), excluding an additional (albeit unknown) signature of time. Single-stem trees were dominant, although multi-stem trees were present at each site, which presumably resulted from post-disturbance resprouting (e.g., fire; Copenheaver and Keyser 2016), and indicative of prior presence of oak stems in those locations. The lack of advanced oak recruitment in the last century—corroborated by the overwhelmingly disparate numbers of oak seedlings vs. saplings—is not well understood, but could be related to a number of factors, including competition from grass cover; browsing by deer, grasshoppers, and small mammals; grazing by domesticated cattle; and canopy shading from the encroachment of Douglas-fir into historically more open oak woodlands. Anecdotal evidence from the study region points to the importance of browsing, as the few young oaks present on the landscape are often found in blackberry (*Rubus armeniacus* Focke) or poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Green) clumps or inside deer fencing (*personal observation*; Dasmann 1971). The exclusion of fire—especially moderate- and high-severity fires—has also affected recruitment of younger age classes of oaks, as fire-induced top kill and subsequent resprouting can reset oak age classes, while simultaneously eliminating competing fire-sensitive trees.

Our findings have important implications for the future of oak woodland ecosystems across a wide range of climate (mesic to xeric) and site conditions throughout northern California.

The process and severity of encroachment was consistent across the study region, resulting in substantial oak woodland losses and shifts toward conifer-dominated forest homogeneity in northwestern California. These transitions appeared most rapid in mesic sites and at the northern end of the study area. These landscape-level changes throughout native oak woodland habitats contribute to a loss of plant and animal

biodiversity, mortality of mature oak trees, reduction in oak regeneration, and shifts in fuel structures that have consequences for re-introduction of fire into these ecosystems (Sugihara and Reed 1987, Agee 1993, Engber et al. 2011, Livingston et al. 2016).

Oak woodland ecosystems are increasingly the focus of conservation and restoration efforts because they provide unique and biodiverse habitats for wildlife, and are culturally important (Long et al. 2017). Recent policy changes in California have opened up new management options for private landowners, whose oak restoration efforts were previously limited by the California Forest Practice Rules (Valachovic et al. 2015). In places where oak woodland persistence is a major goal, active management may be an option to curb conifer encroachment, conserve living oaks, and promote oak regeneration. In stands where encroaching conifers are beginning to establish, or where conifers are reestablishing after removal, prescribed fire can be an effective management tool (Engber and Varner 2012). In stands with larger conifers, mechanical removal is likely necessary. Wildfire will also play an important role in the persistence of deciduous oaks, and managed wildfire could be an effective tool in the places where it is feasible (Cocking et al. 2012). Management interventions have demonstrated effectiveness in maintaining oaks and increasing oak growth in other regions (Devine and Harrington 2006, 2013); however, more science-based information is necessary to help guide conservation and restoration efforts at regional scales. This study focused on the arboreal component of oak woodlands in northern California, and any management actions and/or recommendations from our findings related to prescribed fire or removal of trees should also carefully consider the importance, and less well-known, consequences for understory and wildlife species.

ACKNOWLEDGMENTS

We thank A. Livingston, B. Twieg, B. Hodge, and R. Glebocki for their help in the field and O. Zotter, C. Neuenschwander, A. Potts, and D. Snow for processing tree cores. We also thank many of the private and public landowners who let us survey their land. J. Kane, R. Standiford, and A. Livingston provided feedback on the research project and K. Muth, D. Nemens, D. Peters

and two anonymous reviewers provided editorial and review comments that improved the manuscript. Funding for the research was provided by a University of California Agriculture and Natural Resources grant, the USDA National Institute of Food and Agriculture McIntire-Stennis Cooperative Forestry Research Program Project #160, and the National Fire Plan.

LITERATURE CITED

- Agee, J. K. 1993. Fire ecology of pacific northwest forests. Island Press, Washington, D.C., USA.
- Amoroso, M. M., L. D. Daniels, M. Bataineh, and D. W. Anderson. 2011. Evidence of mixed-severity fires in the foothills of the Rocky Mountains of west-central Alberta, Canada. *Forest Ecology and Management* 262:2240–2249.
- Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial vegetation of California. University of California Press, Berkeley and Los Angeles, California, USA.
- Bond, W. G., and G. F. Midgley. 2000. A proposed CO₂ controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* 6:865–869.
- Cocking, M. I., J. M. Varner, and E. E. Knapp. 2014. Long-term effects of fire severity on oak-conifer dynamics in the southern Cascade. *Ecological Applications* 24:94–107.
- Cocking, M. I., J. M. Varner, and R. L. Sherriff. 2012. California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. *Forest Ecology and Management* 270:25–34.
- Connor, L. G. 1921. A brief history of sheep industry in the United States. *Agricultural History Society Papers* 1:88–197.
- Copenheaver, C. A., N. E. Fuhrman, L. S. Gellerstedt, and P. A. Gellerstedt. 2004. Tree encroachment in forest openings: a case study from Buffalo Mountain, Virginia. *Castanea* 69:297–308.
- Copenheaver, C. A., and T. L. Keyser. 2016. Frequency of sprout-origin trees in pre-European settlement forests of the southern Appalachian Mountains. *Canadian Journal of Forest Research* 46:1019–1025.
- Copes-Gerbitz, K., K. Arabas, E. Larson, and S. Gildehaus. 2018. A multi-proxy environmental narrative of Oregon white oak (*Quercus garryana*) habitat in the Willamette Valley, Oregon. *Northwest Science* 91:160–185.
- Dasmann, W. 1971. If deer are to survive. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Devine, W. D., and C. A. Harrington. 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. *Trees* 20:747–756.

- Devine, W. D., and C. A. Harrington. 2013. Restoration release of overtopped Oregon white oak increases 10-yr growth and acorn production. *Forest Ecology and Management* 291:87–95.
- Devine, W. D., C. A. Harrington, and L. P. Leonard. 2007. Post-planting treatments increase growth of Oregon white oak (*Quercus garryana* Doug. Ex Hook.) seedlings. *Restoration Ecology* 15:212–222.
- D’Odorico, P., J. D. Fuentes, W. T. Pockman, S. L. Collins, Y. He, J. S. Medeiros, S. DeWekker, and M. E. Litvak. 2010. Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. *Ecosphere* 1:art17.
- Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment core in Kahikatea (*Dacrydium dacrydioides*). *New Zealand Natural Sciences* 16:31–37.
- Engber, E. A., and J. M. Varner. 2012. Reversing conifer encroachment with prescribed fire: shifting mortality models toward restoration targets. *Restoration Ecology* 20:665–668.
- Engber, E. A., J. M. Varner, L. Arguello, and N. G. Sugihara. 2011. The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. *Fire Ecology* 7:32–50.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, London, UK.
- Gavin, D. G. 2010. K1D: multivariate Ripley’s K-function for one-dimensional data. University of Oregon, Department of Geography, Eugene, Oregon, USA.
- Gavin, D. G., F. S. Hu, K. Lertzman, and P. Corbett. 2006. Weak climatic control of stand-scale fire history during the late Holocene. *Ecology* 87:1722–1732.
- Gedalof, Z., M. Pellatt, and D. J. Smith. 2006. From prairie to forest: three centuries of environmental change at Rocky Point, Vancouver Island, British Columbia. *Northwest Science* 80:34–46.
- Gilligan, L. A., and P. S. Muir. 2011. Stand structures of Oregon white oak woodlands, regeneration, and their relationships to the environment in Southwestern Oregon. *Northwest Science* 85:141–158.
- Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213–229.
- Holmes, R. L. 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69–78.
- Hothorn, T., K. Hornik, and A. Zeileis. 2006. Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics* 15:651–674.
- Hunter, J. C., and M. G. Barbour. 2001. Through-growth by *Pseudotsuga menziesii*: a mechanism for change in forest composition with forest gaps. *Journal of Vegetation Science* 12:445–452.
- Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179–1188.
- Little Jr, E. L. 1971. *Atlas of United States trees*, volume 1, conifers and important hardwoods: Misc. Pub. 1146. U.S. Department of Agriculture, Washington, D.C., USA.
- Livingston, A. C., J. M. Varner, E. S. Jules, J. M. Kane, and L. Arguello. 2016. Prescribed fire and conifer removal promote positive understory vegetation responses in *Quercus garryana* woodlands. *Journal of Applied Ecology* 53:1604–1612.
- Long, J. W., R. W. Goode, R. J. Gutierrez, J. J. Lackey, and M. K. Anderson. 2017. Managing California black oak for tribal ecological restoration. *Journal of Forestry* 115:426–434.
- McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603–606.
- McDonald, P. M. 1990. *Quercus kelloggii* Newb. California Black Oak. Pages 1281–1289 in R. M. Burns, and B. H. Honkala, editors. *Silvics of North America*. Volume 2: Hardwoods. Agriculture Handbook 654, USDA, Washington, D.C., USA.
- Moore, M. M., and D. W. Huffman. 2004. Tree encroachment on meadows of the North Rim, Grand Canyon National Park, Arizona, U.S.A. *Arctic, Antarctic, and Alpine Research* 36:474–483.
- Müller, J., and T. Hothorn. 2004. Maximally selected two-sample statistics as a new tool for the identification and assessment of habitat factors with an application to breeding-bird communities in oak forests. *European Journal of Forest Research* 123: 219–228.
- National Climate Assessment. 2014. <https://nca2014.globalchange.gov/>
- Pinchot, G. 1898. Report on the survey and examination of forest reserves (March, 1898). Senate Document No. 189, 55th Congress, 2nd Session, Washington, D.C., USA.
- Pyne, S. J. 2001. *Year of the Fires: story of the Great Fires of 1910*. Viking Press, New York.
- Ripley, B. D. 1977. Modelling spatial patterns. *Journal of the Royal Statistical Society B* 39:172–212.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.
- Ripley, B. D. 1977. Modelling spatial patterns. *Journal of the Royal Statistical Society, Series B* 39:172–192.
- Roberts, D. W., and S. V. Cooper. 1989. Concepts and techniques of vegetation mapping. *Land*

- classifications based on vegetation: applications for resource management. USDA Forest Service General Technical Report INT- 257, Intermountain Research Station, Ogden, Utah, USA.
- Savage, M., and T. W. Swetnam. 1990. Earth 19th century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71:2374–2378.
- Sawyer, J. O. 2007. Forests of Northwestern California. Pages 253–265 in M. Barbour, T. Keeler- Wolf, and A. A. Schoenherr, editors. *Terrestrial vegetation of California*. Third edition. University of California Press, Berkeley, California, USA.
- Schoennagel, T., T. T. Veblen, D. Kulakowski, and A. Holz. 2007. Multidecadal climate variability and interactions among Pacific and Atlantic sea surface temperature anomalies affect subalpine fire occurrence, western Colorado (USA). *Ecology* 88:2891–2902.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- Schrivier, M. R. 2015. Stand and tree growth characteristics of *Quercus garryana* and *Quercus kelloggii* woodlands in northwestern California. Thesis. Humboldt State University, Arcata, California, USA.
- Speer, J. H. 2010. *Fundamentals of tree-ring research*. University of Arizona Press, Tucson, Arizona, USA.
- Stam, B. R., J. C. Malechek, D. L. Bartos, J. E. Bowns, and E. B. Godfrey. 2008. Effect of conifer encroachment into aspen stands on understory biomass. *Rangeland Ecology and Management* 61:93–97.
- Standiford, R. B., and J. L. Purcell. 2015. Proceedings of the Seventh California Oak Symposium: Managing Woodlands in a Dynamic World. Gen. Tech. Report. PSW-GTR-251. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, California, USA.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:230–232.
- Stewman, C. J. 2001. Encroachment patterns of Douglas-fir into oak woodlands in the central Klamath region. Thesis. Humboldt State University, Arcata, California, USA.
- Stokes, M. A., and T. L. Smiley. 1996. *An introduction to tree-ring dating*. University of Arizona Press, Tucson, Arizona, USA.
- Sugihara, N. G., and L. J. Reed. 1987. Vegetation ecology of the Bald Hills oak woodlands of Redwood National Park. Redwood National Park Research and Development, Technical Report 21. Redwood National Park, Arcata, California, USA.
- Tepley, A. J., and T. T. Veblen. 2015. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. *Ecological Applications* 85:583–603.
- Thilenius, J. F. 1968. The *Quercus garryana* forest of the Willamette Valley, Oregon. *Ecology* 49:1124–1133.
- Thysell, D. R., and A. B. Carey. 2001. *Quercus garryana* communities in the Puget Trough, Washington. *Northwest Science* 75:219–235.
- Valachovic, Y., L. Quinn-Davidson, and R. Standiford. 2015. Can the California forest practice rules adapt to address conifer encroachment? Pages 515–520 in R. B. Standiford and K. L. Purcell, tech. cords. 2015. Proceedings of the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World. Gen. Tech. Rep. PSW-GTR-251. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, California, USA.
- Weins, J. A., G. D. Hayward, H. D. Safford, and C. M. Giffen, editors. 2012. *Historical environmental variation in conservation and natural resource management*. Wiley- Blackwell, West Sussex, UK.

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