CONIFER ENCROACHMENT AND REMOVAL IN A NORTHERN CALIFORNIA OAK WOODLAND: INFLUENCES ON ECOSYSTEM PHYSIOLOGY AND BIODIVERSITY

By

Gabriel Steffen Goff

A Thesis Presented to
The Faculty of Humboldt State University
In Partial Fulfillment of the Requirements for the Degree
Master of Science in Natural Resources: Forestry, Watershed, and Wildland Sciences

Committee Membership
Dr. Lucy P. Kerhoulas, Committee Chair
Dr. Nicholas J. Kerhoulas, Committee Member
Dr. Jeffrey M. Kane, Committee Member
Dr. Erin C. Kelly, Program Graduate Coordinator

May 2021

ABSTRACT

CONIFER ENCROACHMENT AND REMOVAL IN A NORTHERN CALIFORNIA OAK WOODLAND: INFLUENCES ON ECOSYSTEM PHYSIOLOGY AND BIODIVERSITY

Gabriel Steffen Goff

Oregon white oak (*Quercus garryana*) woodlands across their range are becoming increasingly threatened by encroaching Douglas-fir encroachment (*Pseudotsuga menziesii*) as a result of fire exclusion. Using water potential (Ψ), stomatal conductance (g_s), xylem water stable isotopes (δD), and three metrics of biodiversity, this study investigates the effects of conifer encroachment and removal at the ecosystem-scale. The study was set in an Oregon white oak woodland in northern California and compared three levels of encroachment before and after conifer removal. Findings indicate that heavily encroached stands have the least amount of water stress and gas exchange. A moderate level of conifer encroachment appears to buffer water stress and support high productivity throughout the growing season. Trends in Ψ and g_s suggest that coniferous shade improves oak water status via reduced evapotranspiration but limits productivity. Further, xylem water δD confirms that oaks and Douglas-firs are likely not directly competing for water, as oaks appear to use a relatively deeper water source. Thus, physiological results indicate that oak mortality to encroachment is likely light due to light, not water, limitation. Following conifer removal, moderately encroached stands did not respond dramatically during the first and second post-treatment years. However, heavily encroached stands increased gas exchange in both post-treatment years compared to unthinned counterparts. For ecosystem biodiversity, plant and bird diversity did not meaningfully differ among encroachment levels or between treatments, but mammal diversity was greatest in encroached stands. Collectively, findings from this work demonstrate that conifer removal is physiologically beneficial for light-limited oaks and that heavier thinning treatments are likely needed to yield long-term responses and influence biodiversity.

ACKNOWLEDGEMENTS

This research would not have been possible without those who came before me on this landscape, those who tended to and shaped its forms since time immemorial. This study was carried out on the traditional homelands of the Wiyot, Whilkut, and Nongatl people. I have enjoyed the company of many fine people while conducting this research project, and without them this whole thing really falls apart at the seams. First and foremost, I thank my parents Kristin and Adam for their unending support; they've made so many things possible for me in this life. My brother Kaleb, who has guided me as a naturalist, scientist, and member of the biotic community for many years now. Of course, all great projects have their mentors, and for that I thank Lucy and Nick Kerhoulas. We've become great friends over the years, spent many a lucid overnighter together in the woods, and are possibly the foremost leaf collectors using ground techniques in Northern California. Furthermore, I thank Jeff Kane, who kindly helped with the many steps of data analysis; your guidance was critical in completing this work. Also, a big thanks to Wade Polda for listening to the birds for us. Furthermore, many thanks to all of the folks who helped with my field work over the years: Kevin Soland, James Lamping, Chance Callahan, Tossa Hayward, Michelle Kunst, and others. Finally, this project would not have been possible without funding from the CSU Agricultural Research Institute, USDA McIntire-Stennis Program (CALZ-164), California Native Plant Society, and space to work on Humboldt Redwood Company property.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Oaks are an important group of plants in the Northern Hemisphere and dominate many forest types within their range (Nixon 2002). Oak-dominated landscapes are essential ecological and cultural resources and support some of the highest biodiversity of any terrestrial ecosystem in California (Bernhardt and Swiecki 2001). Oregon white oak (*Quercus garryana* Doug. Ex Hook.) is one of the dominant oak species in Northern California and is archetypal to the region's landscape. These landscapes are immensely important to local Native people who have been managing them for centuries through burning and clearing (Lightfoot and Parrish 2009). Before the onset of attempted cultural genocide, burning was used to promote diversity of understory plants, facilitate the production of basketry materials, deplete insect populations affecting acorn harvest, and provide habitat for a host of species (Kimmerer and Lake 2001, Underwood *et al.* 2003, Lightfoot and Parrish 2009). These burning practices promoted heterogeneous stand structures that were relatively resilient to subsequent fires and provided conditions that promoted plant diversity (Underwood *et al.* 2003, Long *et al.* 2017). Fire is a significant determining factor in the structure and composition of oak ecosystems (Bond and Keeley 2005); in Northern California, Oregon white oak woodlands have evolved with frequent, low-intensity surface fires (Agee 1998). The high frequency, low-intensity fire regimes that characterize this ecosystem prohibited fire-sensitive species from establishing (Engber and Varner 2012).

Under conditions supported by a traditional fire regime, Oregon white oak woodlands are composed of widely spaced, broad-crowned oaks with a predominantly fire-tolerant understory (Devine *et al.* 2007a). However, when fire is excluded from these systems, structural and compositional changes occur and fire sensitive species are favored (Devine *et al.* 2007a, Engber *et al.* 2011). Without fire, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) conifer saplings have the opportunity to establish and grow, eventually overtopping oaks and leading to oak growth reductions, crown dieback, and mortality (Agee 1998, Devine and Harrington 2006, Engber *et al.* 2011). The result of this type of encroachment is a transition from more open woodland conditions to a closed canopy composed primarily of Douglas-fir (Engber *et al.* 2011, Cocking *et al.* 2012). These impacts are widespread, as Oregon white oak communities are declining between central California and southern British Columbia (Thysell and Carey 2001a, Gedalof *et al.* 2006, Gilligan and Muir 2011). In Northern California, oak woodland habitat has been reduced by as much as 30% due to conifer encroachment (Fritschle 2008). Restoring these landscapes to oak-dominated conditions requires the prioritized retention of existing oak trees coupled with the removal of conifers to release oaks from resource competition (Devine and Harrington 2006, Devine *et al.* 2007a).

Although a number of studies have focused on the growth and understory diversity responses of Oregon white oak woodlands to restoration (Devine and Harrington 2006, 2013, Devine *et al.* 2007a, Livingston *et al.* 2016) and recent ecophysiological research has been used to understand Oregon white oak tolerance to water limitations under natural conditions (Hahm *et al.* 2018), few have investigated responses to restoration at the physiological level. While growth can be used to understand long-term oak responses to treatment, physiological measurements have the potential to detect short-term responses and provide valuable insights about mechanisms underlying growth responses (Skov *et al.* 2004). Stomata on the leaf surface effectively function like a pressure regulator by controlling transpiration (Sperry *et al.* 2002). Stomatal conductance (g_s), which is strongly positively correlated with photosynthesis, is regulated by plant water potential (Ψ) and other environmental factors such as light, air temperature, and vapor pressure deficit (VPD) (Sperry 2000, Augé *et al.* 2001, Sperry *et al.* 2002). Predawn (Ψ_{PD}) and midday (Ψ_{MD}) Ψ, respectively represent the most hydrated and stressed tree water status within a daily period; Ψ_{PD} can be thought of as a surrogate to soil water potential, as trees equilibrate with available soil water overnight. At extremely low Ψ, the threat of embolisms and thus reduced hydraulic conductivity and productivity increases (Tyree and Sperry 1989). Ring-porous species like Oregon white oak produce different sizes of xylem vessels across the growing season: early in the season, they put on a ring of large vessels followed later in the season by a narrower and more dispersed ring of vessels (Taneda and Sperry 2008). For ring-porous species, the early growing season is therefore very important because this is when the primary water conduits for the entire year are created (Ellmore and Ewers 1986, Barbaroux and Bréda 2002). Xylem vessel properties contribute to whole-tree Ψ, which has a strong influence on stomatal regulation via turgor pressure (Tyree and Sperry 1989). Trees regulate their stomata on a continuum between isohydry and anisohydry, where stomatal regulation is largely influenced by interactions with the surrounding environment (Hochberg *et al.* 2018). Isohydric species maintain mostly consistent minimum Ψ, whereas anisohydric species will display larger decreases in Ψ (Tardieu and Simonneau 1998, Klein 2014). Differences in stomatal regulation strategy can have a large influence on plants' ability to survive adverse environmental conditions (McDowell *et al.* 2008, 2010, Klein 2014). Conifer encroachment will likely influence stomatal regulation via competition for light and water shifting relative humidity, VPD, and rates of ecosystem water loss through evapotranspiration. Furthermore, recent work suggests that due to a greater tolerance of water limitation and stressful environmental conditions, Oregon white oak will be an increasingly more important species than Douglas-fir in these ecosystems as the climate continues to warm (Hahm *et al.* 2018, Beckmann *et al.* 2021).

Given recent increases in drought severity and frequency (Swain *et al.* 2018), understanding interspecific competition for water can provide valuable insights about the effects of conifer encroachment on oaks. The complex dynamics among the overstory, evapotranspiration rates, tree physiology, and increasing regional drought begs the question: Are Oregon white oak and Douglas-fir competing for water from the same sources in the soil profile? Stable isotope analyses of water sources and xylem waters are an effective way to understand interactions among plants and the biotic and abiotic environments (Dawson *et al.* 2002) and to identify plant water sources (Ehleringer and Dawson 1992, Dawson 1993, Ehleringer *et al.* 2000). For example, the stable isotope composition of xylem water from a desert in southern Utah indicated that different plant groups used different sources of water seasonally, with woody perennial species being the least dependent on summer rainfall (Ehleringer *et al.* 1991). Similarly, stable isotope analyses demonstrated that sugar maple (*Acer saccharum* Marsh.) can hydraulically lift and redistribute deep groundwater to the upper soil profiles (Dawson 1993). Generally, groundwater represents a long-term pool of local rainfall and is relatively depleted of heavy stable isotopes (D and ^{18}O) such that it has a “light” isotopic signature; in contrast, precipitation is relatively enriched with heavy stable isotopes and therefore has a “heavy” isotopic signature (Dawson *et al.* 2002). Further, within the soil profile, water isotopic signatures decrease due to greater evaporative enrichment in surface soils (Kerhoulas *et al.* 2013). Thus, because water sources can vary isotopically, xylem sap water can identify variations in source water used by different species in an ecosystem (Ehleringer and Dawson 1992). Analyzing stable isotopes in tandem with other plant-water metrics (e.g., Ψ and g_s) offers a powerful lens to improve our understanding about how interspecific competition for essential resources impacts plant performance (Ehleringer and Dawson 1992).

The California floristic province is a biodiversity hotspot that supports an impressive collection of endemic species (Myers *et al.* 2010). Oak woodlands in California represent some of the most species-rich habitats in the state, harboring more than 300 vertebrate species and over 2,000 species of plants (Barbour and Keeler-Wolf, 2007). One of the primary driving forces behind such high levels of diversity in these Mediterranean oak woodlands is a heterogeneous mixture of vegetation conditions that supports a wide range of physical attributes (snags, large woody debris, multiple species cohorts, etc.) for many types of organisms (Walter *et al.* 2013). As conifer encroachment disrupts the historical patterns of stand structure and succession across the landscape, it prompts us to understand how these changed conditions alter understory plant, avian, and mammal populations. However, few studies have attempted to quantify oak woodland diversity under encroached or restored conditions. Related to plant diversity, previous work suggests that in Oregon white oak woodland understories, restoration thinning of encroaching conifers has little effect on native species' cover and can actually increase the abundance of non-native species (Devine *et al.* 2007a). However, related to avian diversity, previous work demonstrates that shifting understory vegetation back to open oak woodlands can increase favorable nesting habitats and therefore the abundance of native songbirds such as Western Kingbirds (*Tyrannus verticalis*), Western Bluebirds (*Sialia mexicana*), and Violet-green Swallows (*Tachycineta thalassina*) (Purcell and Stephens 2005). While quantification of diversity is necessary to adequately assess the benefits of restoration treatments to the whole biotic community, it is crucial to determine the type of diversity fostered. If restoration treatments increase the proportion of non-native or invasive species to native, non-invasive ones, the overall efficacy of the project must be closely evaluated.

The objectives of this study were to 1) understand the physiological effects of conifer encroachment and subsequent removal on Oregon white oak, 2) determine if there is a difference in source water used by conifers and oaks, and 3) assess how plant, mammal, and avian biodiversity vary under different levels of conifer encroachment and removal. Correspondingly, the research questions for this study were: 1) How do oak Ψ and g_s vary across the growing season? 2) How do oak Ψ and g_s vary among encroachment levels? 3) How do physiological responses to conifer removal compare between moderately and heavily encroached oaks? 4) Do Oregon white oak and Douglas-fir compete for water? 5) How does biodiversity of understory plants, mammals, and birds vary among encroachment levels and between thinned and unthinned stands and how does it change with time-since-thinning? Ultimately, these results will be important in understanding the mechanisms leading to oak mortality under encroached conditions, and how oaks respond immediately to conifer removal.

MATERIALS AND METHODS

Study Site

The study site is located in the Iaqua Buttes area near Kneeland, CA, approximately 30 km from the coast at roughly 830 m elevation (Figure 1). The two dominant tree species are Oregon white oak and Douglas-fir, with other tree species including Pacific madrone (*Arbutus menziesii* Pursh.), tanoak (*Notholithocarpus densiflorus* Hook. & Arn.), California black oak (*Quercus kelloggii* Newb.), and California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.). Exhibiting characteristics of a Mediterranean climate, the site receives roughly 127 to 139 cm of rainfall annually (NOAA, 2018), nearly all of which fall during the winter months, and temperatures which range from 4 to 24 °C. Fire has been systematically suppressed at this site since the early 1900's, until recent prescribed fire in late 2019 (California Department of Forestry and Fire Protection, 2017). Historically, this site was an open oak woodland consisting of clumps of oak and open grasslands (Figure 2). Douglas-fir was not a prevalent species at this site until the late 20th century, whereas Oregon white oak establishment dates back to the mid 1800's (Schriver *et al.* 2018). This area sits within the Franciscan Complex portion of the Coast Range, where rocks are primarily sedimentary and meta-sedimentary. The soils consist of fine-loamy alfisols in the Elkcamp series and fine, mixed mollisols in the Kinman series, and are often shallow (UC Davis CSRL, 2018). Data were collected in 2017, 2018, and 2019. Between the

2017 and 2018 growing seasons some plots were thinned utilizing both variable retention and single-tree removal techniques. The goal of the treatment was to remove conifers with a diameter at breast height (1.37 m; DBH) greater than 25 cm. However, the timber harvest did not end up removing all of the marked timber during this thinning treatment, so conifer removal was generally light across the study site.

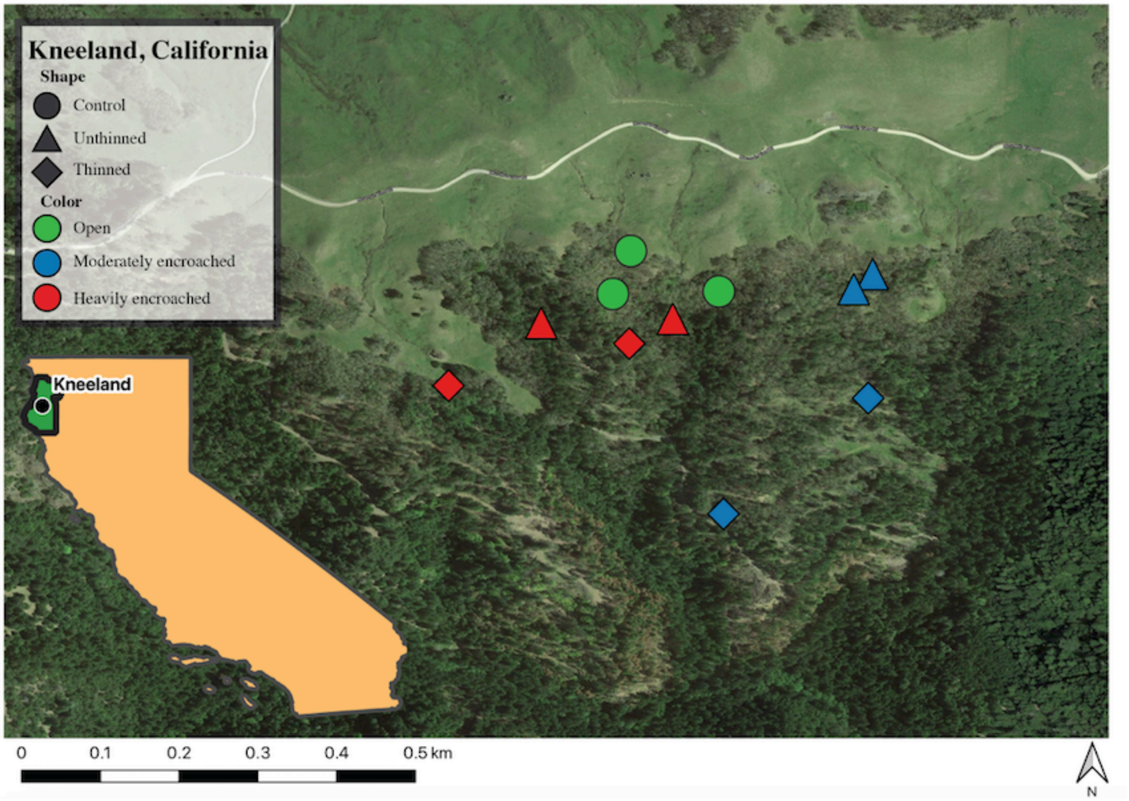

Figure 1. *Study plots (0.1 ha) in an Oregon white oak woodland under three levels of conifer encroachment (open, moderate, heavy) in Kneeland, CA.*

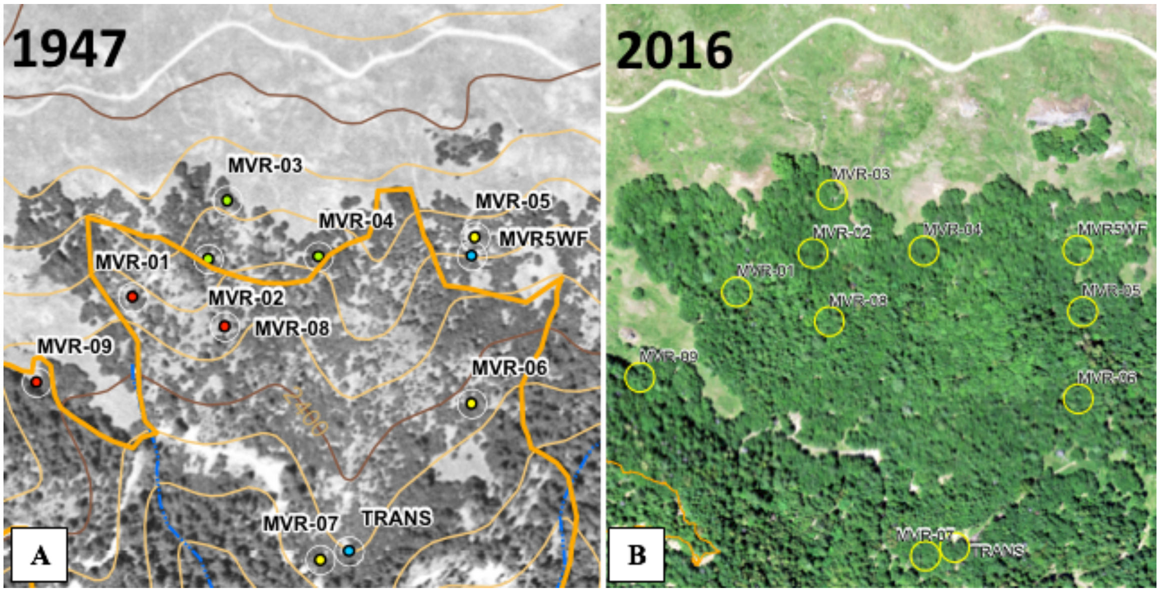

Figure 2. *Study site in Kneeland, CA displaying the encroachment of open oak woodland between 1947 (A) and 2016 (B). Study plot locations on this map represent plots used by previous research, our study utilized a combination of these existing plots, and newly established ones.*

Study Design

The study used a total of ten 0.1 ha circular plots (radius = 17.8 m): two open (unencroached) plots, two moderately encroached unthinned plots, two moderately encroached thinned plots, two heavily encroached unthinned plots, and two heavily encroached thinned plots distributed at varying positions on the slope. In 2017, sampling used nine plots (three per encroachment level). However, in 2018 and 2019, two plots from 2017 were abandoned and two new plots were established due to study trees being damaged during conifer removal treatments and the need for replicates of each encroachment-treatment combination. Although the variability of slope position among plots could have affected plot-level soil moisture and water holding capacity, a soils analysis at this site found that these characteristics did not significantly vary with slope position (Marshall 2017). Plot centers were randomly chosen across the study area and encroachment levels were qualitatively assigned to each plot: open plots had no Douglas-fir in the oak canopy, moderately encroached plots were oak-dominant with Douglas-fir in the canopy, and heavily encroached plots had dominant Douglas-fir trees overtopping oaks (Figure 3). Within each plot, the ten oaks closest to plot center that were pole pruneable and healthy were selected as study trees. Pole pruneability was determined visually in the field and was defined as a maximum live crown base height of approximately 15 m. If there were not ten suitable oaks within the plot boundaries, trees were selected from just outside. For each study tree, diameter at breast height (DBH), crown ratio (CR), the number of stems, and local basal area density (BA) were measured; a prism with a BAF of 20 was used to measure BA. For multi-stemmed oaks, the crown of the largest stem was used for physiological measurements.

Across all study plots, a total of 100 individual oaks were sampled under various levels of encroachment and treatment (

Table 1). All study plots started with 10 study trees. However, between years and at varying points during the growing season, some study trees experienced mortality and some crowns receded beyond a pole prunable height. For this reason, the sample size is not perfectly equal among encroachment levels, and between treatments. The following plot-level results are based on measurements made in summer 2019, after the fall 2017 thinning treatment. Across all plots, mean oak DBH was 30 ± 2 cm, BA density was 124

± 17 m^2 ha^{-1}, and A_L per oak was 178 ± 11 m^2. Oak DBH was not different among encroachment levels ($p = 0.71$, $F = 0.34$), but was slightly higher in thinned plots compared to unthinned plots ($p = 0.02$, $F = 5.61$). Basal area density was higher in heavily encroached stands than in moderately encroached or open stands ($p < 0.0001$, $F = 18.86$) and also was higher in unthinned stands than in thinned stands ($p = 0.02$, $F = 6.07$). Tree-level A_L did not significantly differ among encroachment levels ($p = 0.71$, $F = 0.34$) but was slightly higher in thinned plots compared to unthinned plots ($p = 0.02$, $F = 5.61$). All physiological results for annual comparisons between 2017 and 2018 are based on July through October measurements, as May and June data were not collected in 2017.

Table 1. *Site and tree characteristics (mean ± SE) for Oregon white oaks in Kneeland, CA in 2019: aspect, slope, diameter at breast height (DBH), basal area density (BA), leaf area per tree (A_L), and* N *(number of trees). For each encroachment/treatment combination, two 0.10 ha plots were studied, for a total of 10 plots. Two-Way ANOVA* p*-values are provided to test for significant differences in DBH, BA, and LA among encroachment levels (open, moderate, heavy) and between treatments (thinned, unthinned) for moderate and heavy encroached plots.*

Encroachment	**Treatment**	**Aspect**	**Slope (%)**	**DBH (cm)**	**BA (m^2 ha^{-1})**	**A_L (m^2 $tree^{-1}$)**	***N* (Trees)**
Open	Control	SE	36	31 ± 3	83 ± 5	186 ± 19	19
Moderate	Unthinned	SE	54	24 ± 2	115 ± 8	142 ± 12	19
Moderate	Thinned	S	35	34 ± 4	95 ± 9	208 ± 27	20
Heavy	Unthinned	S	47	29 ± 5	180 ± 16	173 ± 37	17
Heavy	Thinned	E	22	30 ± 2	146 ± 12	183 ± 15	19
All Plots			39	30 ± 2	124 ± 17	178 ± 11	94
p (Encroachment)				0.71	< 0.0001	0.71	
p (Treatment)				0.02	0.02	0.02	

Figure 3. *Oregon white oak stands with no conifer encroachment (A), and under heavily encroached stand conditions (B) in Kneeland, CA.*

Physiology Sampling

During the 2017, 2018, and 2019 growing seasons (May-October), Ψ and g_s were measured monthly in all study trees over two to three consecutive sunny days; in 2017, no measurements were taken in May and June due to a delayed study start. In the predawn (0200-0500), leaf Ψ_{PD} was measured using a pressure chamber (Model 600, PMS Instruments, Corvallis, OR) and at midday (1030-1400), leaf Ψ_{MD} and g_s were measured using a pressure chamber and leaf porometer (SC-1, Decagon Devices Inc., Pullman, WA), respectively. All samples were collected from the lower crown using a pole pruner, with midday samples taken from fully illuminated portions of the crown as possible (this was often difficult in heavily encroached sites due to high live crown bases). Once a small branch was pruned from the crown, three to five Ψ measurements were taken from different sub-branchlets and averaged into one value. At midday, in addition to leaf Ψ measurements on each pruned branch, three g_s measurements were taken from different leaves and averaged into one value.

To understand the implications of gas exchange measurements on whole-tree productivity, leaf-level gas exchange measurements were scaled to the whole-tree level. To do this, the total leaf area (A_L, m^2 $tree^{-1}$) for each study tree was first calculated using an allometric equation relating oak and beech DBH to total A_L (Le Dantec *et al.* 2000). Leaf-level g_s measurements (mmol H_2O m^{-2} s^{-1}) were then multiplied by A_L (m^2) to calculate crown-level stomatal conductance (G_s), or the rate of H_2O leaving leaf surfaces across each study tree crown (mol H_2O $tree^{-1}$ s^{-1}).

During the 2019 growing season, stem psychrometers (Model PSY1, ITC International, Australia) were used to continuously measure stem xylem Ψ during the middle of August. These measurements were conducted on one tree per plot that was closest to average tree diameter across the entire study site. Stem psychrometers ran for a total of two weeks, yielding a roughly eight-day period of time where continuous Ψ values were usable (July 29th – August 5th, 2019). Two five-hour time periods were identified during each 24-hour period as encompassing the highest (pre-dawn, 0000 - 0500) and lowest (midday, 1130 - 1630) Ψ values.

Isotopic Analysis

To determine the source water for Oregon white oak and Douglas-fir trees, small twig samples for xylem water analysis were collected during August 2018, a hydraulically stressful time in the growing season. At each plot, a pole pruner was used to collect small branches from the five white oaks closest to plot center; small branches were also collected from the Douglas-fir tree closest to each sampled oak. The small branches excised from each tree were cut into small sections (approximately 1 x 7 cm); bark was then removed from these short segments and twigs were placed into a glass vial with a screw top lid, wrapped with a wax film (Parafilm; Pechiney Plastic Packaging, Chicago, IL), stored in a dark cool bag, and transported to a -20 °C freezer in the Humboldt State University (HSU) Core Lab until ready for water extraction. Water from each sample ($n = 100$) was extracted using the cryogenic vacuum extraction line in the HSU Forest Physiology Lab and then sent to the University of New Mexico Center for Stable Isotopes for δD and $\delta^{18}O$ analysis via wavelength-scanned cavity ring-down spectroscopy (PL1102-I Water Isotope Analyzer, Picarro Inc., Santa Clara, CA) using a micro-combustion module to eliminate interference with organic solutes in plant water samples.

Biodiversity Sampling

In July of 2018 and 2019, subplots were used to assess understory plant diversity. Within each 0.1 ha plot, six circular 1 m^2 subplots were placed using a random azimuth and random distance from plot center. Within each subplot, the following information was recorded: slope, aspect, species present, and cover class for each species present using modified Daubenmire cover classes adapted from the UC Cooperative Extension methods (Lenya Quinn-Davidson, Unpublished Data). Cover class categories for each species present within each subplot were as follows: 1 = 0-1%, 2 = 2-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75%, 6 = 76-95%, and 7 = 96-100%. Cover values were for all plants under 1 m tall rooted in or hanging over the subplot boundary. Dead portions of living plants were considered live. Samples of each species present were collected and bagged for later identification.

To evaluate mammal abundance and diversity (IACUC No. 17/18.FWR.37-A), camera traps were used. In October of 2018 and 2019, three camera traps (ENKEEO PH770) were installed at 1 m height on a rebar stake at 0°, 120° and 240° 10 m away from plot center facing outwards at each study plot. Camera traps were out for three weeks and checked approximately every week. In 2018, use of Sherman live traps to quantify small mammal diversity was attempted, but this method was aborted due to bear activity destroying traps. Data were used to calculate indices of diversity and abundance (see below) and evaluate possible effects of conifer encroachment and removal on mammalian communities.

To evaluate bird abundance and biodiversity, point count surveys were used. More specifically, in each 0.1 ha plot, three consecutive 10 minute surveys were conducted within 5 hours after sunrise during May and June of 2018 and 2019. All avian species were identified by sight and sound. One individual (Wade Polda) conducted all avian surveys to control for variation in species identification. Using these data, species richness and abundance indices were calculated (see below) and used to investigate the influence of conifer encroachment and removal on avian communities.

For the 10 study plots, diversity was evaluated among encroachment levels and between thinned and unthinned stands for both sampling years using three metrics. These metrics included species richness (S, a sum of species present), species evenness (E) calculated using the following equation:

$$E = 1 - \frac{\sum_{i=1}^{S} n_i(n_i - 1)}{N(N - 1)}$$

and the Shannon – Wiener diversity index (H') using the following equation:

$$H' = -\sum_{i=1}^{S} \frac{n_i}{N} * ln\frac{n_i}{N}$$

where n_i equals the relative cover/sightings for each species, and N equals the total number of species.

Data Analysis

All statistical analyses were conducted using R statistical software (RCore Team, 2020). To investigate the differences in oak tree and stand structural components (DBH, BA, A_L) among plots, 2-way ANOVA tests were conducted (*n* = 98). Paired *t*-tests, and 2-way ANOVA were used to test for differences in xylem water isotopic signature between paired oak and Douglas-fir (*n* = 56). Linear mixed effects (LME, package *lme4*) and generalized linear mixed effects (GLME, gamma distribution, package *lme4*) models were used to investigate the effects of year, seasonality, encroachment level, thinning treatment, and all possible interactions on Ψ, g_s, G_s (with random effects of plot and tree), and three indices of biodiversity (S, E, H') among plants, mammals, and birds (with random effect of plot). To investigate the effects of encroachment (*n* = 650) and treatment (*n* = 628) on leaf Ψ in 2017 and 2018, May and June were excluded from 2018 because they were not measured in 2017. To analyze the effects of encroachment (*n* = 620) and treatment (*n* = 208) on g_s and G_s, data from 2018 and 2019 were used, as these two years had measurements from all months of the growing season. All analyses investigating encroachment effects excluded thinned stands to avoid any influence of treatment. Analyses investigating treatment effects excluded data from May and June in 2018 and 2019 due to these months being missing in 2017; however, the model considered all three growing seasons (2017, 2018, 2019). Open stands were also excluded from analyses of treatment effects as no thinning occurred at these sites across the duration of the study. To account for repeated measurements on the same individual oak throughout the duration of the study period, a random term of plot and tree was used to account for the lack of independence. To determine differences between groups where interactions existed, Tukey's multiple comparisons were used (package *emmeans*). Model selection was conducted by comparing all model combinations to a null model, and then using Akaike information criterion (AIC) values to determine the best model. Model assumptions were assessed graphically for violations of homogeneity of variance, and normality.

RESULTS

Water Potential

Encroachment Effects

Pre-dawn leaf water potential

Woodland encroachment by conifers influenced leaf Ψ_{PD} across multiple time scales (Figure 4, **Error! Reference source not found.**). A linear mixed effects model investigating the influence of encroachment level, month, and year on Ψ_{PD} found that encroachment level was a determining factor of Ψ_{PD} ($p < 0.0001$, $F = 46.66$) across multiple years ($p < 0.0001$, $F = 239.20$), and among months within those years ($p < 0.0001$, $F = 468.90$). Furthermore, interactions existed between encroachment level and month ($p < 0.001$, $F = 30.27$), as well as between encroachment level and year ($p = 0.003$, $F = 6.01$).

For leaf $\Psi_{PD,}$ the effect of encroachment level was different between 2017 and 2018. In 2017, leaf Ψ_{PD} was higher than in 2018 ($p < 0.0001$, $t = 15.41$) and was higher in heavily encroached stands compared to moderately encroached ($p < 0.0001$, $t = 6.77$) and open ($p < 0.0001$, $t = 6.55$) stands. In 2018, heavily encroached stands again had higher Ψ_{PD} than moderately encroached ($p = 0.0001$, $t = 4.259$) and open ($p < 0.0001$, $t = 7.995$) stands and moderately encroached stands had higher Ψ_{PD} than open stands ($p = 0.001$, $t = 3.80$).

Monthly trends in leaf Ψ_{PD} among encroachment levels were quite similar across the 2017 and 2018 growing seasons. Early in the growing season (May and June of 2018), there was little difference in Ψ_{PD} among encroachment levels. As stands progressed into the middle of the growing season (July and August for both years), open stands experienced the lowest Ψ_{PD}, followed by moderately, and then heavily encroached stands. In the final two months of the growing season (September and October for both years), Ψ_{PD} was low compared to the early and middle growing season and maintained the same trend among encroachment levels, being lowest in open stands and highest in heavily encroached stands.

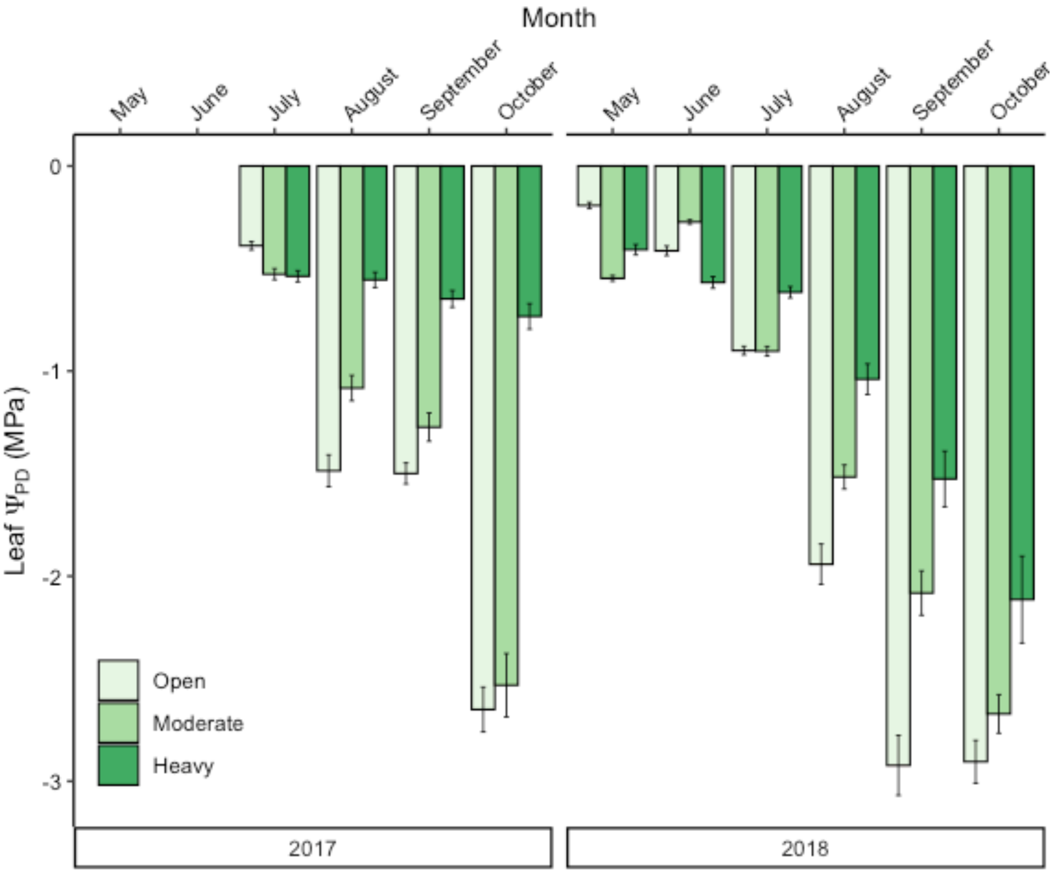

Figure 4. *Oregon white oak leaf predawn water potential (Ψ_{PD}, mean ± standard error) under three levels of conifer encroachment (open, moderate, heavy) across the 2017 and 2018 growing seasons (May – October) in Kneeland, CA. Due to a delayed study start, May and June data were not collected in 2017.*

Midday leaf water potential

Oak woodland encroachment level influenced Ψ_{MD} differently than Ψ_{PD} on both annual and monthly time scales (Figure 5, **Error! Reference source not found.**). A linear mixed effects model found that encroachment level ($p < 0.0001$, $F = 68.06$) was a determining factor of Ψ_{MD} across both years ($p < 0.0001$, $F = 153.51$) and among months ($p < 0.0001$, $F = 487.22$) within those years. Furthermore, there were interactions between encroachment level and month ($p < 0.0001$, $F = 10.83$) as well as between encroachment level and year ($p = 0.004$, $F = 5.57$).

Between years, similar to the trend in leaf Ψ_{PD}, leaf Ψ_{MD} was lower during the 2018 growing season than during the 2017 growing season ($p < 0.0001$, $t = 12.35$). In 2017, while Ψ_{MD} did not significantly differ between open and moderately encroached stands, it was higher in heavily encroached stands compared to moderately encroached ($p < 0.0001$, $t = 9.22$) and open ($p < 0.0001$, $t = 9.76$) stands. During the 2018 growing season, this same trend among encroachment levels was maintained: open and moderately encroached stands did not meaningfully differ from one another, while heavily encroached stands had higher Ψ_{MD} values compared to moderately encroached ($p < 0.0001$, $t = 6.58$) and open ($p < 0.0001$, $t = 6.32$) stands.

Monthly trends in leaf Ψ_{MD} were similar between the 2017 and 2018 growing seasons. Early in the growing season, Ψ_{MD} did not differ meaningfully among encroachment levels. However, during the middle of the growing season, differences in Ψ_{MD} among encroachment levels emerged, with open and moderately encroached stands having the lowest values and heavily encroached stands having the highest values. These patterns continued through the end of the growing season, with moderately encroached and open stands volleying between having the lowest Ψ_{MD} values.

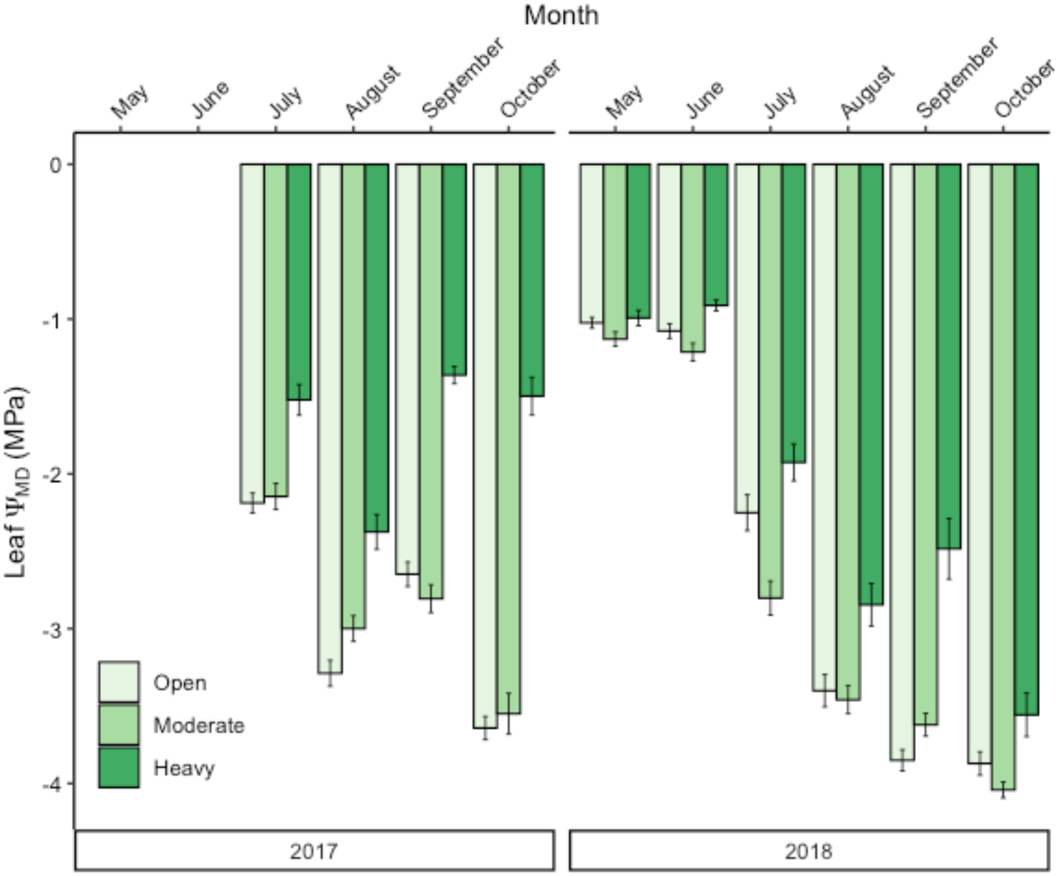

Figure 5. *Oregon white oak predawn leaf water potential (Ψ_{MD}, mean ± standard error) under three levels of conifer encroachment (open, moderate, heavy) across the 2017 and 2018 growing seasons (May – October) in Kneeland, CA. Due to a delayed study start, May and June data were not collected in 2017.*

Treatment Effects

Pre-dawn leaf water potential

Conifer removal influenced leaf Ψ_{PD} differently between moderately and heavily encroached stands one-year post treatment (Figure 6, Appendix B). A linear mixed effects model determined that treatment ($p = 0.01$, $F = 5.04$), encroachment level ($p < 0.0001$, $F = 83.54$), and year ($p < 0.0001$, $F = 29.37$) were all strong predictors of Ψ_{PD}. No interactions existed between predictor variables for Ψ_{PD}. Moderately encroached stands where conifers were removed had slightly higher Ψ_{PD} one-year post treatment (2018) compared to pretreatment (2017, $p < 0.0001$, $t = 8.15$). However, there was no difference between thinned and unthinned stands during either year ($p = 0.25$, $t = -1.82$). In heavily encroached stands where conifer removal occurred, Ψ_{PD} values were lower one-year post treatment compared to pretreatment ($p < 0.0001$, $t = 8.15$). Under heavily encroached conditions, thinned stands had slightly higher Ψ_{PD} values than unthinned stands ($p = 0.04$, $t = -2.62$).

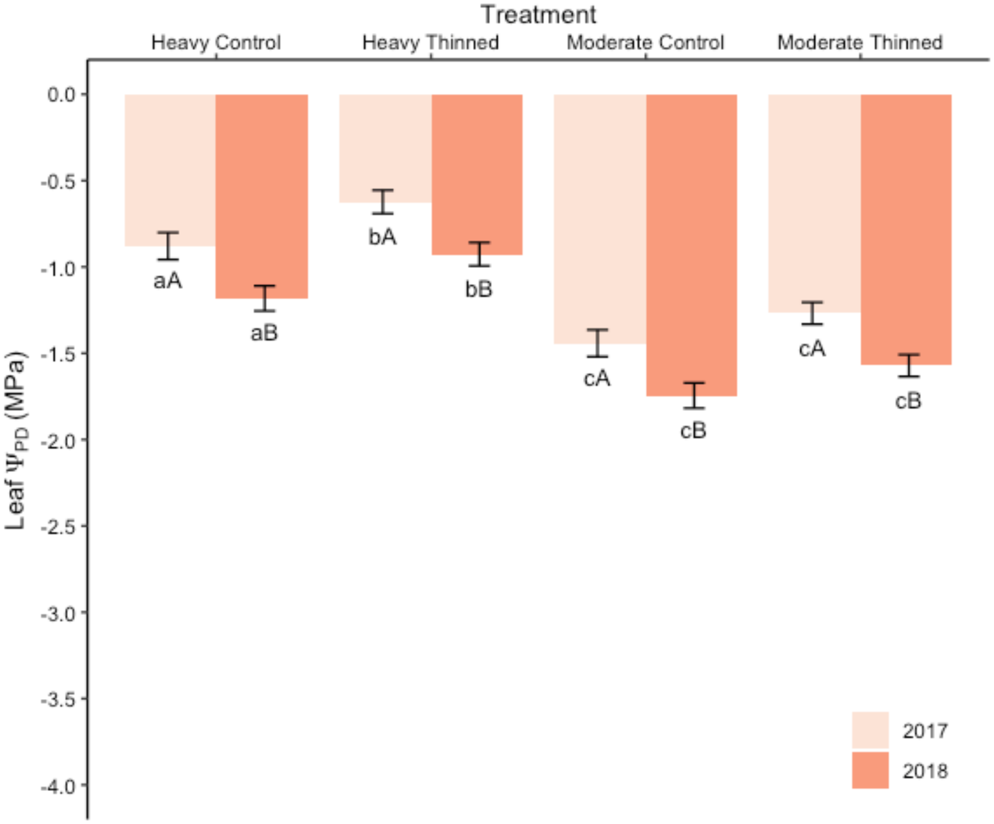

Figure 6. *Predawn leaf water potential (Ψ_{PD}, mean ± standard error) for Oregon white oak in thinned (moderate thinned, heavy thinned) and unthinned (moderate control, heavy control) stands in Kneeland, CA. Year 2017 represents pre-treatment stand conditions and year 2018 represents post-treatment conditions. For comparability between years, only July, August, September, and October data were used in this figure. Thinning treatments were conducted in the Fall of 2017. Within a year, treatments not sharing the same lower-case letter were significantly different. Within a treatment, years not sharing the same upper-case letter were significantly different.*

Midday leaf water potential

During midday, leaf Ψ_{MD} responses to confer removal were similar to those of Ψ_{PD} (Figure 7, Appendix B). The results of a linear mixed model found that treatment ($p < 0.0001$, $F = 11.14$), encroachment level ($p < 0.0001$, $F = 126.21$), and year ($p = 0.003$, $F = 9.53$) were all strong predictors of Ψ_{MD}. No interactions existed between predictor variables for Ψ_{MD}. In moderately encroached stands where conifer removal occurred, Ψ_{MD} was slightly higher one-year post treatment compared to pre-treatment ($p < 0.001$, $t = 7.263$). However, in the control moderately encroached stands, Ψ_{MD} also increased between 2017 and 2018 and this increase was larger than the increase in treated stands ($p < 0.001$, $t = 7.263$). In thinned heavily encroached stands, Ψ_{MD} decreased one-year post treatment compared to pre-treatment ($p < 0.001$, $t = 7.263$), with the magnitude of this decrease being comparable between treated and untreated stands.

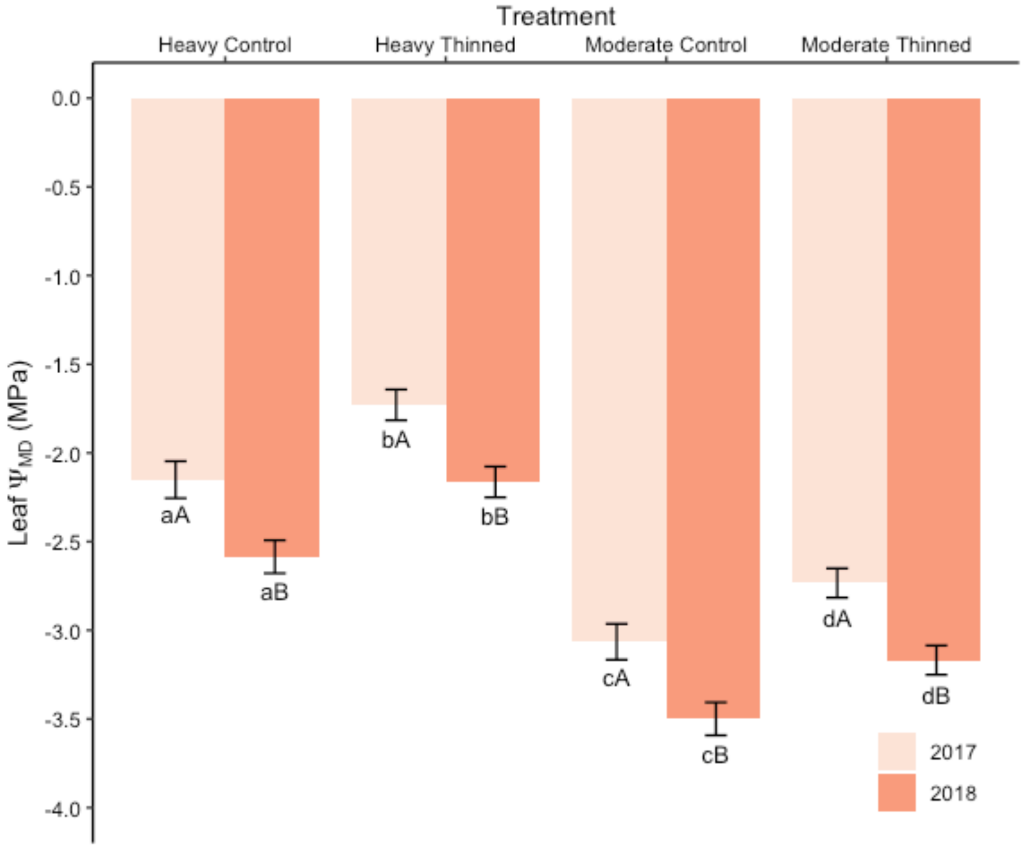

Figure 7. *Midday leaf water potential (*Ψ_{MD}*, mean ± standard error) for Oregon white oak in thinned (moderate thinned, heavy thinned) and unthinned (moderate control, heavy control) stands in Kneeland, CA. Year 2017 represents pre-treatment stand conditions and year 2018 represents post-treatment conditions. For comparability between years, only July, August, September, and October data were used in this figure. Thinning treatments were conducted in the Fall of 2017. Within a year, treatments not sharing the same lower-case letter were significantly different. Within a treatment, years not sharing the same upper-case letter were significantly different.*

Stem Psychrometer Series

During the 2019 growing season, in lieu of predawn and midday leaf Ψ measurements, xylem Ψ was measured continuously over a two-week period on oak trees using stem psychrometers. Stem psychrometers yielded approximately eight days of xylem Ψ measurements recorded every 30 minutes (Figure 8, Appendix C

Appendix C). From July 29th through August 5th, xylem Ψ_{PD} was comparable across all encroachment levels and treatment types with the exception of moderately encroached unthinned stands, which had consistently lower values. During midday, open stands consistently had the lowest Ψ_{MD} relative to all other stands, while Ψ_{MD} remained largely comparable among thinned and unthinned moderately and heavily encroached stands.

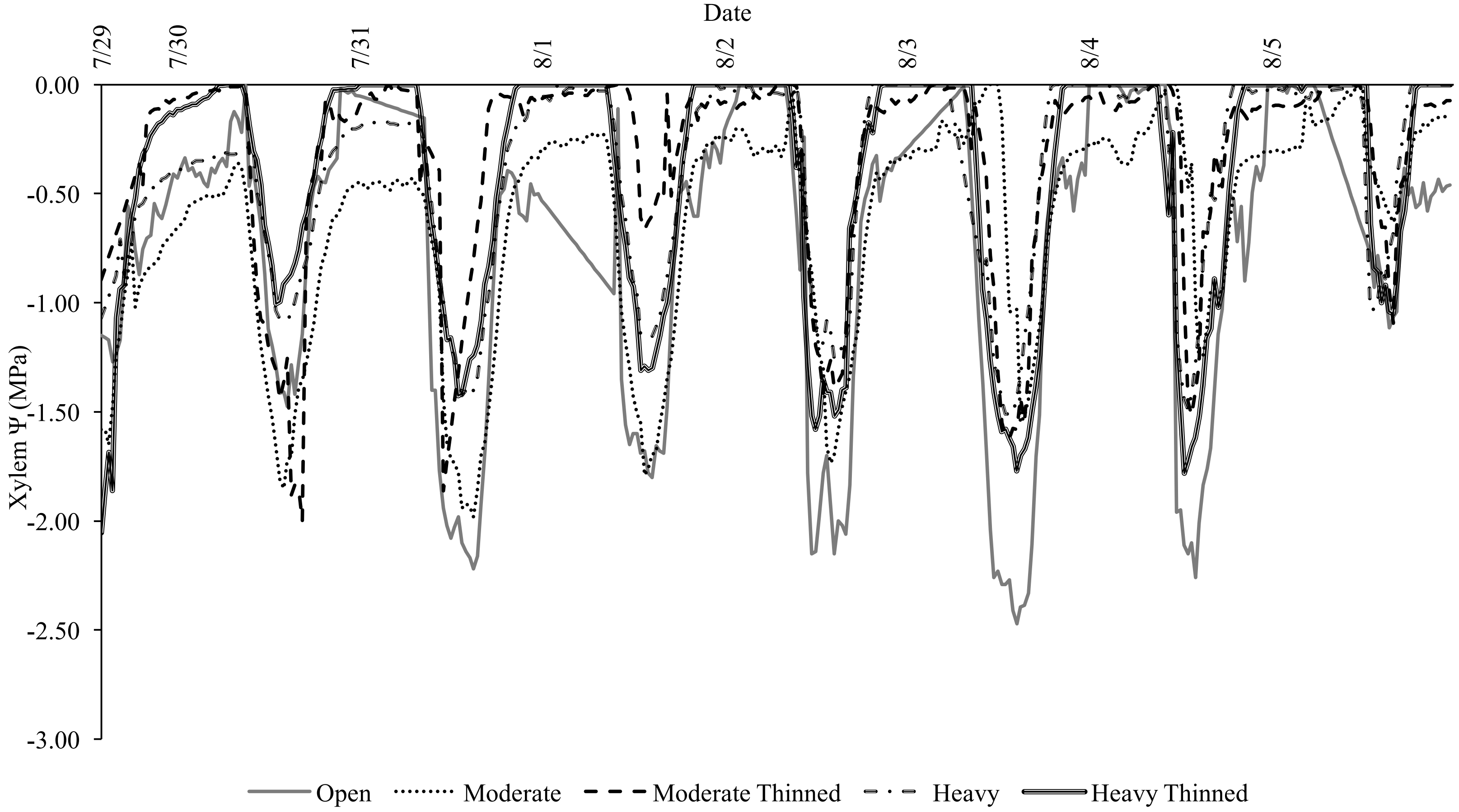

Figure 8. *Daily xylem water potential (Ψ) for Oregon white oak trees under open (solid blue), moderate (solid maroon), moderate thinned (dashed maroon), heavy (solid orange), and heavy thinned (dashed orange) stand conditions in Kneeland, CA. Measurements were taken with stem psychrometers every 30 minutes from July 29th through August 5th, 2019.*

Stomatal Conductance

Encroachment Effects

Leaf-level

Woodland encroachment level had a strong impact on oak g_s across multiple time scales (Figure 9, Appendix D). The results from a linear mixed effects model found that encroachment level was a determining factor of leaf-level g_s ($p < 0.0001$, $F = 24.47$) across multiple years ($p < 0.0001$, $F = 70.58$) and among months ($p < 0.0001$, $F = 44.05$) within those years. Furthermore, there existed interactions between encroachment level and month ($p < 0.0001$, $F = 5.61$), as well as between encroachment level and year ($p < 0.0001$, $F = 20.22$).

Between years, g_s was lower in 2018 than in 2019 ($p < 0.0001$, $t = -8.40$). In 2018, g_s across the growing season was lower in heavily encroached stands compared to moderately encroached stands ($p = 0.0001$, $t = -4.49$) and was higher in moderately encroached stands compared to open stands ($p < 0.0001$, $t = 4.85$). In 2019, g_s across the growing season was lower in heavily encroached stands compared to moderately encroached ($p < 0.001$, $t = -6.57$) and open stands ($p < 0.0001$, $t = -6.64$).

There were notable monthly trends in g_s. For 2018, general trends were: in May, heavily encroached stands had the highest g_s; in June, heavily encroached stands had the lowest g_s; in July, g_s was comparable among all stand types; in August and September, open stands had the lowest g_s; and in October, moderately encroached stands had the highest g_s. During the 2019 growing season, g_s rates followed a clearer trend. From May through July, open stands had higher g_s than moderate and heavily encroached stands. During August and September this relationship changed; moderately encroached stands during these months had the highest g_s rates compared to heavily encroached and open stands.

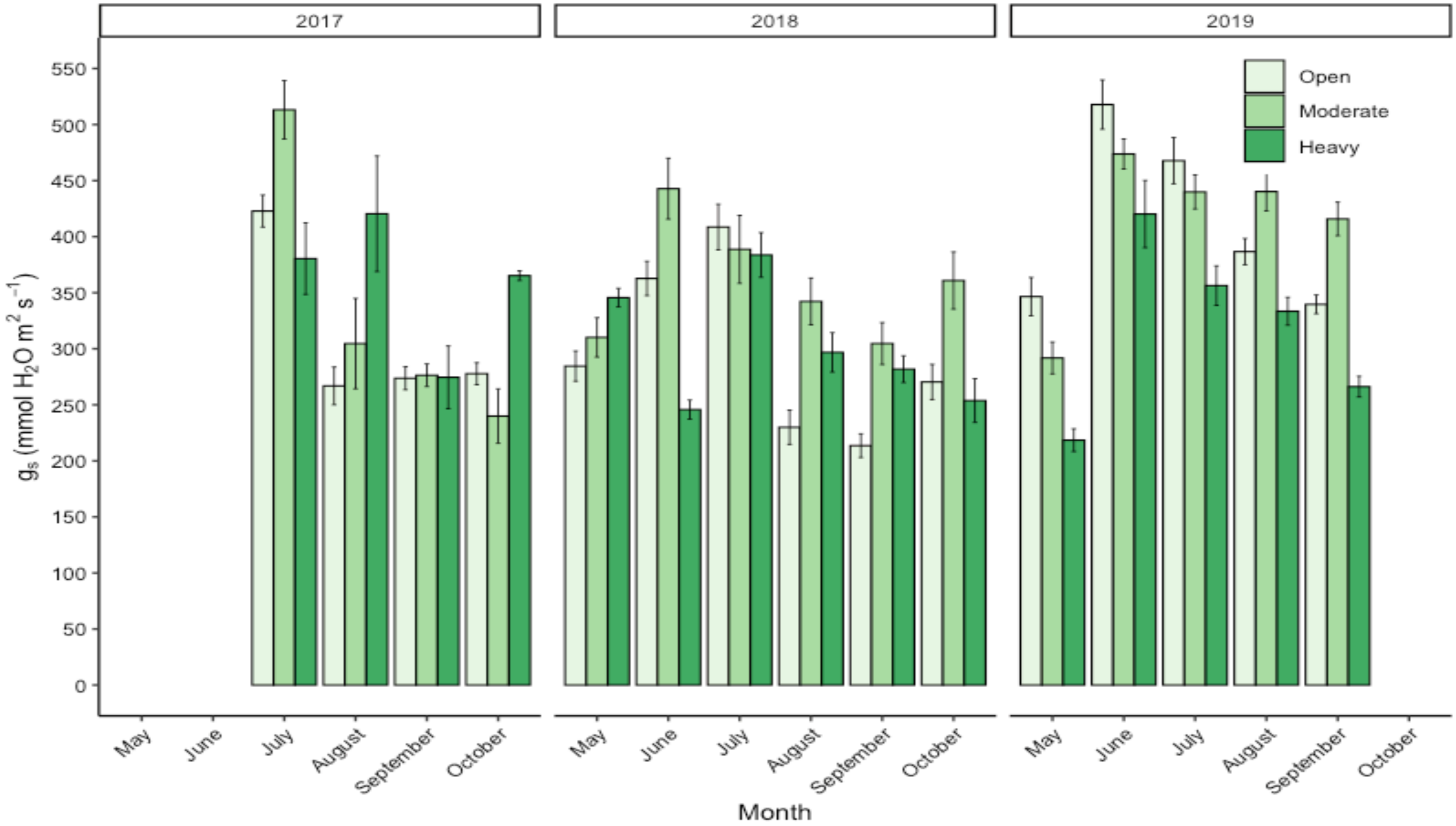

Figure 9. *Oregon white oak leaf-level stomatal conductance rates (g_s, mean ± standard error) under three levels of conifer encroachment (open, moderate, and heavy) across the 2017, 2018, and 2019 growing seasons (May – October) in Kneeland, CA. Due to a delayed study start, May and June data were not collected in 2017 and due to leaf senescence in this deciduous species, October 2019 data were not collected.*

Tree-level

Encroachment level was not individually influential on tree-level g_s (G_s), but depended on seasonality and year (Figure 10, Appendix D). The results from a generalized linear mixed effects model found that encroachment level alone did not have a strong influence on G_s ($p = 0.62$, $X^2 = 0.96$). Temporally, G_s was not strongly influenced by year ($p = 0.93$, $X^2 = 0.01$), but was by month ($p < 0.0001$, $X^2 = 46.72$). Furthermore, there existed significant interactions between month and encroachment level ($p < 0.0001$, $X^2 = 56.50$), as well as between encroachment level and year ($p < 0.0001$, $X^2 = 51.17$). Similar to interannual leaf-level findings, G_s was lower during the 2018 growing season compared to the 2019 growing season ($p < 0.0001$, $z = -7.77$). Although G_s did not meaningfully differ among encroachment levels in 2018, in 2019 open stands had higher G_s than heavily encroached stands ($p = 0.002$, $z = -3.43$).

The influence of encroachment level on G_s varied with month ($p < 0.0001$, $X^2 = 56.50$). During the 2018 growing season, G_s was highest in open stands from May through July, with heavily encroached stands having the lowest G_s during June and July. During the second half of the 2018 growing season (August through October), moderately encroached stands had the highest G_s. In 2019, the relationship between encroachment level, month, and G_s was more consistent, with open and heavily encroached stands supporting the highest and lowest G_s, respectively, during all months.

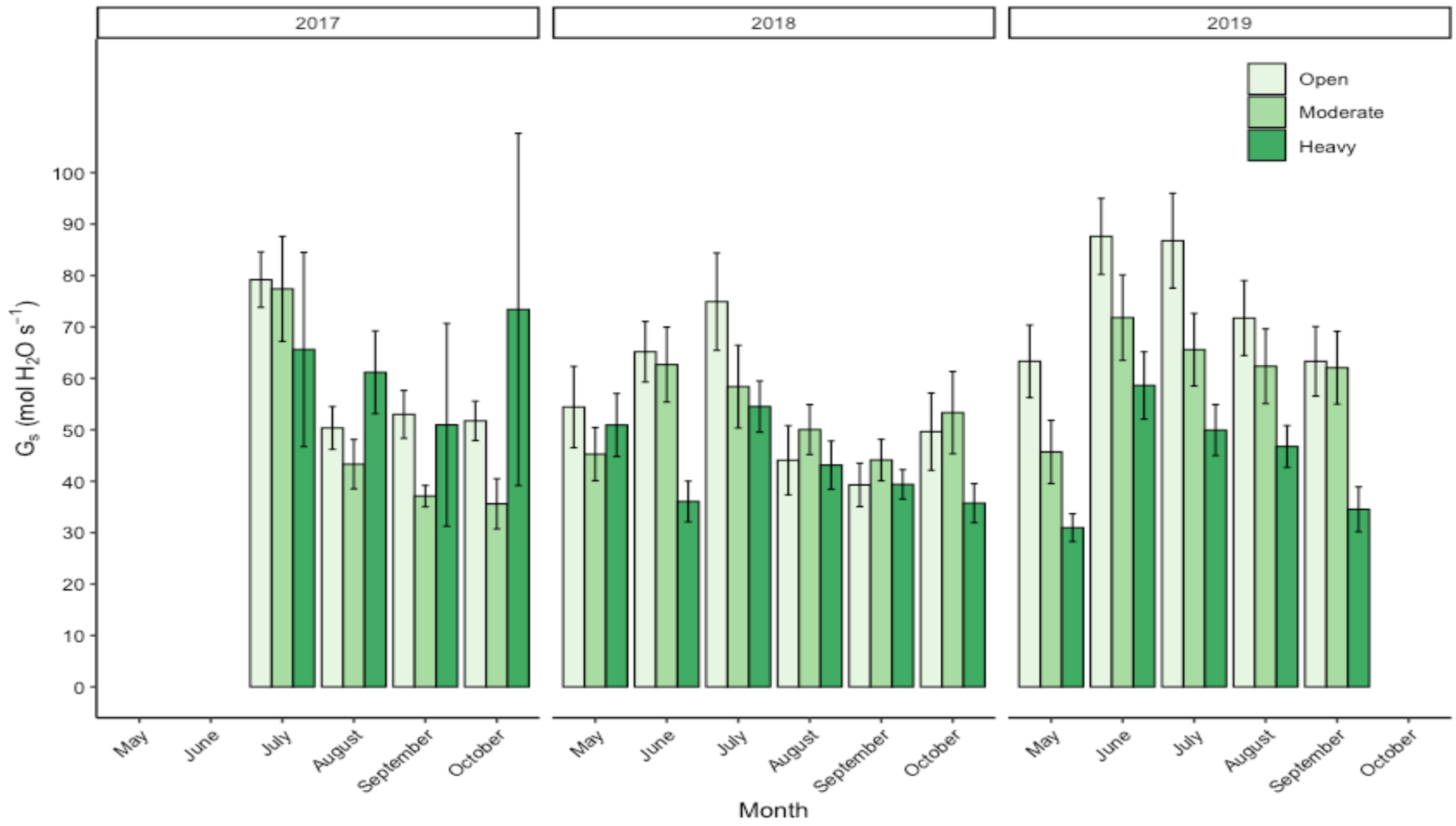

Figure 10. *Oregon white oak tree-level stomatal conductance rates (G_s, mean ± standard error) under three levels of conifer encroachment (open, moderate, heavy) across the 2017, 2018, and 2019 growing seasons (May – October) in Kneeland, CA. Due to a delayed study start, May and June data were not collected in 2017 and due to leaf senescence in this deciduous species, October 2019 data were not collected.*

Influences of Water Potential and Encroachment on Stomatal Conductance

Stomatal regulation strategies appeared to differ during the midday among different levels of encroachment during the 2017 growing season. There was a significant, positive, weakly correlated relationship between g_s and Ψ in open ($p < 0.0001$, $R^2 = 0.24$) and moderately ($p = 0.001$, $R^2 = 0.09$) encroached stands (Figure 11). In heavily encroached stands, the midday relationship between Ψ_{MD} and g_s was negative ($p < 0.0001$, $R^2 = 0.31$), meaning that trees increased water use as water status became more stressed.

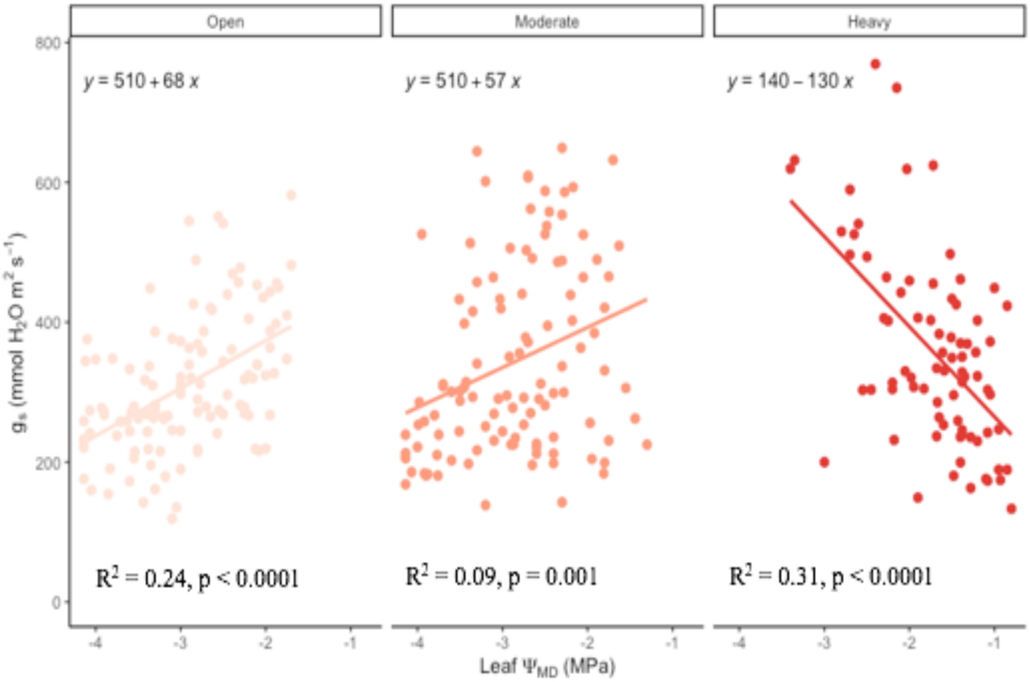

Figure 11. *Relationship between leaf-level stomatal conductance* (g_s) *and midday leaf water potential* (Ψ_{MD}) *in open, moderately encroached, and heavily encroached stands. Measurements were taken across the 2017 growing season (July – October) on Oregon white oak trees near Kneeland, CA.*

Treatment Effects

Post- vs. pre-treatment stomatal conductance

The impacts of conifer removal on stomatal conductance affected moderately and heavily encroached stands differently across time and can be effectively evaluated using a ratio of post-/pre-treatment g_s rates (Figure 12, Appendix E). Analyses done for g_s and G_s yielded nearly identical trends, so only g_s results are reported. A linear mixed effects model found that treatment ($p = 0.04$, $F = 4.31$) was a significant determining factor for the change in g_s between pre- and post-treatment stand conditions. The model did not find that encroachment level, year, nor any interactions were significant determining factors of post-/pre-treatment g_s. In unthinned moderately encroached stands, g_s was comparable in 2017 and 2018 and higher in 2019 compared to 2017. In thinned moderately encroached stands, g_s was higher in both post-treatment years (2018 and 2019) compared to pretreatment (2017). In heavily encroached, unthinned stands, g_s was lower in 2018 and 2019 compared to 2017. In thinned, heavily encroached stands, g_s increased in first post-treatment year (2018) and essentially returned to pre-treatment rates in second post-treatment year (2019).

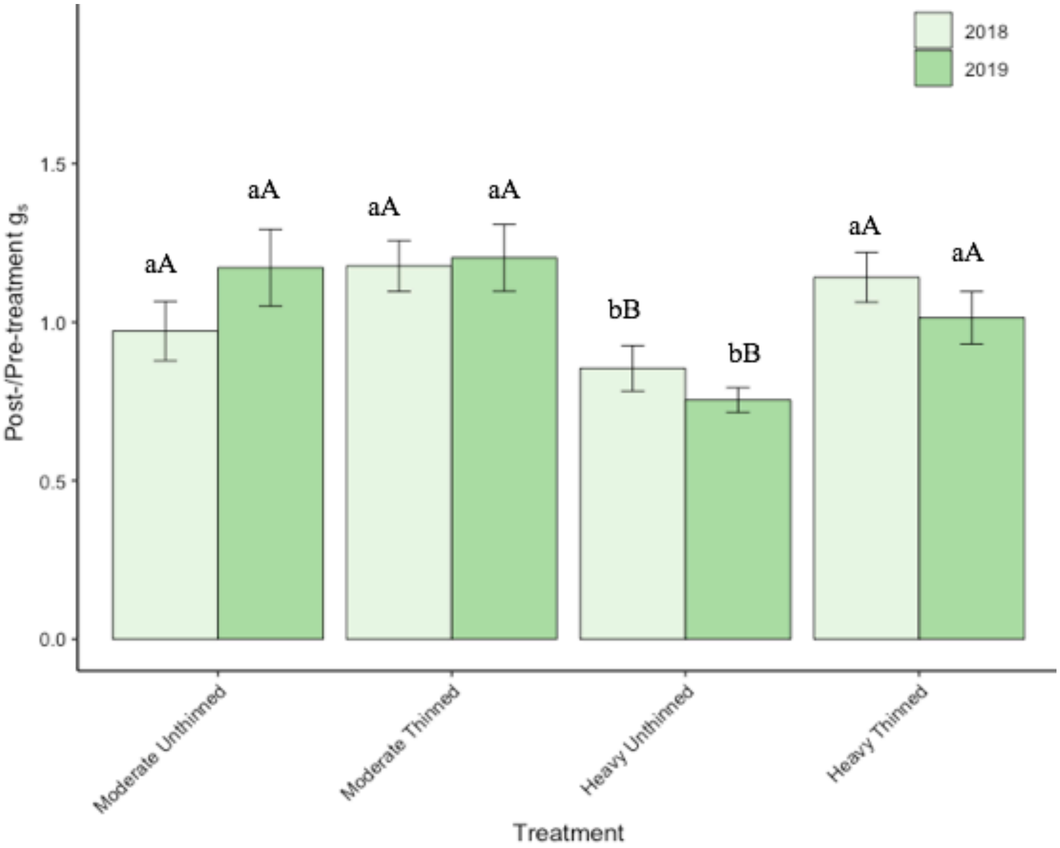

Figure 12. *Post-/pretreatment leaf-level stomatal conductance (g_s, mean ± standard error) for oaks in moderate and heavily encroached stands under thinned and unthinned conditions in Kneeland, CA. Pre-treatment year was 2017 and post-treatment years were 2018 and 2019. Values greater than one represent an increase in g_s and values less than one represent a decrease in g_s. Between years, treatments not sharing the same lower-case letter were significantly different. Between treatments, years not sharing the same upper-case letter were significantly different.*

Stable Isotopes

A paired *t*-test determined that oak xylem water δD was significantly lower than xylem water δD from the nearest Douglas-fir (p = 0.0001, t = 4.20, Figure 13, Figure 14, Appendix F). Furthermore, results from a two-way ANOVA indicated that species ($p < 0.0001$, F = 28.06) and encroachment level ($p < 0.0001$, F = 23.15) were both significant determining factors of tree xylem water δD.

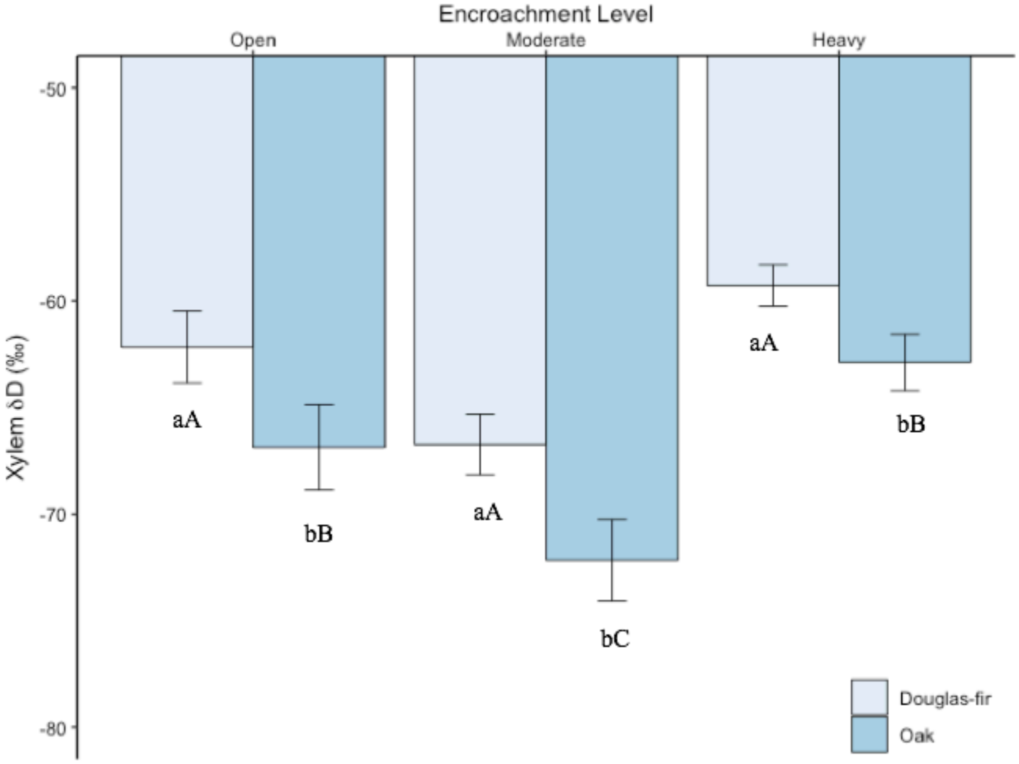

Figure 13. *Xylem water hydrogen stable isotope (δD) signature (mean ± standard error) for Oregon white oak and Douglas-fir trees under three levels of conifer encroachment (open, moderate, heavy) in Kneeland, CA in August 2018. For each evaluated oak, the nearest Douglas-fir was sampled. Among encroachment levels, species not sharing the same lower-case letter were significantly different. Between species, encroachment levels not sharing the same upper-case letter were significantly different.*

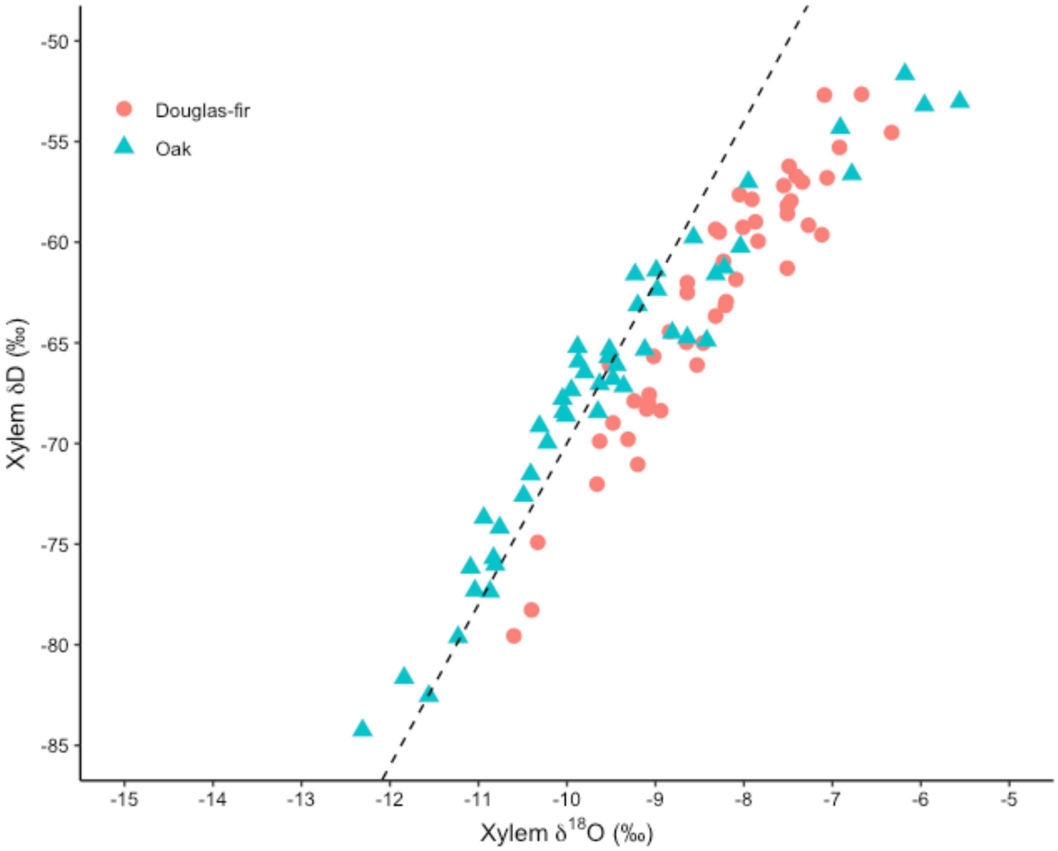

Figure 14. *Oregon white oak and Douglas-fir xylem water hydrogen (δD) and oxygen (δ^{18}O) stable isotope signatures. Dashed line represents global meteoric water line. Trees were sampled in Kneeland, CA in August 2018.*

Biodiversity

Over the course of two years, 59 species of vascular plants (Appendix G), 15 species of mammals (Appendix H

Appendix H), and 39 bird species (Appendix I) were identified among three levels of conifer encroachment, between thinned and unthinned stand conditions. Eleven of the 59 vascular plants found across the study sites were non-native, with seven of those non-natives also being listed invasive species. However, there were no meaningful differences in the distribution of non-native invasive plants across the site. No non-native, or non-native invasive mammal or bird species were detected. Notably, one fisher (*Pekania pennanti*), a federally listed threatened species, was observed via camera trap.

Plants

Understory plant diversity did not significantly vary by encroachment level during either of the sampling years (Table 2). Although S, E, and H' tended to be higher in open and moderately encroached stands, a linear mixed effects model indicated that none of these metrics of biodiversity were different among encroachment levels. Furthermore, there was no difference in these metrics between the 2018 and 2019 sampling years.

Similar to the encroachment effects, treatment had few statistically discernable differences in understory plant S, E, and H', and no interaction existed between encroachment level and thinning treatment. Although S, E and H' were higher on average in thinned stands compared to unthinned stands, treatment was not a significant determining factor for plant diversity (Table 10). Furthermore, there was no effect of time since treatment for S and E, but H' was higher in 2018 than in 2019 (p = 0.02, t = -2.95).

Mammals

Conifer encroachment impacted mammalian diversity, and that effect was different between the two sampling years (**Error! Reference source not found.**). Species richness was significantly less in open stands than in moderate or heavily encroached ones (p = 0.01, F = 10.19), and lower in 2018 than in 2019 (p = 0.01, F = 10.56). Similarly, E was lower in open stands than in moderate or heavily encroached stands and was generally higher in 2019, although neither of these trends were statistically significant. Finally, H' was highest in heavily encroached stands, and lowest in open stands (p = 0.01, F = 7.65), but did not vary between years.

Treatment influenced diversity metrics broadly, but did not vary by encroachment level. Results from a linear mixed effects model indicated that S was higher in unthinned stands than in thinned stands (p = 0.003, F = 14.07) and was higher in 2019 than in 2018 (p = 0.001, F = 17.18). However, encroachment level had no effect on this relationship, and no interactions existed between any combination of encroachment level, treatment, or year. Neither treatment nor encroachment level had significant effects on D or H', but both of these metrics varied between years. Species evenness was generally higher in 2019 compared to 2018 (p = 0.02, F = 8.52), while H' was often higher in 2018 compared to 2019 (p = 0.02, F = 7.62).

Birds

Encroachment level was not an important predictor of bird diversity, as measured by S, E, and H', and these three metrics did not vary between years (Table 2). Although S, E, and H' were generally higher in heavily encroached stands and in 2019, a linear mixed effects model found no significant effect of encroachment, year, or interactions between those terms.

Similar to encroachment level effects, treatment and time since treatment played an insignificant role in predicting bird diversity. Results from a linear mixed effects model found encroachment level, treatment, and year to be poor predictors of S and H'. However, when considering only thinned or unthinned stands, the model found E to be slightly higher in heavily encroached stands than in moderately encroached stands ($p = 0.01$, $F = 11.16$). Furthermore, no interactions existed between encroachment level, treatment, or year across the study period.

Table 2. *Species richness (S), evenness (E), and Shannon – Wiener diversity index (H') of plants, mammals, and birds identified under three levels of conifer encroachment with and without thinning treatment in and Oregon white oak woodland in Kneeland, CA. Surveys for each group were conducted during 2018 and 2019 after a 2017 thinning treatment. Each row is based on 2 plots, except for the birds open 2018 values, which are based on 4 plots.*

Encroachment	**Year**	**Treatment**	**S**	**E**	**H'**
Plants					
Open	2018	Control	18 ± 2	0.64 ± 0.00	1.86 ± 0.08
	2019		19 ± 1	0.93 ± 0.03	2.71 ± 0.11
Moderate	2018	Unthinned	18 ± 3	0.71 ± 0.03	2.05 ± 0.21
	2019		14 ± 4	0.83 ± 0.04	2.14 ± 0.34
Moderate	2018	Thinned	18 ± 2	0.68 ± 0.05	1.98 ± 0.23
	2019		21 ± 3	0.89 ± 0.00	2.70 ± 0.13
Heavy	2018	Unthinned	10 ± 6	0.59 ± 0.11	1.27 ± 0.61
	2019		12 ± 9	0.66 ± 0.05	1.31 ± 0.55
Heavy	2018	Thinned	13 ± 4	0.62 ± 0.04	1.53 ± 0.10
	2019		13 ± 4	0.80 ± 0.02	2.01 ± 0.22
Mammals					
Open	2018	Control	4 ± 1	0.28 ± 0.07	0.55 ± 0.09
	2019		4 ± 1	0.38 ± 0.14	0.13 ± 0.49
Moderate	2018	Unthinned	6 ± 1	0.69 ± 0.00	1.24 ± 0.01
	2019		11 ± 1	0.72 ± 0.04	0.34 ± 0.04
Moderate	2018	Thinned	4 ± 1	0.64 ± 0.05	1.09 ± 0.10
	2019		7 ± 1	0.64 ± 0.05	0.13 ± 0.30
Heavy	2018	Unthinned	6 ± 1	0.63 ± 0.04	1.19 ± 0.11
	2019		9 ± 1	0.65 ± 0.03	1.25 ± 0.14
Heavy	2018	Thinned	5 ± 1	0.56 ± 0.07	0.98 ± 0.18
	2019		6 ± 2	0.59 ± 0.07	0.82 ± 0.39
Birds					
Open	2018	Control	15 ± 1	0.90 ± 0.00	2.36 ± 0.05
	2019		15 ± 1	0.90 ± 0.01	2.36 ± 0.11
Moderate	2018	Unthinned	11 ± 2	0.87 ± 0.00	2.09 ± 0.08
	2019		18 ± 1	0.91 ± 0.00	2.55 ± 0.01
Moderate	2018	Thinned	11 ± 1	0.88 ± 0.01	2.15 ± 0.02
	2019		15 ± 1	0.89 ± 0.00	2.35 ± 0.08
Heavy	2018	Unthinned	14 ± 3	0.91 ± 0.01	2.36 ± 0.16
	2019		14 ± 1	0.90 ± 0.01	2.35 ± 0.05
Heavy	2018	Thinned	19 ± 2	0.93 ± 0.00	2.65 ± 0.03
	2019		17 ± 2	0.92 ± 0.01	2.53 ± 0.11

DISCUSSION

Oregon White Oak Physiology

The impacts of conifer encroachment were mediated by seasonality, and fluctuated by year, but nevertheless patterns emerged as to how encroachment impacts Oregon white oak physiology. Data indicated that oaks under the highest severity of conifer encroachment had the lowest gas exchange rates, but also maintained the least amount of water stress. Furthermore, moderately encroached oak stands often had gas exchange rates comparable to open stands and higher water potentials. In part, these findings are likely attributable to encroachment-induced changes in stand conditions. Increased tree density likely changes the microclimate of encroached stands by decreasing temperature, VPD, and evaporative water loss from the soil (Devine and Harrington 2007). As soil water dries out across the growing season, a moderate level of encroachment could support a beneficial combination of these environmental conditions, allowing oaks in these stands to display comparable gas exchange rates to open stands while maintaining relatively low water stress. However, densification of these stands is likely only beneficial to a certain point. Under heavily encroached conditions, oaks invest more energy in height growth than in diameter growth in an attempt to access limited light resources (Schriver *et al.* 2018). Once overtopped and under increased competitive pressure, the possibility of oak mortality increases (Devine *et al.* 2007b, Engber *et al.* 2011, Ruiz-Benito *et al.* 2013).

Physiological results may also reflect variability in stomatal regulation strategies among oaks under different levels of conifer encroachment. Oaks under heavily encroached conditions generally maintained higher Ψ and lower g_s rates compared to oaks in moderately encroached and open stands. The positive correlation between Ψ and g_s in open and moderately encroached stands demonstrates that oaks in these stand conditions regulated stomata to conserve water. Oaks under these higher light conditions behaved relatively isohydrically, using stomatal regulation to avoid embolisms resulting from very low Ψ. Contrastingly, the negative correlation between Ψ and g_s for oaks in light-limited, heavily encroached stands indicates that these oaks behaved more anisohydrically, maintaining stomatal conductance even under very low Ψ to maximize CO_2 uptake. While once understood as a fixed trait, recent work suggests that woody plants can alter stomatal regulation in response to environmental conditions (Hochberg *et al.* 2018). The contrasting relationships measured in this study between Ψ and g_s in oaks under different stand conditions is a compelling demonstration of plasticity in tree stomatal regulation strategy. Under dry stand conditions (open and moderately encroached stands), oaks in this woodland regulated stoma to conserve water; under wet, shaded conditions (heavily encroached stands), oaks allowed Ψ to decrease without regulating stomata, likely to maximize carbon assimilation when light was available. These findings are interesting and deserve further investigation, as differences in stomatal regulation strategy can have a large influence on plant survival under adverse environmental conditions (McDowell *et al.* 2008, 2010, Klein 2014).

Although this investigation did not evaluate findings as they related to climate, climatic variables such as temperature and precipitation undoubtedly influenced physiology. At this study site, spring maximum temperatures are lowest in stands with the highest amounts of Douglas-fir (Beckmann *et al.* 2021). Ring-porous species such as oak typically produce a ring of large vessels early in the growing season; later in the growing season, a narrower ring is produced with smaller, more dispersed vessels (Taneda and Sperry 2008). Further, in ring-porous stems, the outermost growth ring often transports more than 90% of the water conducted up the tree stem, with the vast majority of this water flowing through the large earlywood vessels (Ellmore and Ewers, 1986). Early season growth is therefore very important because during this time the tree creates the primary water conduits for the entire year (Barbaroux and Bréda 2002). Low spring temperatures due to increased shading in heavily encroached stands could limit xylem development, which would influence tree hydraulic capacity, Ψ, and g_s throughout the year. At this site, winter and rare, late-summer precipitation inputs have a significantly positive effect on Oregon white oak growth (Beckmann *et al.* 2021), likely due to the presence of deep taproots and shallow lateral roots allowing access to different water resources throughout the year (Allen 2014). This study's isotopic analysis indicated that oaks draw water from a deeper source in the soil profile than Douglas-fir, suggesting that oak mortality in response to encroaching conifers is likely due to competition for light, not water resources.

Removal of encroaching Douglas-fir did not induce meaningful physiological responses in Ψ under either encroachment level when compared to controls. Rather, differences between encroachment levels seemed to be independent of treatment, as thinned and unthinned stands of either encroachment level displayed strikingly similar trends. However, under heavily encroached conditions, the drop in Ψ_{pd} between 2017 and 2018 was less for treated stands than controls, perhaps indicating that treatment had a positive influence on oak water status. The similarity of interannual Ψ trends in treated and control stands of both encroachment levels suggests that differences between 2017 and 2018 were more related to climate than to conifer removal. Thus, the lower Ψ in 2018 compared to 2017 is likely due to the fact that it was a drier year (2017 Palmer Drought Severity Index [PDSI] at this site = 3.33, while 2018 PDSI = -0.07) (NOAA, 2021). While thinning can potentially increase water stress in residual trees due to increased evapotranspiration, residual oaks following treatment in this woodland did not have lower Ψ than oaks in controls. The lack of Ψ response to treatment might be attributed to the generally light intensity of treatment at this site. Greater reductions in stand density would likely increase evapotranspirational water loss by exposing the stand to more light and wind (Breda *et al.* 1995, Aussenac 2000), which could induce more notable decreases in post-treatment Ψ.

Stomatal conductance increased in response to thinning in both moderately and heavily encroached stands. In the first post-treatment year, g_s in moderately and heavily encroached conditions was higher than pre-treatment rates in thinned stands and lower than pre-treatment rates in unthinned stands. Moderately encroached stands likely responded positively to treatment during the first post-treatment year due to broader, thicker crowns with the ability to photosynthesize more rapidly following conifer removal (Aussenac 2000). Furthermore, moderately encroached stands experienced a shorter duration of encroached conditions, a strong factor when attempting to understand release effects (Wright *et al.* 2000). For moderately encroached stands, g_s in the second post-treatment year was higher than pre-treatment rates for both thinned and unthinned stands, suggesting that the second-year increase was independent of treatment and likely driven by climate. In heavily encroached stands, although g_s during the first post-treatment year was higher for thinned stands compared to controls, in the second post-treatment year oak g_s in thinned stands returned to pre-treatment rates. However, for oaks in unthinned heavily encroached stands, g_s was lower than pre-treatment rates during the second post-treatment year, indicating that thinning allowed oaks to maintain gas exchange during dry conditions (2019 PDSI = -0.43), while oaks in the unthinned stands had to use more stomatal regulation. The difference in response to thinning during the second post-treatment year between heavily and moderately encroached stands could be due to the hot, dry 2019 conditions. Because thinning can increase soil temperature and evaporative water loss (Covington *et al.* 1997, Chase *et al.* 2016), these post-treatment changes may have induced a greater reduction of gas exchange in heavily encroached stands acclimated to wetter conditions compared to moderately encroached stands. While oaks can respond positively and quickly to reduced competition via growth and physiology (Lamson *et al.* 1990, Devine and Harrington 2013), the longevity of these responses is unclear, thus, short- and long-term monitoring of responses are useful to improve the understanding of management efficacy in encroached oak woodlands (Devine and Harrington 2006).

Finally, it is important to consider the light intensity of thinning that occurred at these sites. The thinning treatment removed trees >25 cm DBH, and therefore only removed a fairly small number of encroaching Douglas-firs. Generally, tree removal increases vigor in residual trees via improved resource availability, and more intense treatments produce larger post-treatment growth responses (Breda *et al.* 1995). In Oregon white oak woodlands, heavier thinning treatments confer a larger positive response compared to lighter thinning treatments (Devine and Harrington 2006). Stand-level responses to thinning treatments are often determined by size, age, physiological attributes, and the availability of resources (Bose *et al.* 2018). Further, individual tree characteristics, pre- and post-thinning stand conditions, and time since treatment can also temper responses to treatment (Girona *et al.* 2017). Findings from this work suggest that thinning conferred a positive response under heavily encroached conditions, whereas moderately encroached stands remained mostly unchanged in comparison to their unthinned counterparts. Conifer removal was likely more intense under heavily encroached conditions, which could explain the responses to treatment measured in this study. Additionally, without sufficiently aggressive thinning, residual Douglas-fir crowns likely grew to quickly close recently-opened gaps, potentially explaining the return to pre-treatment conditions during the second post-treatment year observed in the heavily encroached stands (Wardman and Schmidt 1998).

Woodland Biodiversity

Oak woodlands are renowned for supporting high levels of biodiversity, particularly in the understory plant community (Thysell and Carey 2001a, Devine *et al.* 2007a, Livingston *et al.* 2016). Changes in stand structure due to conifer encroachment should negatively impact these understory communities (Klinka *et al.* 1996, Bailey *et al.* 1998), while restoration thinning should promote a resurgence of understory species (Devine and Harrington 2006, Devine *et al.* 2007a). However, this study found very muted reductions in understory plant diversity in encroached stands compared to open stands. These uncharacteristic results could be due to the fact that understory surveys were conducted only during peak flowering and not also during peak fruiting, as some oak woodland studies investigating plant diversity sample during both time periods (Devine *et al.* 2007a, Livingston *et al.* 2016). Thus, this study's results from peak flowering season reflect a mid-summer inventory of woodland understory plant diversity and are likely missing species that would have been detected if sampling had also occurred during peak fruiting season. This study also found small understory plant responses to treatment. While part of this minimal response to treatment may be attributable to sampling only during peak flowering and not also during peak fruiting, many ecosystems do not experience dramatic increases in understory plant diversity within the first few years after restoration thinning treatments (Wayman and North 2007, Perchemlides *et al.* 2008, Davis and Puettmann 2009, Dodson and Peterson 2010, Bassett *et al.* 2020). It could take many years to see the impacts of thinning treatments on the understory, as slow-growing, long-lived, and endemic plants often recover very slowly (Veldman *et al.* 2015). The impacts of treatment are further tempered and will also vary based on site conditions and past history of fire suppression and grazing practices (Reid *et al.* 2020). Although our sites were actively grazed over the duration of this study, the effects of grazing are variable and depend on time and intensity (Watkinson and Ormerod 2001, Hayes and Holl 2003, Bartolome *et al.* 2014).

Mammal diversity varied among encroachment levels and was often higher in moderately encroached stands compared to heavily encroached and open stands. These results can likely be attributed to the abundance of variable forest structures associated with the different levels of conifer encroachment. Wildlife diversity is largely influenced by the ecological structures of forests (e.g., spaces between patches, continuity of communities, variability of physical structures, etc.) on both local and landscape scales (Hayes *et al.* 1996). Thus, wildlife diversity is commonly higher in stands with complex conditions compared to stands with more homogeneous conditions (Thysell and Carey 2001b). However, ecosystems that don't support species over long periods of time can still provide crucial linkages to lands with more suitable habitats and thus remain important (Beier 1993, Manning *et al.* 2006, Thornton *et al.* 2011). The mosaic of conditions supported by an encroached oak woodland might therefore provide a range of habitats suitable for numerous mammal species, possibly explaining why unthinned stands in this study had the highest mammal richness and diversity. Unfortunately, this study did not assess pre-treatment mammal diversity, which would have provided a valuable baseline for long-term post treatment mammal monitoring. Other studies have recorded increased small mammal diversity following thinning treatments where new structures such as slash or large downed wood are created (Wilson and Carey 2000, Converse *et al.* 2006). Perhaps the fact that treatments at this study site removed merchantable timber and left minimal coarse woody debris limited mammal responses to treatment.

As with understory plant and mammal diversity, the impacts of conifer encroachment and removal were similarly muted on bird diversity. Habitat configuration on the landscape strongly impacts vertebrate populations and their interactions (Wiens 1976). One possible explanation for the lack of encroachment or treatment effects on bird diversity is that although conifer encroachment negatively impacts oak trees, the variable conditions between encroached and open stands likely support a wide range of avian species with different survival strategies (McGarigal and McComb 1995, Ries 2004). The lack of difference between thinned and unthinned stands may reflect the short time period (first and second post-treatment years) during which responses to treatment were examined, as it can take several years to detect the impacts of habitat alteration for many species (Allen *et al.* 2002). Furthermore, these results could also be attributed to the generally light thinning treatment previously discussed. Overall, these findings highlight a need for longer-term investigations into how avian species respond to conifer encroachment and removal.

Climate and Management Implications

There is broad agreement that climate will become increasingly volatile as the 21st century progresses (Swain *et al.* 2016, 2020, Diffenbaugh *et al.* 2017). In our Mediterranean climate this will likely include more frequent drought and also more extreme hydrological activity (Swain *et al.* 2018). Understanding how different species respond to stressful climatic events, especially those involving water use, will become increasingly important for adaptive management under warming and drying conditions (Peñuelas *et al.* 2001, West *et al.* 2012). Oregon white oaks, much like other oak species throughout the United States, are considered drought-tolerant (Johnson *et al.* 2009, D'Amato *et al.* 2013, Hahm *et al.* 2018). Although findings from this study suggest that a moderate level of conifer encroachment might buffer oak water status, a moderate level of encroachment is ephemeral and will inevitably progress to a heavier level of encroachment as the conifers continue to grow taller and overtop the oaks. And, increased Douglas-fir density reduces growth-based drought resistance (Beckmann *et al.* 2021), suggesting that dry conditions have a greater negative impact on encroached oaks compared to oaks in open stands. This study's findings that gas exchange is most limited under heavily encroached conditions despite trees having higher Ψ and that oaks and Douglas-firs draw water from different soil depths together indicate that oaks under encroached conditions are likely inhibited by limited carbon assimilation via shading, and not via competition for water. Related to encroachment, drought, and/or competition, reduced productivity and thus growth can increase tree vulnerability to mortality (Cailleret *et al.* 2017, DeSoto *et al.* 2020). Reducing Douglas-fir density in woodlands will support Oregon white oak future climate resilience, as synergies between drought and competition continue to threaten these landscapes (Beckmann *et al.* 2021; Bradford and Bell, 2017).

A primary objective of ecological restoration is to return ecosystems to their historic range of variability while enhancing resiliency and sustainability into the future (Holling and Meffe 1996). However, care is needed to use historic baselines as guidelines, not gospel (Landres *et al.* 1999). The management activities that occurred at this study site were largely a positive side-effect from harvesting merchantable timber. To effectively restore these ecosystems, a combination of manual removal, girdling, and prescribed fire are likely needed

(Hastings *et al.* 1997, Nielsen *et al.* 2003, Harrington and Devine 2006, Devine *et al.* 2007a, Engber *et al.* 2011, Kabrick *et al.* 2014, Lettow *et al.* 2014, Vander Yacht *et al.* 2017, Kane *et al.* 2019). Diameter growth assessments of ecosystem responses to treatments may not yield results on a time scale that is helpful to understand the impacts of restoration (Drobyshev *et al.* 2019). Findings from this work indicate that removing conifers in heavily encroached oak stands can confer a physiologically positive response in residual hardwoods. However, these heavily encroached stands are often the most difficult to restore for both economic and procedural reasons (Cocking *et al.* 2014). Thus, although physiologically able to respond to restoration, heavily encroached woodlands may not be the logical focus for treatment efforts. As such, when evaluated holistically, it seems that moderately encroached stands that are physiologically responsive and structurally accessible for treatment implementation likely have the greatest chance for successful restoration and are where management efforts should be directed.

LITERATURE CITED

Agee, J.K., 1998. The landscape ecology of western forest fire regimes. *Northwest Science*. 72 (Special Issue): 24–34.

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., and Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: A broad perspective. *Ecological Applications* 12 (5): 1418–1433.

Allen, M.F., 2014. How oaks respond to water limitation. *USDA General Technical Report*. PSW-GTR-251: 13–21.

Augé, R.M., Green, C.D., Stodola, A.J., Saxton, A.M., Olinick, J.B., and Evans, R.M., 2001. Correlations of stomatal conductance with hydraulic and chemical factors in several deciduous tree species in a natural habitat. *New Phytologist* 145 (3): 483–500.

Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science* 57 (3): 287–301.

Bailey, J.D., Mayrsohn, C., Doescher, P.S., St. Pierre, E., and Tappeiner, J.C., 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. *Forest Ecology and Management* 112 (3): 289–302.

Barbaroux, C. and Bréda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree physiology* 22: 1201–1210.

Bartolome, J.W., Allen-Diaz, B.H., Barry, S., Ford, L.D., Hammond, M., Hopkinson, P., Ratcliff, F., Spiegal, S., and White, M.D., 2014. Grazing for biodiversity in californian mediterranean grasslands. *Rangelands* 36 (5): 36–43.

Bassett, T.J., Landis, D.A., and Brudvig, L.A., 2020. Effects of experimental prescribed fire and tree thinning on oak savanna understory plant communities and ecosystem structure. *Forest Ecology and Management* 464 (February): 118047.

Beckmann, J.J., Sherriff, R.L, Kerhoulas L.P., Kane, J.M. 2021. Douglas-fir encroachment reduces drought resistance in Oregon white oak of northern California. *Forest Ecology and Management*: *accepted*.

Beier, P., 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7 (1): 94–108.

Bernhardt, E.A. and Swiecki, T.J., 2001. Restoring oak woodlands in California : Theory and practice. *Phytosphere* 8 (15): 1–24.

Bond, W.J. and Keeley, J.E., 2005. Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20 (7): 387–394.

Bose, A.K., Weiskittel, A., Kuehne, C., Wagner, R.G., Turnblom, E., and Burkhart, H.E., 2018. Does commercial thinning improve stand-level growth of the three most commercially important softwood forest types in North America? *Forest Ecology and Management* 409: 683–693.

Bradford, J.B. and Bell, D.M., 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. *Frontiers in Ecology and the Environment* 15 (1): 11–17.

Breda, N., Granier, A., and Aussenac, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology* 15 (5): 295–306.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* 23 (4): 1675–1690.

Chase, C.W., Kimsey, M.J., Shaw, T.M., and Coleman, M.D., 2016. The response of light, water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir forests. *Forest Ecology and Management* 363: 98–109.

Cocking, M.I., Varner, J.M., and Engber, E.A., 2014. Conifer encroachment in California oak woodlands. *The Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World*: 505–514.

Cocking, M.I., Varner, J.M., and Sherriff, R.L., 2012. California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. *Forest Ecology and Management* 270: 25–34.

Converse, S.J., Block, W.M., and White, G.C., 2006. Small mammal population and habitat responses to forest thinning and prescribed fire. *Forest Ecology and Management* 228 (1–3): 263–273.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., and Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal of Forestry* 95 (4): 23–29.

D'Amato, A.W., Bradford, J.B., Shawn, F., and Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications* 23 (8): 1735–1742.

Le Dantec, V., Dufrêne, E., and Saugier, B., 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. *Forest Ecology and Management* 134 (1–3): 71–81.

Davis, L.R. and Puettmann, K.J., 2009. Initial response of understory vegetation to three alternative thinning treatments. *Journal of Sustainable Forestry* 28 (8): 904–934.

Dawson, T.E., 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95 (4): 565–574.

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., and Tu, K.P., 2002. Stable Isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.

DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T., Amoroso, M.M., Bigler, C., Camarero, J.J., Čufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hereş, A.M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanič, T., Linares, J.C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner, B., Sangüesa-Barreda, G., Stojanovic, D.B., Suárez, M.L., Villalba, R., and Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nature Communications* 11 (1): 1–9.

Devine, W.D. and Harrington, C.A., 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. *Trees - Structure and Function* 20 (6): 747–756.

Devine, W.D. and Harrington, C.A., 2007. Release of Oregon white oak from overtopping Douglas-fir: Effects on soil water and microclimate. *Northwest Science* 81 (2): 112–124.

Devine, W.D. and Harrington, C.A., 2013. Restoration release of overtopped Oregon white oak increases 10-year growth and acorn production. *Forest Ecology and Management* 291: 87–95.

Devine, W.D., Harrington, C.A., and Peter, D.H., 2007a. Oak woodland restoration: Understory response to removal of encroaching conifers. *Ecological Restoration* 25 (4): 247–255.

Diffenbaugh, N.S., Singh, D., Mankin, J.S., Horton, D.E., Swain, D.L., Touma, D., Charland, A., Liu, Y., Haugen, M., Tsiang, M., and Rajaratnam, B., 2017. Quantifying the influence of global warming on unprecedented extreme climate events. *Proceedings of the National Academy of Sciences of the United States of America* 114 (19): 4881–4886.

Dodson, E.K. and Peterson, D.W., 2010. Dry coniferous forest restoration and understory plant diversity: The importance of community heterogeneity and the scale of observation. *Forest Ecology and Management* 260 (10): 1702–1707.

Drobyshev, I., Koch Widerberg, M., Andersson, M., Wang, X., and Lindbladh, M., 2019. Thinning around old oaks in spruce production forests: current practices show no positive effect on oak growth rates and need fine tuning. *Scandinavian Journal of Forest Research* 34 (2): 126–132.

Ehleringer, J.R. and Dawson, T.E., 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell & Environment* 15: 1073–1082.

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., and Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88 (3): 430–434.

Ehleringer, J.R., Roden, J., and Dawson, T.E., 2000. Assessing ecosystem-level water relations through stable isotope ratio analyses. *Methods in ecosystem science*: 181–198.

Ellmore, G.S. and Ewers, F.W., 1986. Fluid flow in the eutermost xylem increment of a ring-porous tree , *Ulmus americana*. *American Journal of Botany* 73 (12): 1771–1774.

Engber, E.A., Morgan Varner, J., Arguello, L.A., and Sugihara, N.G., 2011. The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. *Fire Ecology* 7 (2): 32–50.

Engber, E.A. and Varner, J.M., 2012. Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research* 42 (11): 1965-1975.

Fritschle, J.A., 2008. Reconstructing historic ecotones using the public land survey: The lost prairies of Redwood National Park. *Annals of the Association of American Geographers* 98 (1): 24–39.

Gedalof, Z., Pellat, M., and Smith, D.J., 2006. From prairie to forest: three centuries of environmental change at Rocky Point, Vancouver Island, British Columbia. *Northwest Science* 80 (1): 34–46.

Gilligan, L.A. and Muir, P.S., 2011. Stand structures of Oregon white oak woodlands, regeneration, and their relationships to the environment in Southwestern Oregon. *Northwest Science* 85 (2): 141-158.

Girona, M.M., Rossi, S., Lussier, J.M., Walsh, D., and Morin, H., 2017. Understanding tree growth responses after partial cuttings: A new approach. *PLoS ONE* 12 (2): 1-18.

Hahm, W.J., Dietrich, W.E., and Dawson, T.E., 2018. Controls on the distribution and resilience of Quercus garryana: ecophysiological evidence of oak's water-limitation tolerance. *Ecosphere* 9 (5): 1-27.

Harrington, C.A. and Devine, W.D., 2006. A practical guide to oak release. *USDA General Technical Report*. PNW-GTR-666: 1-24.

Hastings, M.S., Barnhart, S., and McBride, J.R., 1997. Restoration Management of Northern Oak Woodlands. *USDA Forest Service General Technical Report*. PSW-GTR-16: 275–280.

Hayes, B.J.P., Chan, S., Emmingham, H., Tappeiner, C., Kellogg, L.D., and Bailey, D., 1996. Wildlife response to thinning young forest in the Pacific northwest. *Journal of Forestry* 95(8): 28-33.

Hayes, G.F. and Holl, K.D., 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* 17 (6): 1694–1702.

Hochberg, U., Rockwell, F.E., Holbrook, N.M., and Cochard, H., 2018. Iso/anisohydry: A plant–environment interaction rather than a simple hydraulic trait. *Trends in Plant Science* 23 (2): 112–120.

Holling, C.S. and Meffe, G.K., 1996. Command and control and the pathology of natural resource management. *Conservation Biology* 10 (2): 328–337.

Johnson, D.M., Woodruff, D.R., McCulloh, K.A., and Meinzer, F.C., 2009. Leaf hydraulic conductance, measured in situ, declines and recovers daily: Leaf hydraulics, water potential and stomatal conductance in four temperate and three tropical tree species. *Tree Physiology* 29 (7): 879–887.

Kabrick, J.M., Dey, D.C., Kinkead, C.O., Knapp, B.O., Leahy, M., Olson, M.G., Stambaugh, M.C., and Stevenson, A.P., 2014. Silvicultural considerations for managing fire-dependent oak woodland ecosystems. GTR NRS-P-142: 1-15.

Kane, J.M., Engber, E.A., and McClelland, J.E., 2019. Effectiveness and impacts of girdling treatments in a conifer-encroached Oregon white oak woodland. *Forest Ecology and Management* 447: 77–86.

Kerhoulas, L.P., Kolb, T.E., and Koch, G.W., 2013. Tree size, stand density, and the source of water used across seasons by ponderosa pine in northern Arizona. *Forest Ecology and Management* 289: 425–433.

Kimmerer, R.W. and Lake, F.K., 2001. The role of indigenous burning in land management. *Journal of Forestry* 99 (11): 36–41.

Klein, T., 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Functional Ecology* 28 (6): 1313–1320.

Klinka, K., Chen, H.Y.H., Wang, Q., and De Montigny, L., 1996. Forest canopies and their influence on understory vegetation in early- seral stands on west Vancouver Island. *Northwest Science* 70 (3): 193–200.

Lamson, N.I., Smith, H.C., Perkey, A.W., and Brock, S.M., 1990. Crown release increases growth of crop trees. *USDA Research Paper Northeastern Forest Experimentation Station* 635.

Landres, P.B., Morgan, P., and Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9 (4): 1179.

Lettow, M.C., Brudvig, L.A., Bahlai, C.A., and Landis, D.A., 2014. Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management* 329: 89–98.

Lightfoot, K.G. and Parrish, O., 2009. *California Indians and their environment: an introduction*. Univ of California Press, Berkley, California.

Livingston, A.C., Varner, J.M., Jules, E.S., Kane, J.M., and Arguello, L.A., 2016. Prescribed fire and conifer removal promote positive understorey vegetation responses in oak woodlands. *Journal of Applied Ecology* 53 (5): 1604–1612.

Long, J.W., Goode, R.W., Gutteriez, R.J., Lackey, J.J., and Anderson, M.K., 2017. Managing California black oak for tribal ecocultural restoration. *Journal of Forestry* 115 (5): 426-434.

Manning, A.D., Fischer, J., and Lindenmayer, D.B., 2006. Scattered trees are keystone structures - Implications for conservation. *Biological Conservation* 132 (3): 311–321.

Marshall, S., 2017. Technical soil report for Kneeland site. *Unpublished Research*.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., and Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? 178 (4): 719–739.

McDowell, N.G., Sevanto, S., Phytologist, S.N., and April, N., 2010. The mechanisms of carbon starvation : how, when, or does it even occur at all? *New Phytologist* 186 (2): 264–266.

McGarigal, K. and McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* 65 (3): 235–260.

Michael Barbour, Todd Keeler-Wolf, A.S., 2007. *Terrestrial Vegetation of California*. University of California Press, Berkley, California.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., and Kent, J., 2010. Biodiversity hotspots for conservation politics. *Nature* 468 (7326): 895.

Nielsen, S., Kirschbaum, C., and Haney, A., 2003. Restoration of midwest oak barrens: Structural manipulation or process-only? *Ecology and Society* 7 (2): 2-15.

Nixon, K.C., 2002. The oak (Quercus) biodiversity of California and adjacent regions. *USDA Forest Service General Technical Report*. PSW-GTR-184: 3-20.

Peñuelas, J., Lloret, F., and Montoya, R., 2001. Severe drought effects on mediterranean woody flora in Spain. *Forest Science* 47 (2): 214–218.

Perchemlides, K.A., Muir, P.S., and Hosten, P.E., 2008. Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in southwestern Oregon. *Rangeland Ecology and Management* 61 (1): 98–109.

Purcell, K.L. and Stephens, S.L., 2005. Changing fire regimes and the avifauna of California oak woodlands. *Studies in Avian Biology* 30 (30): 33–45.

Reid, J.L., Holmberg, N.J., Albrecht, M., Arango-Caro, S., Hajek, O., Long, Q., and Trager, J., 2020. Annual understory plant recovery dynamics in a temperate woodland mosaic during a decade of ecological restoration. *Natural Areas Journal* 40 (1): 23–24.

Ries, T.D.S., 2004. A predictive model of edge effects. *Ecology* 85 (11): 2917–2926.

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., and Coomes, D.A., 2013. Patterns and drivers of tree mortality in Iberian forests: Climatic effects are modified by competition. *PLoS ONE* 8 (2): 1-10.

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

Skov, K.R., Kolb, T.E., and Wallin, K.F., 2004. Tree size and drought affect ponderosa pine physiological response to thinning and buring treatments. *Forest Science* 50 (1): 1–11.

Sperry, J.S., 2000. Hydraulic constraints on plant gas exchange. *Agricultural and Forest Meteorology* 104 (1): 13–23.

Sperry, J.S., Hacke, U.G., Oren, R., and Comstock, J.P., 2002. Water deficits and hydraulic limits to leaf water supply. *Plant, Cell and Environment* 25 (2): 251–263.

Swain, D.L., Horton, D.E., Singh, D., and Diffenbaugh, N.S., 2016. Trends in atmospheric patterns conducive to seasonal precipitation and temperature extremes in California. *Science Advances* 2 (4): 1–14.

Swain, D.L., Langenbrunner, B., Neelin, J.D., and Hall, A., 2018. Increasing precipitation volatility in twenty-first-century California. *Nature Climate Change* 8 (5): 427–433.

Swain, D.L., Singh, D., Touma, D., and Diffenbaugh, N.S., 2020. Attributing extreme events to climate change: A new frontier in a warming world. *One Earth* 2 (6): 522–527.

Taneda, H. and Sperry, J.S., 2008. A case-study of water transport in co-occurring ring- versus diffuse-porous trees: Contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiology* 28 (11): 1641–1651.

Tardieu, F. and Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany* 49 (Special): 419–432.

Thornton, D.H., Branch, L.C., and Sunquist, M.E., 2011. The influence of landscape, patch, and within-patch factors on species presence and abundance: A review of focal patch studies. *Landscape Ecology* 26 (1): 7–18.

Thysell, D.R. and Carey, A.B., 2001a. Quercus garryana communities in the Puget Trough, Washington. *Northwest Science* 75 (3): 219–235.

Thysell, D.R. and Carey, A.B., 2001b. Manipulation of density of Pseudotsuga menziesii canopies: Preliminary effects on understory vegetation. *Canadian Journal of Forest Research* 31 (9): 1513–1525.

Tyree, M.T. and Sperry, J.S., 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* 40 (1): 19–36.

Underwood, S., Arguello, L., and Siefkin, N., 2003. Restoring ethnographic landscapes and natural elements in Redwood National Park. *Ecological Restoration* 21 (4): 278–283.

Veldman, J.W., Buisson, E., Durigan, G., Fernandes, G.W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G.E., Veldman, R.G., Zaloumis, N.P., Putz, F.E., and Bond, W.J., 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13 (3): 154–162.

Walter, K., Roig, S., Evett, R.R., Gea-izquierdo, G., and Cañellas, I., 2013. Mediterranean Oak Woodland Working Landscapes. *Springer Landscape Series 16*: 1-21.

Wardman, C.W. and Schmidt, M.G., 1998. Growth and form of Douglas-fir adjacent to persistent vine maple gaps in southwestern British Columbia. *Forest Ecology and Management* 106 (2–3): 223–233.

Watkinson, A.R. and Ormerod, S.J., 2001. Grasslands, grazing and biodiversity: Editors' introduction. *Journal of Applied Ecology* 38 (2): 233–237.

Wayman, R.B. and North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *Forest Ecology and Management* 239 (1–3): 32–44.

West, A.G., Dawson, T.E., February, E.C., Midgley, G.F., Bond, W.J., and Aston, T.L., 2012. Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phytologist* 195 (2): 396–407.

Wiens, J.A., 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7 (1): 81–120.

Wilson, S.M. and Carey, A.B., 2000. Legacy retention versus thinning: Influences on small mammals. *Northwest Science* 74 (2): 131–145.

Wright, E.F., Canham, C.D., and Coates, K.D., 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research* 30 (10): 1571–1580.

Vander Yacht, A.L., Barrioz, S.A., Keyser, P.D., Harper, C.A., Buckley, D.S., Buehler, D.A., and Applegate, R.D., 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. *Forest Ecology and Management* 390: 187–202.

APPENDIX A

Appendix A. *Oregon white oak leaf predawn (Ψ_{PD}) and midday (Ψ_{MD}) water potential (mean ± standard error) among three levels of conifer encroachment (open, moderate, heavy) across the 2017 and 2018 growing seasons in Kneeland, CA. Due to a delayed study start, May and June data were not collected in 2017.*

Encroachment	**Year**	**Month**	**Ψ_{PD} (MPa)**	**Ψ_{MD} (MPa)**	***N* (Trees)**
Open	2017	July	-0.39 ± 0.02	-2.18 ± 0.06	30
Moderate	2017	July	-1.48 ± 0.08	-2.15 ± 0.08	30
Heavy	2017	July	-1.50 ± 0.05	-1.52 ± 0.09	17
Open	2017	August	-2.65 ± 0.11	-3.28 ± 0.08	30
Moderate	2017	August	-0.53 ± 0.03	-2.98 ± 0.08	30
Heavy	2017	August	-1.08 ± 0.06	-2.37 ± 0.11	25
Open	2017	September	-1.27 ± 0.07	-2.65 ± 0.08	30
Moderate	2017	September	-2.53 ± 0.15	-2.81 ± 0.09	28
Heavy	2017	September	-0.54 ± 0.03	-1.36 ± 0.06	21
Open	2017	October	-0.56 ± 0.04	-3.64 ± 0.08	30
Moderate	2017	October	-0.65 ± 0.04	-3.55 ± 0.13	25
Heavy	2017	October	-0.73 ± 0.06	-1.50 ± 0.12	20
Open	2018	May	-0.19 ± 0.02	-1.02 ± 0.03	20
Moderate	2018	May	-0.41 ± 0.02	-1.13 ± 0.05	20
Heavy	2018	May	-0.90 ± 0.02	-0.99 ± 0.05	17
Open	2018	June	-1.94 ± 0.10	-1.08 ± 0.05	20
Moderate	2018	June	-2.92 ± 0.14	-1.21 ± 0.05	20
Heavy	2018	June	-2.91 ± 0.10	-0.91 ± 0.03	19
Open	2018	July	-0.55 ± 0.01	-2.25 ± 0.12	20
Moderate	2018	July	-0.27 ± 0.01	-2.80 ± 0.11	20
Heavy	2018	July	-0.90 ± 0.02	-1.93 ± 0.12	19
Open	2018	August	-1.52 ± 0.06	-3.40 ± 0.10	20
Moderate	2018	August	-2.08 ± 0.11	-3.46 ± 0.09	18
Heavy	2018	August	-2.67 ± 0.10	-2.85 ± 0.14	19
Open	2018	September	-0.41 ± 0.03	-3.85 ± 0.07	20
Moderate	2018	September	-0.57 ± 0.03	-3.62 ± 0.07	17
Heavy	2018	September	-0.62 ± 0.03	-2.48 ± 0.20	15
Open	2018	October	-1.04 ± 0.07	-3.87 ± 0.08	18
Moderate	2018	October	-1.52 ± 0.14	-4.04 ± 0.05	18
Heavy	2018	October	-2.11 ± 0.21	-3.56 ± 0.14	14

APPENDIX B

Appendix B. *Oregon white oak predawn (Ψ_{PD}) and midday (Ψ_{MD}) leaf water potential (mean ± standard error) under unthinned, pre-treatment (2017), and post-treatment (2018) conditions in moderate and heavily encroached stands in Kneeland, CA. Data are based on July through October measurements.*

Encroachment	**Year**	**Ψ_{PD} (MPa)**	**Ψ_{MD} (MPa)**	***N* (Trees)**
Moderate Control	2017	-1.40 ± 0.12	-3.17 ± 0.10	40
	2018	-1.29 ± 0.08	-2.65 ± 0.11	113
Heavy Control	2017	-0.69 ± 0.05	-1.92 ± 0.14	19
	2018	-0.99 ± 0.07	-2.06 ± 0.10	103
Moderate Thinned	2017 (Pre)	-1.25 ± 0.10	-2.67 ± 0.08	73
	2018 (Post)	-1.17 ± 0.08	-2.54 ± 0.11	114
Heavy Thinned	2017 (Pre)	-0.60 ± 0.03	-1.68 ± 0.08	64
	2018 (Post)	-0.78 ± 0.05	-1.83 ± 0.08	102

APPENDIX C

Appendix C. *Daily xylem water potential at predawn (Ψ_{PD}) and midday (Ψ_{MD}) for Oregon white oak trees under open, moderate, moderate thinned, heavy, and heavy thinned conditions in Kneeland, CA. Measurements were taken with a stem psychrometer every 30 minutes from July 29th through August 5th, 2019. Ψ_{PD} occurred from 0000 – 0500 and Ψ_{MD} from 1130 – 1630. No Ψ_{PD} values exist on July 29th as instruments were installed that day. All Ψ_{MD} values are in MPa. "T" indicated stands were thinned after 2017 growing season.*

	Open		**Moderate**		**Moderate (T)**		**Heavy**		**Heavy (T)**	
Date	**Ψ_{PD}**	**Ψ_{MD}**	**Ψ_{PD}**	**Ψ_{MD}**	**Ψ_{PD}**	**Ψ_{MD}**	**Ψ_{PD}**	**Ψ_{MD}**	**Ψ_{PD}**	**Ψ_{MD}**
29-Jul	/	-1.27	/	-1.65	/	-0.90	/	-1.07	/	-2.05
30-Jul	-0.34	-1.48	-0.51	-1.85	-0.02	-2.00	-0.33	-1.08	-0.03	-1.01
31-Jul	-0.05	-2.22	-0.44	-1.98	-0.01	-1.73	-0.17	-1.43	0.00	-1.43
1-Aug	-0.53	-1.80	-0.25	-1.79	-0.03	-0.67	-0.01	-1.16	0.00	-1.31
2-Aug	0.00	-2.15	-0.20	-1.74	-0.05	-1.42	-0.01	-1.26	0.00	-1.58
3-Aug	-0.11	-2.47	-0.17	-1.55	0.00	-1.62	0.00	-1.51	0.00	-1.77
4-Aug	0.00	-2.26	-0.25	-1.26	-0.04	-1.52	0.00	-1.49	0.00	-1.78
5-Aug	0.00	-1.12	-0.10	-0.63	-0.06	-1.10	-0.01	-1.03	0.00	-1.05

APPENDIX D

Appendix D. *Oregon white oak leaf- (g_s) and tree-level (G_s) stomatal conductance rates (mean ± standard error) among three levels of conifer encroachment (Open, Moderate, Heavy) across the 2018 and 2019 growing seasons in Kneeland, CA. Due to leaf senescence in this deciduous species, October 2019 data were not collected.*

Encroachment	**Year**	**Month**	**g_s (mmol H_2O m^{-2} s^{-1})**	**G_s (mol H_2O s^{-1})**	***N* (Trees)**
Open	2018	May	285 ± 14	54 ± 8	20
Moderate	2018	May	310 ± 18	45 ± 5	20
Heavy	2018	May	346 ± 8	51 ± 6	20
Open	2018	June	363 ± 15	65 ± 6	20
Moderate	2018	June	443 ± 27	62 ± 7	19
Heavy	2018	June	246 ± 9	36 ± 4	20
Open	2018	July	409 ± 20	75 ± 9	20
Moderate	2018	July	389 ± 30	58 ± 8	20
Heavy	2018	July	384 ± 20	55 ± 5	20
Open	2018	August	230 ± 15	44 ± 7	20
Moderate	2018	August	342 ± 21	50 ± 5	20
Heavy	2018	August	297 ± 18	43 ± 5	20
Open	2018	September	214 ± 11	39 ± 4	20
Moderate	2018	September	305 ± 19	44 ± 4	20
Heavy	2018	September	281 ± 12	39 ± 3	20
Open	2018	October	270 ± 16	50 ± 8	18
Moderate	2018	October	361 ± 26	53 ± 8	17
Heavy	2018	October	254 ± 20	36 ± 4	18
Open	2019	May	347 ± 17	63 ± 7	20
Moderate	2019	May	292 ± 14	46 ± 6	20
Heavy	2019	May	219 ± 10	31 ± 3	19
Open	2019	June	518 ± 22	88 ± 7	19
Moderate	2019	June	474 ± 13	72 ± 8	20
Heavy	2019	June	420 ± 30	59 ± 7	17
Open	2019	July	468 ± 21	87 ± 9	20
Moderate	2019	July	440 ± 15	66 ± 7	20
Heavy	2019	July	356 ± 18	50 ± 5	17
Open	2019	August	387 ± 12	72 ± 7	20
Moderate	2019	August	440 ± 17	62 ± 7	15
Heavy	2019	August	334 ± 12	47 ± 4	16
Open	2019	September	340 ± 8	63 ± 7	20
Moderate	2019	September	416 ± 15	62 ± 7	16
Heavy	2019	September	266 ± 9	35 ± 4	12

APPENDIX E

Appendix E. *Post/pretreatment leaf-level stomatal conductance (mean ± standard error) for oaks in moderate and heavily encroached stands under thinned and unthinned conditions in Kneeland, CA. The pre-treatment year was 2017.*

Encroachment	**Year**	**Treatment**	**Ratio (Pre vs. Post)**	***N* (Trees)**
Moderate	2018	Unthinned	0.97 ± 0.09	18
	2019		1.17 ± 0.12	18
Moderate	2018	Thinned	1.17 ± 0.08	31
	2019		1.20 ± 0.11	31
Heavy	2018	Unthinned	0.85 ± 0.08	11
	2019		0.75 ± 0.04	11
Heavy	2018	Thinned	1.14 ± 0.08	36
	2019		1.01 ± 0.08	36

APPENDIX F

Appendix F. *Oregon white oak and Douglas-fir hydrogen (δD) and oxygen ($\delta^{18}O$) stable isotope signatures under three levels of conifer encroachment (open, moderate, heavy) in Kneeland, CA in August 2018.*

Encroachment	**Species**	**δD (‰)**	**$\delta^{18}O$ (‰)**	***N* (Trees)**
Open	Oak	-66.86 ± 2.00	-9.37 ± 0.51	9
Open	Douglas-fir	-62.16 ± 1.69	-8.33 ± 0.33	9
Moderate	Oak	-72.17 ± 1.91	-10.29 ± 0.33	20
Moderate	Douglas-fir	-66.74 ± 1.43	-8.80 ± 0.23	20
Heavy	Oak	-62.88 ± 1.32	-8.78 ± 0.30	19
Heavy	Douglas-fir	-59.28 ± 0.97	-7.84 ± 0.17	19

APPENDIX G

Appendix G. *Vascular plants observed among three levels of conifer encroachment under thinned and unthinned conditions in an Oregon white oak woodland in Kneeland, CA. Understory plant surveys were conducted during early summer of 2018 and 2019, one and two years following a 2017 thinning treatment that removed conifers. "X" denotes species present, "*" denotes non-native species, and "**" indicates invasive, non-native species.*

Species	**Common Name**	**Open**	**Moderate Unthinned**	**Moderate Thinned**	**Heavy Unthinned**	**Heavy Thinned**
Achillea millefolium	common yarrow	X	X	X		
Acmispon americanus	American bird's foot trefoil			X		
Acmispon parviflorus	hill lotus	X	X	X	X	X
Agoseris heterophylla	mountain dandelion		X	X		
Agrostis capillaris	colonial bentgrass *	X	X	X		
Anisocarpus madioides	woodland madia	X	X	X	X	X
Anthoxanthum aristatum	annual vernalgrass *	X	X	X	X	X
Arbutus menziesii	madrone		X			
Asyneuma prenanthoides	California harebell		X			
Avena barbata	slender oat **	X	X			
Brodiaea coronaria	crown brodiaea		X	X		
Bromus carinatus	California bromegrass	X	X	X	X	X
Calochortus tolmiei	hairy star tulip	X	X	X		
Chlorogalum pomeridianum	soaproot	X	X			
Clarkia purpurea	purple clarkia		X			
Claytonia perfoliata	miners lettuce			X		X

Species	**Common Name**	**Open**	**Moderate Unthinned**	**Moderate Thinned**	**Heavy Unthinned**	**Heavy Thinned**
Clinopodium douglasii	yerba buena		X	X	X	X
Collomia heterophylla	variableleaf collomia		X	X	X	X
Cynoglossum grande	hounds tongue	X	X	X	X	X
Cynosurus echinatus	dogtail grass **	X	X	X	X	X
Dactylis glomerata	orchardgrass **	X	X	X	X	X
Dichelostemma ida-maia	firecracker flower	X		X		X
Elymus glaucus	blue wildrye	X				
Eriophyllum lanatum	woolly sunflower		X		X	
Euthamia occidentalis	western goldenrod			X		
Fragaria vesca	wild strawberry	X	X	X	X	X
Galium aparine	cleavers	X	X	X	X	X
Galium californicum	California bedstraw			X		X
Geranium robertianum	Robert's geranium *	X		X	X	X
Helminthotheca echioides	bristley ox tongue **			X		X
Hieracium albiflorum	white hawkweed		X	X	X	X
Holodiscus discolor	oceanspray		X		X	
Hypochaeris radicata	hairy cats ear **		X	X	X	X
Lasthenia californica	common goldfield		X			
Lathyrus polyphyllus	Oregon pea		X		X	
Leptosiphon androsaceus	false babystars		X	X		
Lonicera hispidula	pink honeysuckle		X		X	
Madia gracilis	grassy tarweed	X	X	X		
Osmorhiza berteroi	sweet cicely	X	X	X	X	X
Osmorhiza occidentalis	mountain sweet cicely	X	X	X	X	X

Species	**Common Name**	**Open**	**Moderate Unthinned**	**Moderate Thinned**	**Heavy Unthinned**	**Heavy Thinned**
Pentagramma triangularis	goldback fern		X		X	
Plantago lanceolata	ribwort **	X	X		X	
Pseudotsuga menzeisii	Douglas-fir		X	X	X	X
Quercus garryana	Oregon white oak	X	X	X	X	X
Ranunculus californicus	California buttercup	X		X		X
Rosa gymnocarpa	wood rose	X		X		X
Rumex acetosella	sheep sorrel **	X	X		X	
Scutellaria antirrhinoides	skullcap	X	X	X		
Silene laciniata	indian pink	X	X			
Solidago elongata	west coast goldenrod	X	X	X	X	X
Stachys ajugoides	hedge nettle	X	X		X	
Stachys bullata	southern hedge nettle	X	X	X	X	X
Taraxacum officinale	red seeded dandelion *			X		X
Toxicodendron diversilobum	poison-oak	X	X	X	X	X
Trifolium albopurpureum	Indian clover			X		X
Triteleia laxa	Ithuriel's spear	X	X	X	X	X
Umbellularia californica	California bay		X	X	X	X
Veronica americana	American brooklime	X	X		X	
Vicia americana	American vetch	X	X	X	X	X

APPENDIX H

Appendix H. *Mammals observed among three levels of conifer encroachment under thinned and unthinned conditions in an Oregon white oak woodland in Kneeland, CA. Mammals were inventoried in the Fall of 2018 and 2019, one and two years after a 2017 thinning treatment that removed conifers. Rodents were identified as mammals smaller than squirrels, as we could not identify to species from photos. "X" denotes species present in specific stand condition type, and "*" indicates species of special concern.*

Species	**Common Name**	**Open**	**Moderate Unthinned**	**Moderate Thinned**	**Heavy Unthinned**	**Heavy Thinned**
Bassariscus astutus	ring-tailed cat		X			
Glaucomys oregonensis	Humboldt's flying squirrel		X	X	X	X
Lynx rufus	bobcat		X		X	X
Mephitis mephitis	striped skunk	X	X			
Odocoileus hemionus	mule deer	X	X	X	X	X
Pekania pennanti	fisher*				X	
Procyon lotor	racoon			X	X	
Puma concolor	mountain lion		X		X	
Rodentia spp.	rodent	X	X	X	X	
Sciurus griseus	grey squirrel	X	X	X	X	X
Spilogale gracilis	spotted skunk				X	
Sylvilagus bachmani	brush rabbit	X	X	X	X	
Tamiasciurus douglasii	Douglas squirrel		X		X	
Ursus americanus	black bear	X	X	X	X	X
Urocyon cinereoargenteus	grey fox	X	X	X	X	X

APPENDIX I

Appendix I. *Birds identified via call and observation among three levels of conifer encroachment under thinned and unthinned conditions in an Oregon white oak woodland in Kneeland, CA. Surveys were conducted in early June in 2018 and 2019, one and two years following a thinning treatment that removed conifers. "X" denotes species present in each stand condition.*

Species	**Common Name**	**Open**	**Moderate Unthinned**	**Moderate Thinned**	**Heavy Unthinned**	**Heavy Thinned**
Melanerpes formicivorus	acorn woodpecker	X	X			
Selasphorus sasin	Allen's hummingird		X		X	
Corvus brachyrhynchos	American crow	X	X	X	X	X
Turdus migratorius	American robin		X			
Calypte anna	Anna's hummingbird	X	X	X	X	X
Pheucticus melanocephalus	black-headed grossbeak			X	X	
Patagioenas fasciata	band-tailed pigeon					X
Callipepla californica	California quail	X	X			
Vireo cassinii	Cassin's vireo	X	X	X	X	X
Poecile rufescens	chestnut-backed chickadee	X	X	X	X	X
Bombycilla cedrorum	cedar waxwing		X			
Spizella passerina	chipping sparrow	X			X	
Chaetura pelagica	chimney swift				X	
Corvus corax	common raven	X			X	X
Junco hyemalis	dark-eyed junco	X	X	X	X	X
Regulus satrapa	golden-crowned kinglet				X	
Dryobates villosus	hairy woodpecker		X	X		
Setophaga occidentalis or *Setophaga nigrescens*	hermit/black throated gray warbler	X		X	X	X

Species	**Common Name**	**Open**	**Moderate Unthinned**	**Moderate Thinned**	**Heavy Unthinned**	**Heavy Thinned**
Catharus guttatus	hermit thrush	X	X	X		X
Haemorhous mexicanus	house finch				X	X
Vireo huttoni	Hutton's vireo	X	X	X	X	X
Passerina amoena	lazuli bunting	X	X			
Zenaida macroura	mourning dove	X			X	
Oreortyx pictus	mountain quail	X	X	X	X	X
Colaptes auratus	Northern flicker	X	X	X	X	X
Glaucidium gnoma	Northern pygmy-owl	X			X	
Contopus cooperi	olive-sided flycatcher	X				
Dryocopus pileatus	pileated woodpecker	X	X		X	X
Empidonax difficilis	Pacific-slope flycatcher			X		
Sitta canadensis	red-breasted nuthatch	X	X	X	X	X
Sphyrapicus ruber	red-breasted sapsucker				X	
Buteo lineatus	red-shouldered hawk			X		
Buteo jamaicensis	red-tailed hawk	X				
Dendragapus fuliginosus	sooty grouse	X	X	X	X	X
Cyanocitta stelleri	Steller's jay	X	X	X	X	X
Sialia mexicana	Western bluebird	X			X	
Sturnella neglecta	Western meadowlark	X	X	X	X	X
Piranga ludoviciana	Western tanager	X		X	X	X
Contopus sordidulus	Western wood-pewee		X			
Troglodytes hiemalis	winter wren			X		X