

Establishment Patterns of Oregon White Oak and California Black Oak Woodlands in Northwestern California¹

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Abstract

Mixed-Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*) woodlands are unique ecosystems that support high biodiversity in the Pacific Northwest, yet little is known about their current and historical stand establishment patterns in northwestern California. With concerns of local extirpation due to Douglas-fir (*Pseudotsuga menziesii*) succession, research objectives were to characterize the variability of age structure, stand structure, and current tree regeneration in four mixed oak-conifer woodlands in northwestern California. Each site varied in stand type from open-oak woodland to transitional woodland-forest to closed mixed hardwood-conifer forest. While very low densities of white and black oak saplings (>30 cm tall and <5 cm DBH) characterized all stand types, regeneration of shade-tolerant tree species in closed-forest stands was common. Across all four sites most living white and black oak trees (≥ 5 cm DBH) established during the mid-to late 1800s with no establishment since 1937. Conversely, the majority of Douglas-fir trees have been continuously establishing since around 1950. Within sites, most oaks established over a relatively narrow period of time (40 years), suggesting a stand-level disturbance during the mid-to-late 1800s that promoted regeneration. Less commonly (6 percent of plots), oaks established over a longer period of time (100 years) with plot-level age distributions indicating evidence of more localized stand-initiation events. The establishment of shade-tolerant tree species in some plots at each site, and the lack of oak tree establishment for the last 70 to 100 years, likely reflects the effects of altered disturbance regimes. Tree establishment patterns appear to be consistent with findings in Oregon and Washington, where studies suggest Oregon white oak ecosystems are transitioning into conifer-dominant stands due to land use changes, representing a loss of endemic biodiversity and structural heterogeneity on the landscape.

Key words: age structure, California black oak, conifer encroachment, Oregon white oak, stand dynamics

Introduction

Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*) woodlands are unique ecosystems in the Pacific Northwest, interspersed primarily throughout a mixed Douglas-fir (*Pseudotsuga menziesii*)-hardwood landscape. They represent important refugia for one of the richest diversities of vertebrates, invertebrates, and native plant species in California (for example, Block and others 1990, Sugihara and Reed 1987). In the Pacific West studies suggest that Oregon white oak (Gedalof and others 2006, Gilligan and Muir 2011) and California black oak (Skinner and others 2009) ecosystems are at risk for local extirpation due to a lack of recent oak establishment and native conifer succession where open-oak woodlands transition between conifer-hardwood forests and more xeric ecosystems

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such as oak savanna. For example, in relatively intact oak ecosystems in Oregon studies show most conifer establishment post-dates oak establishment (Gilligan and Muir 2011, Thilenius 1968). Limited information exists on northwestern California to assess if there are similar patterns of tree establishment, forest structure, and oak regeneration as found in Oregon and Washington. Thus, the primary objective of this study was to characterize the variability of age and stand structure in oak woodlands interspersed within conifer-dominated stands in northwestern California. The specific research questions were: **(1) What tree age and stand structures characterize mixed-oak conifer woodlands in northwestern California? (2) Are there similar temporal patterns of oak and conifer establishment in mixed oak-conifer woodlands throughout northwestern California? And (3) what are the current tree regeneration patterns across stands throughout the study region?**

Methods

Study area

The study area was located in the North Coast range of California, which hosts a mosaic of plant community types, ranging from conifer-dominated, mixed-evergreen forests to oak woodlands and savannas (Stein 1990). We focused on the mixed-white oak and black oak woodlands that transition between open oak stands and closed mixed-hardwood conifer forest stands. Additional tree species of this region include California bay laurel (*Umbellularia californica*), Pacific madrone (*Arbutus menziesii*), white fir (*Abies concolor*), big leaf maple (*Acer macrophyllum*), canyon live oak (*Quercus chrysolepis*), and tanoak (*Notholithocarpus densiflorus*). The climate is temperate Mediterranean with cool, moist winters, and warm, dry summers.

Site selection and field sampling

Four sites were sampled in 2013 in contiguous woodland community types dominated by white oak and black oak, with Douglas-fir as the primary co-dominant species that ranged between 500 m and 1500 m in elevation (table 1), and excluded stands with visible signs of past harvesting and other major land use disturbances (in other words, mining) (fig.1). In each site, nine 0.1-ha circular plots were selected from randomly-generated locations and stratified by open-oak woodland (3 plots), transitional woodland-forest (3 plots) and closed mixed hardwood-conifer forest (3 plots) stand types based on visual assessment in the field. In each 0.1-ha plot, we tallied overstory (≥ 5 cm at 1.37 m above ground (DBH)) trees, each tree's DBH, and recorded the physical environment (slope, aspect, slope position, elevation). The 10 closest white and black oak trees from plot center were mapped and cored at 30-cm height above the root-shoot interface to determine tree age (Stokes and Smiley 1996). Multi-stem trees were tallied, and when cored, the largest stem was selected to determine the tree age. Additionally, the 10 closest evergreen conifer/hardwood tree species from plot center were also mapped and cored. Up to five of the largest and closest living trees outside of the plot were also cored in order to best estimate the oldest establishment dates within the sampling area. Within each 0.1-ha plot, we also tallied seedlings (<30 cm tall) and saplings (<5 cm DBH and >30 cm tall) by species using six randomly-located nested 2-m² plots and one nested 0.025-ha plot, respectively.

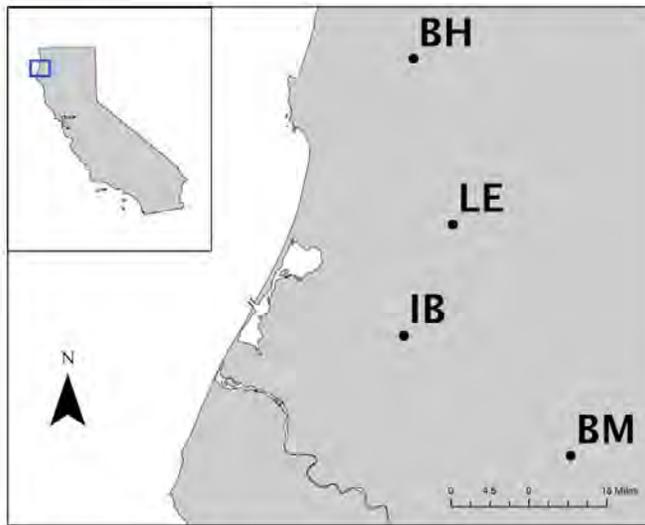


Figure 1—Study area in Humboldt County, California. Bald Hills (BH), Lord-Ellis Summit (LE), Iaqua Buttes (IB), and Blake Mountain (BM). (map credit: M. Eitzel)

Table 1—Site information for contiguous mixed-oak woodlands in northwestern California. Site codes come from USGS quadrangle maps

Site Name (Code)	Latitude (°N)	Longitude (°W)	Area (ha)	Elevation (m)	Aspect ^a	Slope (°)
Bald Hills (BH)	41.18	123.89	152	500	NW	15
Lord-Ellis Summit (LE)	40.90	123.79	162	600	W	20
Iaqua Buttes (IB)	40.71	123.90	86	750	S	25
Blake Mountain (BM)	40.51	123.53	169	1200	SW	15

^a Aspect: NW northwest, W west, S south, SW southwest.

Data analysis

Tree cores were mounted, sanded, and counted following standard dendrochronology techniques (Fritts 1979). When a tree core missed the pith a geometric model of annual tree growth was used to estimate the number of years to pith (Duncan 1989). Tree ages could be older than reported if seedlings or sprouts were browsed or lacked a single dominant stem dating to establishment (Hibbs and Yoder 1993), and due to the lack of correction for tree age at coring height. Thus, we summarized tree establishment dates into 20-year age bins. For oak trees annual growth was measured with a tree-ring scanning system (WinDendro software, Regent Instruments, version 2009b) in order to quantitatively crossdate annual ring widths using the COFECHA program (Holmes 1983).

At each site the proportion of tree establishment was examined for equal time periods prior to and during regional fire decline (a significant decline in fire frequency occurred around 1900 in nearby locations; Taylor and Skinner 1998). Fire is traditionally thought to have maintained oak woodlands in some locations; thus, altered fire regimes during the 20th century could have altered tree establishment dynamics. The youngest tree established in 2006, therefore this was our cutoff year for analysis. A chi-squared test was used to assess whether tree establishment was significantly different between tree types (in other words, oaks and evergreen conifer/hardwoods) prior to and during regional fire decline (1805-1904 and 1905-2006). All statistical analyses were conducted using R-studio.

Basal area (m² per hectare), stem density (trees per hectare), and sapling and seedling densities (per hectare) were calculated for each tree species in each stand type (in other words, open-oak woodland, transitional woodland-forest, closed mixed hardwood-conifer forest). Differences between basal area and stem density among stand types were examined using a one-way analysis of variance (ANOVA; $\alpha = 0.05$). A pair-wise t-test using the Bonferroni correction was used when stand type showed a significant effect. The median proportion of dead versus live tree stems were calculated for each oak species to assess the average oak-tree mortality in each stand type ($n = 12$ plots per stand type across four sites; 3 plots per stand type at each of the sites).

Results

Tree establishment patterns

In total, 672 trees were sampled for age structure. The youngest tree (Douglas-fir; site IB) was 7 years old and the oldest tree (black oak; site: BM) was over 316 years old. However, the oldest tree and other trees that had rotten centers were excluded from future analysis for tree age structure (16 percent of all cored trees, mostly oaks). Across all four sites, the median tree age of oaks was 132 years (range: 75 to over 316 years). The median tree age of Douglas-fir was 45 years (range: 6 to 125 years). Only 2 percent of cored trees composed of evergreen hardwood species (bay laurel and canyon live oak) whose median age was 35 years (range: 28 to 72 years).

Across all sites, the majority (75 percent) of live white oak and black oak trees established before regional fire decline (pre-1905), whereas the majority (97 percent) of evergreen conifer/hardwood trees established during regional fire decline (fig. 2; $\chi^2 = 310.777$, $df = 1$, p -value ≤ 0.001). Across all sites, the majority of oak trees established between 1850 and 1937. At a stand-scale, each site shows the majority of establishment occurred during a relatively short (~40 years) period of time (fig. 2). None of the oaks sampled established after 1937 at any of the sites. Douglas-fir trees established from 1890 to 2006 with the majority occurring after 1950 across all sites (fig. 2).

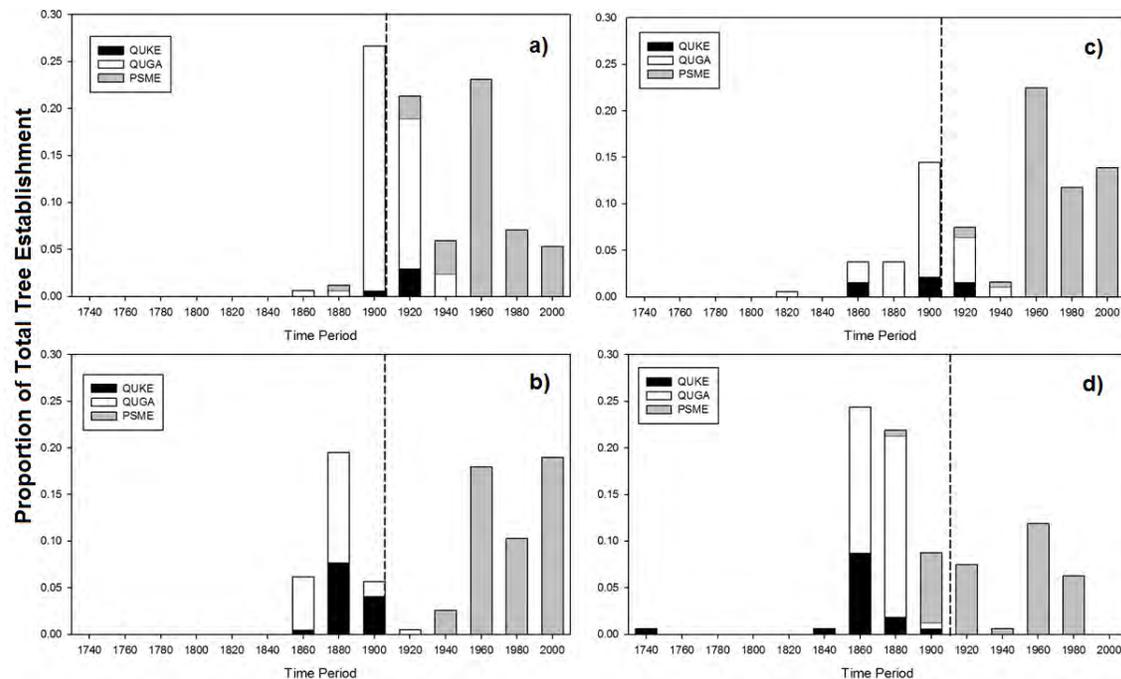


Figure 2—Proportion of tree establishment by tree species at each site (a) BH, b) LE, c) IB, and d) BM). Vertical-dashed line indicates the beginning of regional fire decline (1905). Species codes: QUKE, *Quercus kelloggii*; QUGA, *Q. garryana*; PSME, *Pseudotsuga menziesii*.

Stand structure

Across all sites, white oak, black oak, and Douglas-fir trees together accounted for 95 percent of the basal area on average. White oak had higher stem densities and basal areas than black oak across all stand types (fig. 3 a-d). Across sites, the median proportion of white oak and black oak tree mortality was 24 percent and 13 percent, respectively, and greater in closed vs. open stands (table 2). Predictively, Douglas-fir stem density and basal area was highest in closed-forest stands (fig. 3 e, f). Total basal area was greater in closed vs. open stands (fig. 3 h), but total stem density was not significantly different cross stand types (fig. 3 g). On average, open stands were composed of white oak (81 percent), black oak (12 percent), and Douglas-fir (7 percent); transitional stands were composed of white oak (38 percent), and black oak (14 percent), and Douglas-fir (45 percent); and closed stands were composed of white oak (17 percent), black oak (8 percent), Douglas-fir (72 percent), and evergreen-hardwood tree species (3 percent; tanoak, canyon live oak, and bay laurel).

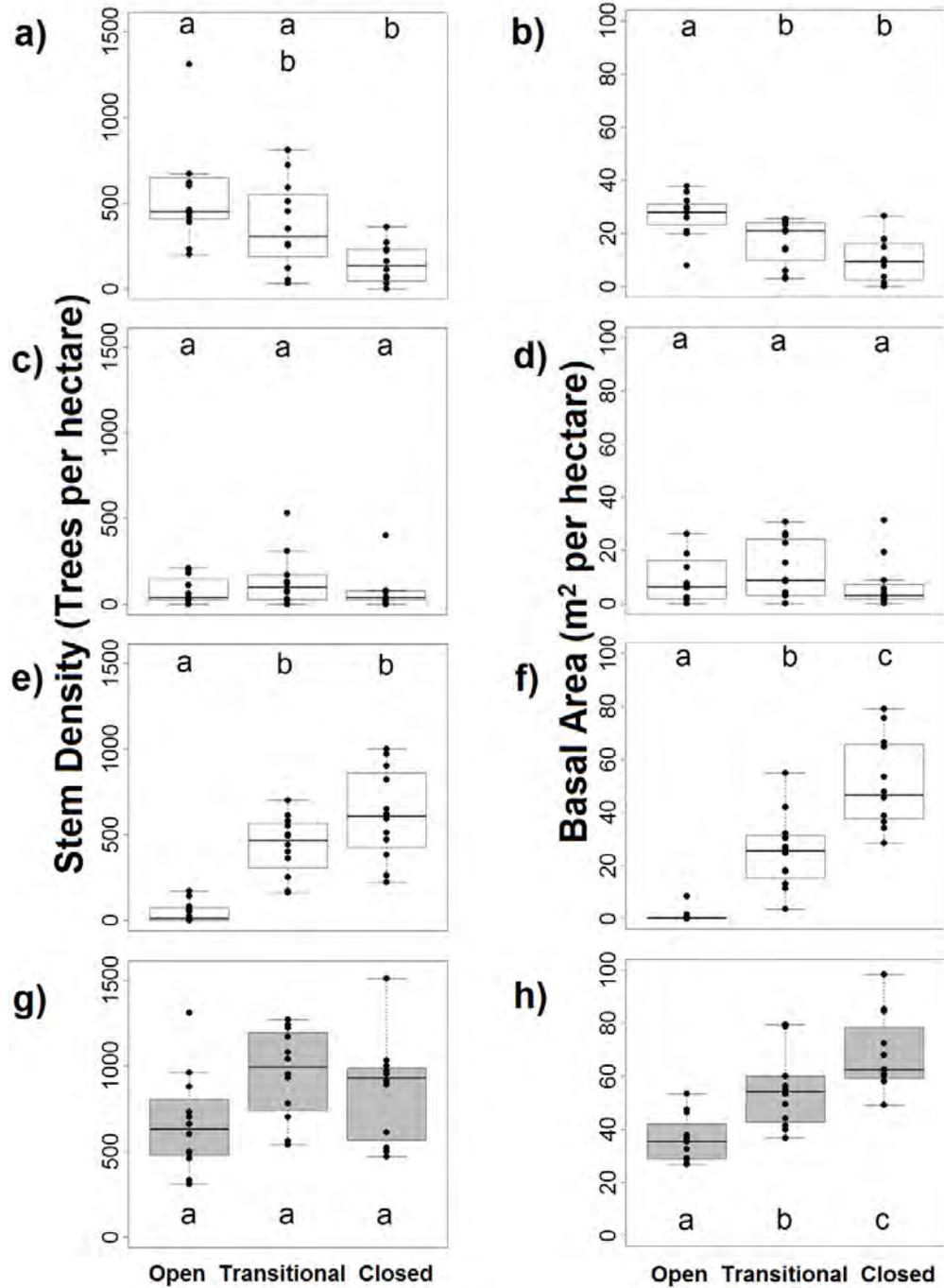


Figure 3 a-h—Stem density and basal area of live trees in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stands in northwestern California ($n = 12$ plots per stand type). Stem density and basal area measurements include white oak (a, b), black oak (c, d), Douglas-fir (e, f), and all tree species (g, h), respectively. In each graph variables with different letters indicate significant differences (Paired t-test, p -value < 0.05).

Table 2—Median proportion of dead Oregon white oak and California black oak trees in open-oak woodland, transitional woodland-forest, closed mixed hardwood-conifer forest, and across all stand types in northwestern California

Stand Type	Oregon white oak	California black oak
Open	0.14	0.10
Transitional	0.25	0.16
Closed	0.45	0.17
Across Stands	0.24	0.13

Current tree regeneration patterns

Density of oak seedlings varied the most between open and closed stands (fig. 4 a, c). White and black oak seedling densities were highest in open stands with white oak composing the vast majority (fig. 4 a, c). On average, seedlings in open stands were composed of white oak (84 percent), black oak (12 percent), and Douglas-fir (3 percent); seedlings in transitional stands were composed of white oak (49 percent), black oak (14 percent), Douglas-fir (26 percent), canyon live oak (5 percent), and bay laurel (5 percent); and seedlings in closed stands were composed of white oak (22 percent), black oak (18 percent), Douglas-fir (7 percent), canyon live oak (14 percent), bay laurel (11 percent), and tanoak (11 percent).

Sapling density did not vary between stand types (fig. 4 b, d, f, h). White and black oak sapling densities were low among all stand types (fig. 4 b, d). The proportion of evergreen conifer and hardwood species did vary between stand types. On average, saplings in open stands were composed of white oak (6 percent), black oak (2 percent), Douglas-fir (88 percent), and bay laurel (4 percent); saplings in transitional stands were composed of white oak (2 percent), Douglas-fir (54 percent), bay laurel (16 percent), and canyon live oak (28 percent); saplings in closed stands were composed of Douglas-fir (4 percent), bay laurel (2 percent), canyon live oak (83 percent), and tanoak (6 percent).

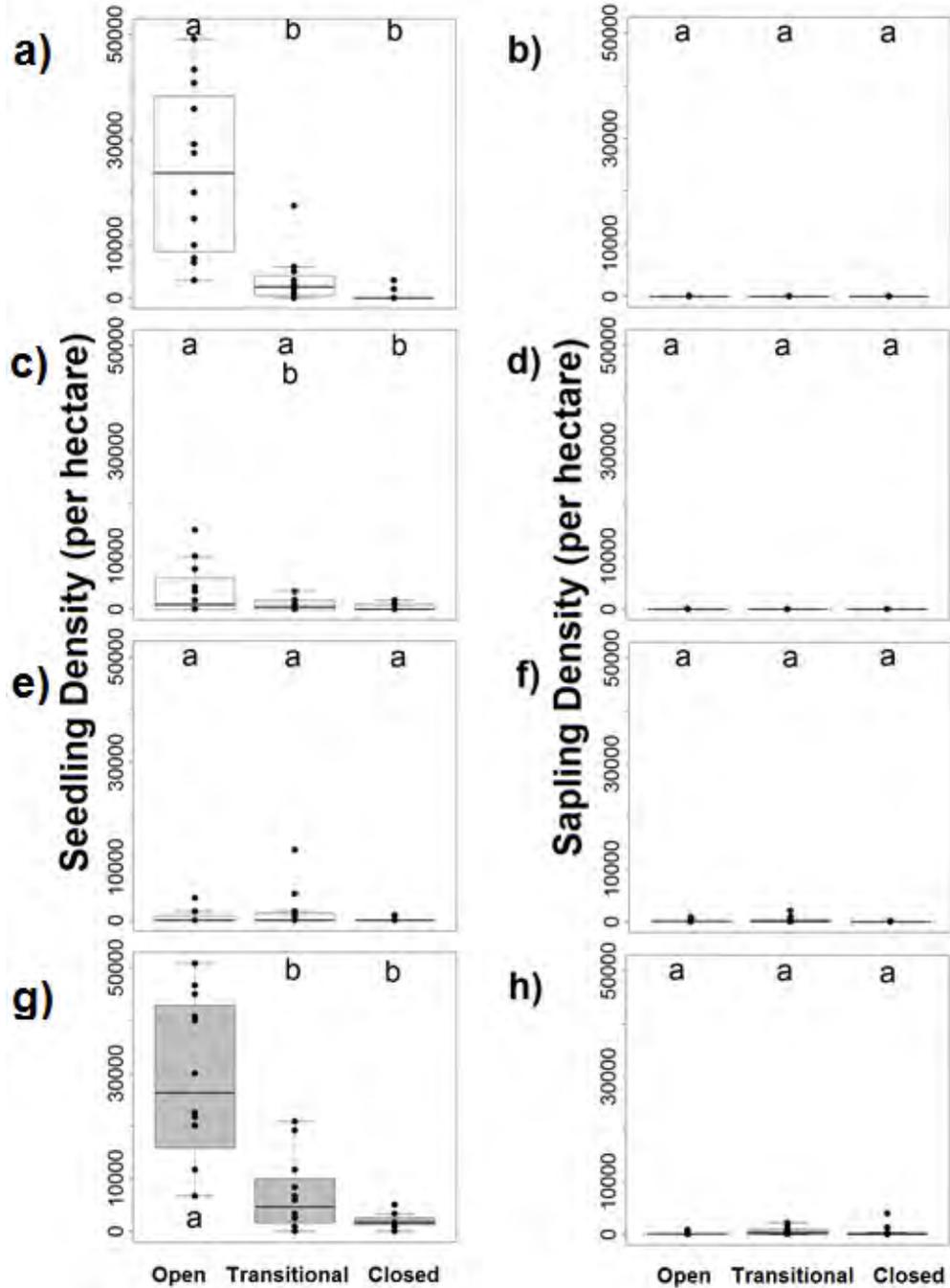


Figure 4 a-h—Density of live seedlings and saplings in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stand types in northwestern California ($n = 12$ plots per stand type). Seedling and sapling densities include white oak (a, b), black oak (c, d), Douglas-fir (e, f), and all species (g, h), respectively. In each graph variables with different letters indicate significant differences (Paired t-test, p -value < 0.05).

Discussion

Temporal patterns of oak and conifer establishment

Across all sites, most live Oregon white oak and California black oak trees established during the mid-to late 1800s, while most Douglas-fir trees established after 1950. These findings are consistent with age distributions of conifer-encroached Oregon white oak ecosystems in Oregon and Washington (Gedalof and others 2006, Gilligan and Muir 2011, Thilenius 1968). Plot-level age distributions within sites indicated varying temporal periods of stand-initiation. Across all plots at individual sites, most oaks established over a relatively narrow period of time (40 years) suggesting a stand-level disturbance during the mid-to late 1800s that promoted regeneration. Less commonly (6 percent of plots; only located at site: IB), oaks established over a longer period of time (100 years) indicating evidence of more localized stand-initiation events. Stand-scale disturbances triggering establishment events may have been fire, livestock grazing, reduced anthropogenic burning (Gedalof and others 2006, Gilligan and Muir 2011), in addition to a favorable climate conditions for tree establishment (Duren and Muir 2012). However, there is a lack of information on the disturbance history at this time needed to evaluate the mechanisms for recruitment.

Stand structure in mixed oak-conifer woodlands

The higher proportion of oak-tree mortality in closed-forest stands suggests low-light conditions are highly unfavorable for oak trees. Where Douglas-fir trees overtop hardwood trees, research has shown reduced growth rates and eventual hardwood tree mortality due to shade intolerance (Hunter and Barbour 2001). While both oak species have higher proportions of mortality in closed-canopy conditions, the lower proportion of California black oak mortality in closed-canopy stands suggests a higher tolerance of low-light conditions than Oregon white oak. This may be due to California black oak's ability to persist in conifer-dominant stands depending on environmental factors, such as soil type and topography (Taylor and Skinner 1998), which have yet to be investigated in these stands.

Regeneration

The lower density of oak seedlings in closed stands compared to open stands supports findings that Oregon white oak seedling survival is strongly associated with open-canopy conditions (Gedalof and others 2006, Thysell and Carey 2001). Low levels of Oregon white oak regeneration for the past half-century have also been noted in Oregon and Washington (Fuchs and others 2000, Gedalof and others 2006, Gilligan and Muir 2011). While the presence of Douglas-fir overstory likely reduces oak regeneration by limiting light resources, there is also a paucity of oak saplings in open stands. For example, the open-oak stands had the highest oak seedling densities but few saplings (99.99 percent reduction) on average, suggesting other limiting factors also contribute to the lack of oak regeneration.

In dry habitats with limited soil moisture, Oregon white oak seedling survival is reduced by herbaceous vegetation dominated by grasses (Devine and others 2007b, Fuchs and others 2000). Due to their fibrous root system, grasses can outcompete oak seedlings for soil water causing oak seedling desiccation and mortality. When grass

cover is controlled, oak seedlings grow more vigorously which allow them to grow above the height of animal browse (Devine and others 2007b).

On-going research

In the face of changing climate patterns and related drought stress (van Mantgem and others 2009), understanding these trends in context of biophysical interactions is important. Further investigations are necessary to evaluate if these findings are consistent across the North Coast region of California. Additional research will also explore if the trends in age, composition, and regeneration between stand types relate to environmental factors (soil type and topography). Recent conifer establishment into oak woodlands could be limited to mesic environments (for example, in and near drainages). Lastly, researchers will examine the interaction between stand structure and tree growth relationship to climate variability.

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