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Douglas-fir encroachment reduces drought resistance in Oregon white oak of northern California

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ABSTRACT

Oregon white oak (*Quercus garryana* Douglas ex Hook.) is experiencing increasing competition from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) across much of its range at the same time as climate variability is increasing, including more frequent and extreme droughts. These combined factors suggest that Douglas-fir encroachment is not only leading to range reduction from competition, but also likely exacerbating drought stress for a keystone oak species in the Pacific West of North America. Our research examines this by evaluating radial tree growth and drought response in Oregon white oak (n = 104 trees) and Douglas-fir (n = 104 trees) along a gradient of encroachment in an oak woodland in the North Coast region of California. Linear mixed-effects models were used to evaluate the effects of tree diameter, Douglas-fir competition, oak competition, and climate on drought resistance (2013–2015) and recent tree growth (2002–2016). Oregon white oak growth was more resistant to prolonged drought than Douglas-fir. However, Oregon white oak drought resistance declined with increasing Douglas-fir competition and increased with increasing oak competition. Oregon white oak and Douglas-fir growth related to different seasonal climate factors, but both species were more strongly limited by Douglas-fir competition than climate. Oregon white oak may be better suited to future climate conditions than Douglas-fir, although Douglas-fir encroachment will likely continue to reduce Oregon white oak resistance to future drought. These results present a strong case for the need to release Oregon white oak by controlling Douglas-fir in areas that were historically oak woodlands with diverse understory species, wildlife, and important traditional ecological values and services.

1. Introduction

In the Pacific West, oak woodlands are highly-valued habitats that support rich and diverse understory communities (Devine et al., 2007; Livingston et al., 2016; Thysell and Carey, 2001), wildlife (Hagar and Stern, 2001; Ryan and Carey, 1995), and traditional ecological values and services (Hosten et al., 2006). Following attempted cultural genocide of Native Americans and the adoption of other fire exclusion practices (Underwood et al., 2003), fire occurrence declined dramatically across these ecosystems that formerly burned frequently. In the prolonged absence of fire, Oregon white oak (*Quercus garryana* Douglas ex Hook.) woodlands declined by as much as 30% (Fritschle, 2008) due to their vulnerability to encroachment by shade-tolerant conifers like Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which can grow quickly through oak canopies (Hunter and Barbour, 2001); this encroachment is occurring throughout much of Oregon white oak's range (Barnhart et al., 1996; Schriver et al., 2018; Thysell and Carey, 2001; Cocking et al., 2015). Unabated, reduced growth from Douglas-fir encroachment leads to oak mortality, and eventually, to complete ecosystem change (Barnhart et al., 1996; Engber et al., 2011; Gould et al., 2011).

At the same time as oak woodland ecosystems are converting to closed conifer forests, climate change is increasing the likelihood of extreme drought conditions throughout California and the Pacific Southwest (Diffenbaugh et al., 2015; Williams et al., 2015). Increased climate variability is projected through the 21st century, including an amplification of the existing annual Mediterranean precipitation pattern in California and more frequent drought and extreme hydrological events (Swain et al. 2018). Conditions during the prolonged drought that occurred in California from 2012 to 2015 may be exemplary of future severe drought conditions (Swain et al., 2016; Williams et al., 2015) and provide a unique opportunity to examine the combined effects of conifer encroachment and climate change in this important ecosystem.

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To predict ecosystem change, it is critical to understand how individual species respond to specific changes in climate throughout the year, as tree species are affected by climate changes unequally due in part to varying seasonality of water use, growth, and repair (Anderegg et al., 2013). Anatomical and physiological differences suggest that oak growth may be more resistant to prolonged drought than Douglas-fir (Abrams, 1990; Allen, 2015; Beedlow et al., 2013; Hahm et al., 2020, 2018; Johnson et al., 2009; Kelly, 2016; Littell et al., 2008). However, Douglas-fir competition may compete for scarce water resources (Devine and Harrington, 2007) and interfere with the drought resistance of Oregon white oak, especially given the shade-intolerance of Oregon white oak and well-documented decline of this species as a result of Douglas-fir encroachment (Barnhart et al., 1996; Cocking et al., 2015; Hunter and Barbour, 2001; Schriver et al., 2018; Thysell and Carey, 2001). Alternatively, increasingly hot and dry climate conditions may be favorable for Oregon white oak relative to Douglas-fir and therefore change the competition dynamics between these species. Increased tree density due to Douglas-fir encroachment might even alter understory microclimate in ways that are beneficial to oaks during drought, such as by reducing air and soil temperatures, vapor pressure deficit, and evaporative demand on soil and vegetation, including oaks (Devine et al., 2007; Devine and Harrington, 2007). Reversals in species performance at high levels of competition under increasingly dry conditions have been observed in other forest ecosystems (Gómez-Aparicio et al., 2011). An improved understanding of how competition, climate, and drought affect tree vigor and stand dynamics in oak woodland ecosystems is therefore needed to inform management under rapidly changing ecological and climate conditions.

Tree-growth responses are known to effectively measure drought resistance, where trees experiencing greater impact may have reduced radial growth compared to pre-drought levels (Bottero et al., 2017; Bradford and Bell, 2017; Gleason et al., 2017; Sohn et al., 2016; Vernon et al., 2018). In contrast, drought resistant individuals illustrate little change in growth patterns (Lloret et al., 2011). Further, drought-induced growth declines may trigger mortality (Allen et al., 2015, 2010; Bigler et al., 2007; Cailleret et al., 2017; DeSoto et al., 2020; Pedersen, 1998), especially when resources are already limited by competition (Bradford and Bell, 2017; Young et al., 2017). The effects of competition and climate on tree growth may interact dynamically and depend, in part, on species interactions (Gómez-Aparicio et al., 2011; Marqués et al., 2021; Pretzsch et al., 2013; Sánchez-Salguero et al., 2015). Few studies have directly examined the effects of competition on tree growth under prolonged and severe drought conditions (except see Vernon et al. 2018).

This study used tree rings to examine how Oregon white oak and Douglas-fir growth respond to drought, competition, and climate in an encroached oak woodland in Northwest California. Based in part on previous research, we asked the following questions: 1) Do oaks have greater drought resistance than Douglas-fir? 2) Does competition reduce drought resistance in both species? 3) Is the effect of competition on tree growth greater than climate in both species? And 4) how do Douglas-fir competition and climate factors interact to affect growth in Oregon white oak? The answers to these questions are critical for managing historical oak woodlands with diverse understory species, wildlife, and important traditional ecological values and services.

2. Methods

2.1. Study area

The study site was located in the Iaqua Buttes area (40.71, −123.90) on the Yager Creek tract of Humboldt Redwood Company, LLC near Kneeland, California, USA in Humboldt County (Fig. 1). The climate is characterized as Mediterranean with most precipitation falling between October and May, a 30-year (1981–2010) mean annual precipitation of 1914 mm (down 44% and 19% in 2014 and 2015), and an average temperature of 7.0 °C in December and 19.0 °C in July (up 2.4 °C, 1.9 °C, 2.0 °C in 2013, 2014, and 2015) (Flint and Flint, 2014). The area is within the Franciscan Complex area of the Coast Range Province, composed primarily of sedimentary and metasedimentary rocks. Soils are fine loamy to loamy skeletal and shallow in some places, as evidenced by occasional nearby rock outcrops. Note that in this setting where soft sandstone bedrock comprises the parent material, different depths to bedrock or rockiness, should not be taken as a significant

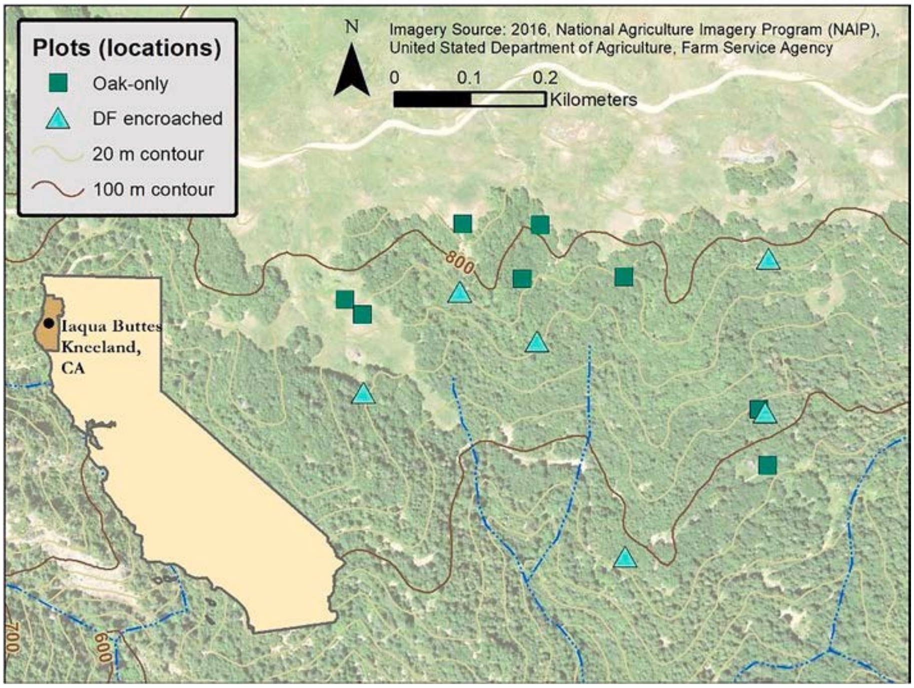

Fig. 1. Locations of trees evaluated in this study including nine plots and four open-grown tree locations at the study site in Humboldt County near Kneeland, California. Points are colored by condition of Oregon white oak trees at each location, oak-only or Douglas-fir (DF) encroached.

variable in explaining woody species distribution (S. Marshall, pers. comm.). Slopes are generally steep (19-35°) with a predominantly southern aspect ranging SE to SW across sample locations (Table 1). An analysis during the 2017 sampling year found no detectable relationships between Douglas-fir encroachment or slope and soil type or water-holding capacity (S. Marshall, unpublished data and pers. comm.). Although there is no evidence of recent windthrow, fire, or harvesting, evidence of periodic cattle grazing disturbance is present. The estimated historic fire return interval within the study area is 6–10 years (LANDFIRE, 2017), but no recorded fire has occurred at our site since 1900 (California Department of Forestry & Fire Protection, 2017) until a prescribed burn in 2019, after this study was conducted. Previous research and historical photos indicate that Douglas-fir was not abundant on the site until the mid to late 20th century (Schriver et al. 2018). This contrasts with the establishment of Oregon white oak which date from the early 1800s, with most establishment occurring between 1865 and 1930 (Schriver et al. 2018).

2.2. Study design

This study used trees sampled from nine plot locations that were randomly selected in 2013 as part of a regional study on conifer encroachment in oak woodland habitats (Schriver et al., 2018). These nine locations were stratified across a gradient of forest conditions (i.e. oak to conifer dominance; Schriver et al., 2018). Five opportunistically located 'open-grown' Oregon white oak trees (at four locations, one multistem) were also included in this study to account for Oregon white oak in conditions absent of competition from other trees, a condition that was present at the site but not represented by the nine randomly selected locations. For this study, Oregon white oak trees were classified into 'oak-only' and 'Douglas-fir (DF) encroached' groups which generally corresponded with stand-level conditions at each location (Table 1; Fig. 1). Oregon white oak trees in oak-only conditions were open-grown or in oak-dominant stands where conifers were not present or limited to the sub-canopy. Douglas-fir encroached white oak trees were in oak stands with Douglas-fir in intermediate, co-dominant, or dominant canopy positions (Schriver et al., 2018).

2.3. Field and lab methods

In 2017 and 2018, all Oregon white oak (120) and Douglas-fir (108) trees (any stem differentiated below breast height, 1.37 m) greater than 10 cm and within a 10 m radius of each plot center were cored perpendicular to the slope at an average height of 0.93 m (SD = 0.18). Tree cores were then mounted, sanded, digitally scanned, and measured using WinDENDRO software (Regent Instruments, 2014). A dissecting microscope was used to identify and confirm visibility of each ring boundary, especially while measuring oak cores with complacent and very narrow rings. Visual and statistical cross-dating methods (COFECHA program; Holmes, 1983) allowed for 104 Oregon white oak trees and 104 Douglas-fir trees to be successfully cross-dated. Douglas-fir series collected for this study had an average length of 37 years (range 11–79) while previous work at this site aged Oregon white oak trees, which in our plots averaged 123 years (range 67–194; Schriver et al. 2018).

Each tree series was converted to basal area increment (BAI) using the package *dplR* in R (Bunn et al., 2018; R Core Team, 2019). Bark thickness was directly measured on mounted cores for 74 Oregon white oak trees that clearly showed complete inner and outer bark. To estimate bark thickness for trees with incomplete bark samples, bark measurement data were used to derive a non-linear model using the form (Eq. (1)):

$$Bark\ thickness = a \times \sqrt{DCH}^{b} \tag{1}$$

where bark was measured in millimeters, *DCH* was diameter at coring height in centimeters, and *a* and *b* were coefficients derived from the data, using the nls function in R (R Core Team, 2019; Zeibig-Kichas et al., 2016). The selected coefficients for white oak were $a = 2.2721$ and $b = 0.6757$, resulting in a standard error of the regression of 2.56 mm for modeled bark measurements with a mean of 7.38 mm. For Douglas-fir, a published model was used to estimate Douglas-fir bark thickness from DBH (Zeibig-Kichas et al., 2016). This model is (Eq. (2)):

$$DF\ bark\ thickness = 0.785 \times \sqrt{DCH} \tag{2}$$

where bark thickness was measured in millimeters and *DCH* was diameter at coring height in centimeters.

To quantify competition around subject trees, all Douglas-fir trees greater than 10 cm diameter at breast height (DBH) and all oak trees greater than 5 cm DBH that were within 15 m radius of each cored tree were mapped with species and DBH recorded. Only 11 mapped oak trees had diameters between 5 and 10 cm. Prior research at the site (Schriver et al. 2018) identified that 5 cm oaks were consistently older than 10 cm DBH Douglas-fir trees, of which the latter were also likely to have less than 15 years of growth at breast height. A 15 m radial distance around each cored tree was chosen to account for crown competition between neighboring trees since it was observed that the largest oak crowns had about a 12 m radius. Stem mapping was completed using a monopod-mounted TruPulse laser range finder and electronic compass placed along four transects radiating from plot center (uphill, downhill, and in contour with the slope). Draft stem-maps were printed and field verified so that noticeable errors could be corrected, resulting in final maps that were highly reflective of the competitive environment.

A total of 1141 competition trees were mapped within 15 m radius of all cored trees. Of these, 532 (47%) were Oregon white oak, 500 (44%) were Douglas-fir, 90 (8%) were California black oak (*Quercus kelloggii* Newb.), 18 (1.6%) were California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.), and 1 (<0.1%) was tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh). Competition trees were grouped into two categories: Douglas-fir and those of other species. This latter group is referred to as "oak competition" and was comprised of only hardwood species with 97% oak species and 83% Oregon white oak.

To estimate Douglas-fir competition and oak competition around each subject tree, the Hegyi index was calculated using the equation (Eq. (3)):

$$Hegyi_t = \sum_{i=1}^{n} \frac{DBH_i}{DBH_t} \times \frac{1}{dist_i} \tag{3}$$

where $Hegyi_t$ represents the competitive strain on the cored subject tree *t*, DBH_t is the DBH of the subject tree, DBH_i is the DBH of each competition tree *i*, and $dist_i$ is the distance between the subject tree and each competition tree, summed for all competition trees (Hegyi, 1974). For each subject tree, the Hegyi index was calculated separately using

Table 1

Condition, species, number, and number of plots (locations) of subject trees. Mean Douglas-fir (DF) competition, oak competition, aspect, slope, and elevation, with ranges of values presented in parenthesis. WO = Oregon white oak.

Condition Group	No. Subject Trees	No. Plots (locations)	DF Competition (Hegyi)	Oak Competition (Hegyi)	Aspect (°)	Slope (°)	Elevation (m)
DF encroached	60 WO	6	4.38 (0.86–14.66)	4.42 (0.58–12.35)	177 (94–231)	30 (16–40)	747 (691–803)
Oak-only	44 WO	8 (4 open-grown)	0.14 (0–0.68)	4.46 (0–17.58)	184 (121–237)	23 (13–32)	790 (696–831)
DF trees	104 DF	7	6.09 (0.56–23.02)	5.20 (0.90–13.42)	165 (94–228)	30 (16–40)	756 (691–803)

Douglas-fir competition and oak competition. We evaluated the optimality of various competition radii lengths and found that Hegyi indices using the full radius of 15 m correlated best with BAI for both species (Pearson correlation coefficient; Sánchez-Salguero et al., 2015). As a comparison to species-specific competition indices, we also summed competition for each subject tree ("total competition") and calculated the percent of total competition from Douglas-fir (see Appendix B for supplementary analyses).

For each plot location, monthly climate data including total precipitation (PPT mm), minimum temperature (TMN °C), maximum temperature (TMX °C), and climatic water deficit (CWD mm) were extracted from the Basin Characterization Model (Flint and Flint, 2014). This downscaled climate model accounts for local topographic and geologic conditions at a 270 m pixel size.

As an exploratory means to identify significant monthly climate relationships for each species, we reviewed climate-growth correlations that also had a biological basis during two 20-year periods (1992–2011 and 1997–2016) just prior to and during the 2013–2015 severe drought in the study area (*treeclim* minimum window size is 20 years). For both Oregon white oak and Douglas-fir, we first developed chronologies of prewhitened ring-width indices using the "Ar" method with the detrend function in *dplR* in R (Bunn et al. 2018). We then created bootstrapped response correlations ($\alpha = 0.05$) with monthly climate data (PPT, TMN, TMX; *treeclim*; Zang and Biondi 2015; R Core Team 2019).

Based on the correlation analysis, the following variables were selected for further analysis for the Oregon white oak series: November-January PPT, September TMX, April-June TMX, and July-August PPT. Variables selected for the Douglas-fir series include: May-June TMX, and June-July PPT. In addition, maximum summer TMX (July, August, or less commonly September TMX; Flint and Flint, 2014), which could not be used in *treeclim* (only a single value per year whereas *treeclim* uses monthly climate data), was also selected for analysis for Oregon white oak trees. To account for lagged climate effects, mean annual CWD for the previous year (November-October) was also selected for further analyses in both species. Mean CWD for the current year was not included because it correlated with significant climate variables ($r > 0.6$) and caused instability in some parameter estimates. Climate variability through the analysis period is shown in Appendix A.

2.4. Drought response

The 2012–2015 California drought led to the most severe moisture deficits in the last millennium (Grantham, 2018; Griffin and Anchukaitis, 2014). In contrast to many other areas of California, the coastal study area was not designated as a moderate or severe drought during 2012 and conditions were normal or above from 2010 to 2012 except for a few brief (weeks) dry periods (PDSI −1 to −1.9) occurring in winter (Jan-Mar) (Palmer Drought Severity Index; National Drought Mitigation Center, 2017). Condsidering that prior conditions in 2008 and 2009 included substantial periods of moderate to severe drought (PDSI −2 to −3.9), we selected 2010 to 2012 to represent growth conditions prior to drought. In Humboldt County, the extended drought period began with dry to severe drought conditions (PDSI −1 to −3.9) in 2013, which intensified to moderate to exceptional levels (PDSI −2 to −5) throughout 2014 and 2015 (National Drought Mitigation Center, 2017). Conditions in 2016 were normal to dry (PDSI 0 to −1.9), so we classified 2016 as a post-drought year to assess drought resilience for the one post-drought year in which radial growth data were available. Therefore, drought resistance and resilience for each subject tree were calculated using the formulas (Eqs. (4) and (5)):

$$\textit{drought resistance} = \frac{\textit{BAI during drought}}{\textit{BAI prior to drought}} \tag{4}$$

$$\textit{drought resilience} = \frac{\textit{BAI post drought}}{\textit{BAI prior to drought}} \tag{5}$$

where radial growth prior to drought (2010–2012), during drought (2013–2015), and post-drought (2016), was measured in basal area increment (Lloret et al., 2011). Drought resistance was calculated for each drought year (2013, 2014, and 2015) and for the entire drought period (mean, 2013–2015) with mean basal area increment for years 2010–2012 indicating radial growth prior to drought in all cases. We recognize that this approach to quantifying drought resistance and resilience has weaknesses (Schwarz et al., 2020); nevertheless these metrics offer valuable insight into Oregon white oak and Douglas-fir response to this record-breaking drought, especially coupled with analyses of species-specific seasonal climate-growth response.

2.5. Statistical methods

For evaluation of drought resistance, analyses of variance (ANOVA) on linear mixed-effects models (package *nlme;* Pinheiro et al. 2017; R Core Team 2019) were used to evaluate log-transformed mean drought resistance over the entire drought period and one-year drought resilience, both with plot as a random effect; and annual drought resistance with random effects of plot and tree. Differences between groups were identified using Tukey's multiple comparisons with packages *emmeans* and *multcomp* in R (Hothorn et al., 2019; Lenth et al., 2018; R Core Team, 2019). Using this framework, we first evaluated the effect of species on mean drought resistance, and again on one-year drought resilience; followed by two-way ANOVA using an interaction of species and drought year to evaluate the effect of species on annual drought resistance. Second, we compared mean drought resistance, and separately one-year drought resilience, for Oregon white oak trees in oak-only verses Douglas-fir encroached conditions; followed by two-way ANOVA to compare annual drought resistance by drought year and white oak condition group.

Third, linear mixed-effects models with a random effect of plot were used to further evaluate the effect of tree size and competition variables on log-transformed mean drought resistance for each species. Continuous predictor variables were transformed using $\log(x + 1)$ to improve residuals. Akaike Information Criterion for small sample sizes (AICc) was used to select the best model for each species with all significant predictor variables ($\alpha = 0.05$) (Burnham et al. 2002).

Finally, to evaluate how climate and competition interact as predictors of recent annual growth (BAI) (the 15-year period of recent growth between 2002 and 2016), we used linear mixed-effects models for log-transformed Oregon white oak and Douglas-fir BAI. We used growth years 2002–2016 to evaluate the effect of competition during a period of known tree age structure and Douglas-fir canopy dominance in encroached conditions (Schriver et al. 2018). Predictors included *treeclim*-identified climate variables, competition variables, and DBH as fixed effects. Plot and tree were included as random effects to account for correlation at the plot and subject tree levels. Temporal autocorrelations of orders 1–4 were compared using AIC and likelihood ratio tests (Pinheiro and Bates, 2000), and a second-order autocorrelation structure by year was determined best for both species. Due to model complexity (many possible fixed effect combinations), we used a backwards model selection process, starting with a full model that included all climate and competition terms for each species. We first determined which combination of tree size and competition variables best predicted growth, and then continued to remove additional non-significant ($\alpha = 0.05$) climate terms while checking for AIC improvement. For Oregon white oak subject trees, each important climate variable was further evaluated for interaction with Douglas-fir competition (encroachment). Significant interaction terms were retained and AIC comparison was used to select the best climate × competition model (Burnham et al., 2002).

To aid in the interpretation and comparison of model coefficients, numeric predictor variables for all models were standardized by subtracting the mean and dividing by two standard deviations (Gelman, 2008). Full (all variables included) and selected 'best' models were evaluated for homogeneity of variance using plots of residual versus fitted values and for normality with quantile-quantile plots. AICc or AIC comparisons of varying fixed effects were conducted on models fit with maximum likelihood while coefficients and *p*-values were evaluated on equivalent models fit with restricted maximum likelihood. Best models improved AICc or AIC by more than 2.5 over the next best model and all variables reported have variance inflation factors of less than 2.

3. Results

3.1. Drought response

Oregon white oak and Douglas-fir had distinct differences in their response to the 2013–2015 drought (Fig. 2). Mean drought resistance was 27% greater for Oregon white oak compared to Douglas-fir (WO = 0.89, DF = 0.71, $p < 0.0001$), and some (32%) Oregon white oak had a positive mean growth response to drought (drought resistance > 1). Oregon white oak trees had increased drought resistance after 2013 despite persistent drought conditions in 2014 and 2015, while Douglas-fir growth declined through the drought period. A two-way ANOVA model confirmed the presence of an interactive effect of species and drought year on drought resistance ($p < 0.0001$) (Fig. 3a). Drought resistance of Oregon white oak in 2014 and 2015 was greater than that of Douglas-fir by 42% and 55% respectively ($p < 0.001$) (Fig. 3a). One-year drought resilience was 83% greater for Oregon white oak than Douglas-fir ($p < 0.0001$) (Fig. 3b).

For Oregon white oak, drought resistance was 19% greater in oak-only conditions than in DF encroached conditions ($p < 0.01$). Drought resistance of Oregon white oak increased in 2014 and 2015 by 7% ($p = 0.017$) and 8% ($p < 0.01$), respectively, but there was no interaction with encroachment condition (Fig. 3c). There was no difference in one-year drought resilience across Oregon white oak condition groups (1.15, SD = 0.05; Fig. 3d). Tree mean drought resistance in Oregon white oak from 2013 to 2015 was negatively related to Douglas-fir competition (effect size −0.19, $p < 0.0001$) and positively related to oak competition (effect size 0.15, $p < 0.01$) (Fig. 4a). The positive relationship between oak competition and Oregon white oak drought resistance was similar for both oak-only (effect size 0.11, $p = 0.11$) and DF encroached trees (effect size 0.12, $p = 0.12$; also see Appendix B). Tree mean drought resistance in Douglas-fir during the same period was negatively related to Douglas-fir competition (effect size −0.25, $p < 0.0001$; Fig. 4b).

3.2. Competition and climate effects

Competition and climate both influenced growth of Oregon white oak and Douglas-fir with competition having the greatest relative influence. The best model for Oregon white oak growth (2002–2016) included positive relationships with DBH, April-June TMX, September TMX, previous year mean CWD, November-January PPT, and July-August PPT; negative relationships with oak competition and maximum summer temperature (Fig. 5a); and interactions of Douglas-fir competition with April-June TMX, July-August PPT, and previous year mean CWD (Fig. 5a and Fig. 6). The best model for Douglas-fir growth (2002–2016) included positive relationships with DBH and May-June PPT; and negative relationships with June-July TMX and Douglas-fir competition (Fig. 5b).

4. Discussion

4.1. Drought resistance

Both Oregon white oak and Douglas-fir responded negatively to drought in 2013–2015, but Douglas-fir responded more strongly than Oregon white oak. We found increased resistance of Oregon white oak and decreased resistance of Douglas-fir after the first year of drought, which suggests that Douglas-fir may not be as physiologically adapted to prolonged drought events as Oregon white oak. The difference in drought resistance may be attributed to differences in root structure and physiology (i.e., seasonal water use, stomatal regulation, hydraulic structure and strategies) (Abrams, 1990; Anderegg et al., 2015; Beedlow et al., 2013; Goff, 2021; Hahm et al., 2020, 2018; Johnson et al., 2009; Kelly, 2016; Littell et al., 2008). These results also may reflect differences in drought resilience strategy between the two species, as survival of Oregon white oak, as with other angiosperms, may relate to drought resistance, while that of Douglas-fir, a gymnosperm, may relate to drought recovery (DeSoto et al., 2020). We were unable to assess growth over a longer post-drought period, but we found that one-year drought resilience was markedly greater in Oregon white oak than in Douglas-fir; the latter did not yet show recovering growth in 2016. Oaks are known to recover quickly from drought events (Anderegg et al. 2015); while Douglas-fir has a lower hydraulic safety margin than that of Oregon white oak (Johnson et al., 2009; Kelly, 2016), a characteristic associated with strong legacy effects (reduced growth in years following drought) (Anderegg et al. 2015). Further, some oaks reduce leaf area in response to drought conditions as part of a conservative strategy that balances low stomatal control and may allow trees to keep a constant, or even increased, leaf-specific hydraulic conductance when submitted to drought stress (Limousin et al., 2009). If present in Oregon white oak, this mechanism could help prevent further damage from continuous drought by limiting tree-level water use and transpiration in later drought years.

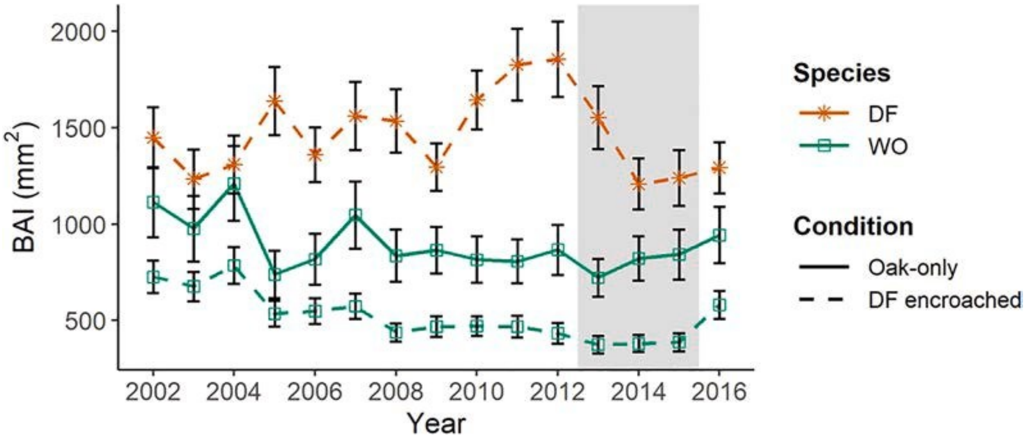

Fig. 2. Radial tree growth (mean basal area increment [BAI] ± standard error) for Douglas-fir (DF) and Oregon white oak (WO) in different conditions. The 2013–2015 drought period is shaded in grey.

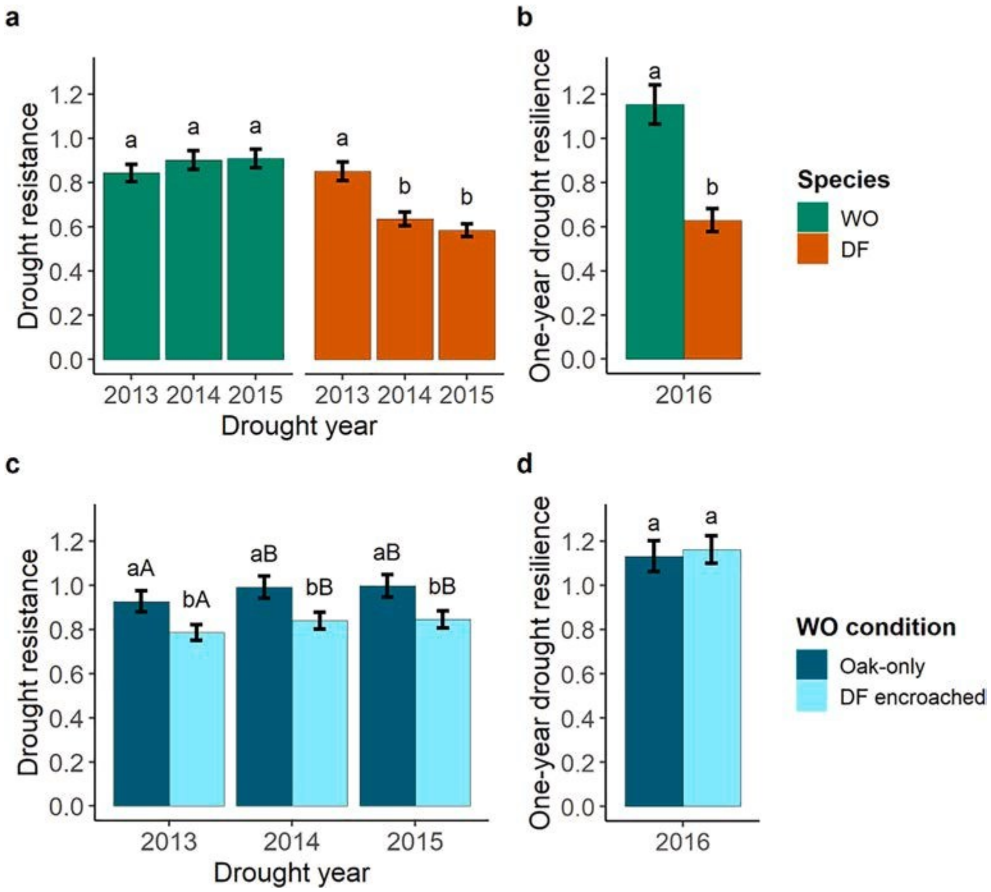

Fig. 3. Mean (±standard error) drought resistance by year (a) and mean one-year drought resilience (b) for all Douglas-fir (DF) and Oregon white oak (WO), and respectively for white oak growing in oak-only conditions compared to DF encroached conditions (c, d). Shared letters indicate similar group means based on a Tukey's adjustment for multiple comparison tests ($\alpha = 0.05$) for two-way (a, c) or one-way (b, d) ANOVA of a linear mixed effect model with random effects plot and tree (a, c), or plot (b, d). Fixed effects were species, year, and their interaction (a); species (b); condition and year with no interaction (c); and condition (d). In panel (c) lower case letters indicate a difference in means between conditions while capital letters indicate a difference in means across drought years.

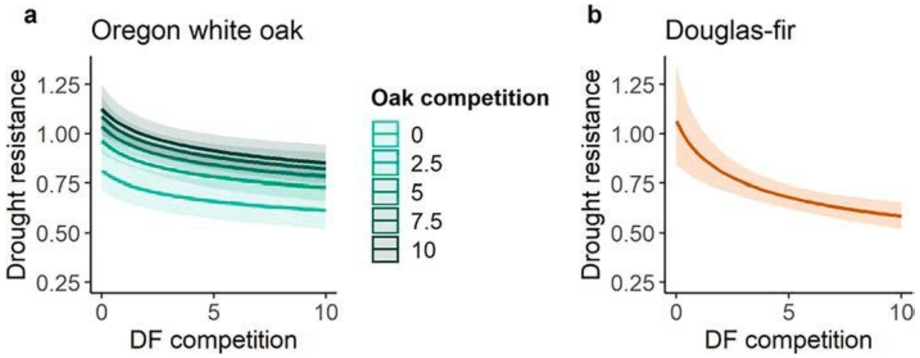

Fig. 4. Back-transformed model predictions for drought resistance (tree mean, 2013–2015) showing the fixed effects of Douglas-fir (DF) competition (Hegyi) and oak competition on Oregon white oak (a) and Douglas-fir competition on Douglas-fir (b). Predictor variables were transformed using $\log(x + 1)$.

Unencroached ('oak-only') Oregon white oak had greater drought resistance than Douglas-fir encroached Oregon white oak, and drought resistance in Oregon white oak was negatively related to Douglas-fir competition. Likely in an effort to capture more direct sunlight under heavy Douglas-fir competition, Oregon white oak trees in encroached conditions invested more in height growth than trees in unencroached conditions (Appendix B; and also see Schriver 2015). This response may shunt carbon resources away from structures that aid in drought resistance, such as roots. Douglas-fir drought resistance was also negatively related to Douglas-fir competition and drought resistance in this species may be similarly affected by reduced availability or reallocation of carbon resources when growing in crowded conditions. Due to increased stem density, there may also be greater competition for subsurface water resources in encroached conditions compared with unencroached conditions. This could affect the drought resistance of both oaks and Douglas-fir in crowded stands when water is limiting. However, because Oregon white oak and Douglas-fir appear to have different patterns of seasonal water use (oak growth being more responsive to winter precipitation and Douglas-fir growth being more responsive to spring precipitation) and because oaks draw water from a deeper source than Douglas-fir at this site (Goff, 2021), it is likely that the negative effect of Douglas-fir competition on Oregon white oak drought resistance relates more to competition for light than for water. We found no difference in drought resilience between encroached and unencroached Oregon white oak trees. These results are broadly consistent with a recent meta-analysis showing that competition tends to negatively affect drought resistance but has inconsistent effects overall on drought resilience (Castagneri et al., 2021).

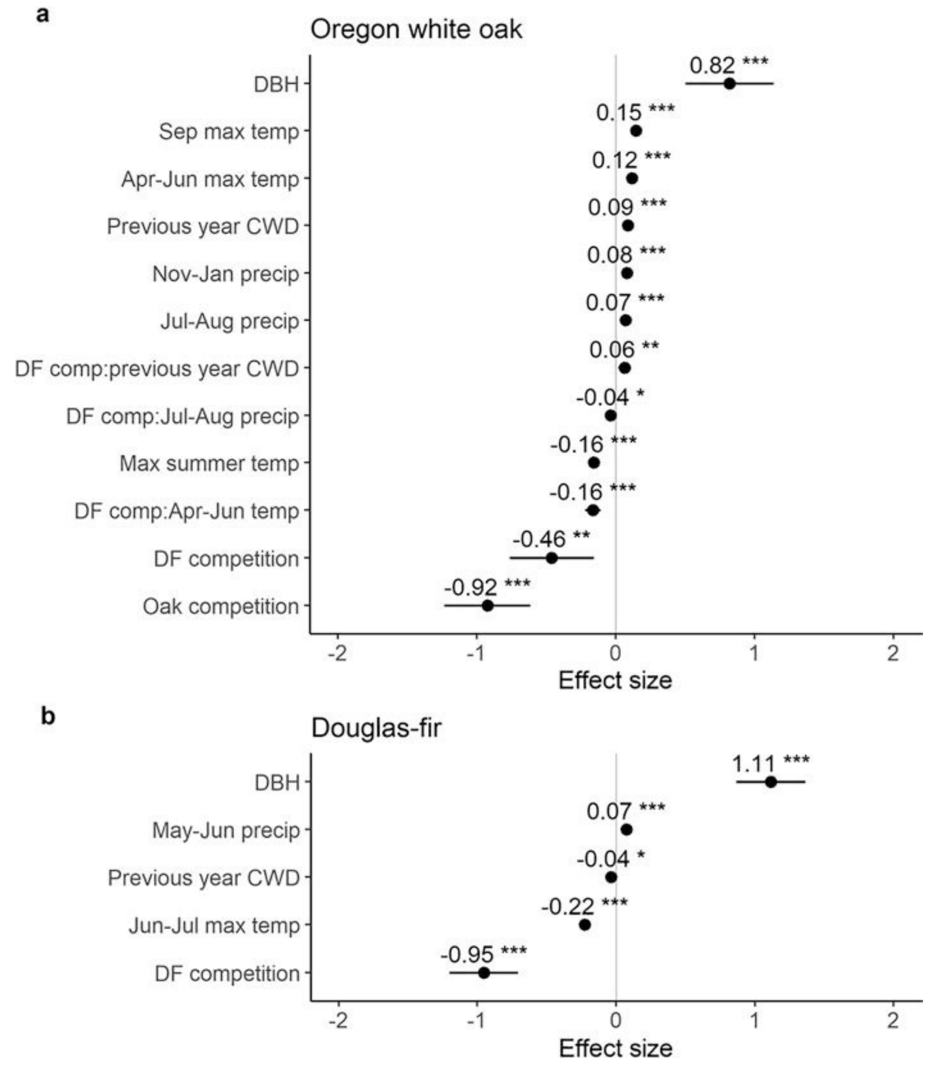

Fig. 5. Back-transformed (e^x-1) effect size and 95% confidence intervals of marginal fixed effects on log-transformed basal area increment in Oregon white oak (a) and Douglas-fir (b), between 2002 and 2016 ($n = 1560$ tree rings). Effect size represents the proportion change in the response variable based on a two standard deviation increase in the predictor variable. Asterisks indicate strength of statistical significance (p-value) of each fixed effect (* < 0.05, ** < 0.01, and *** < 0.001).

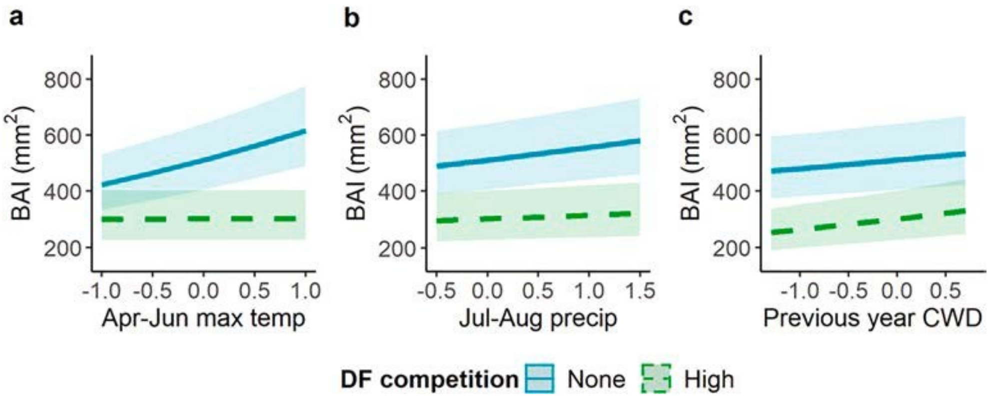

Fig. 6. For Oregon white oak, basal area increment (BAI) growth was influenced by interactions between Douglas-fir (DF) competition and April-June mean maximum temperature (a), July-August total precipitation (b), and previous year mean climatic water deficit (CWD) (c). Model predictions display back-transformed response with predictor variables on a standardized scale and are reflective of the range of observed values. High Douglas-fir competition represents the 90th percentile.

Interestingly, the best drought resistance models for Oregon white oak included a positive relationship with oak competition. High competition may reduce, cancel out, or mask climate effects (Sánchez-Salguero et al., 2015) and can induce phenotypic structural changes (such as increased proportion of latewood) that aid in drought resistance (Carnwath et al., 2016). In our study system, the beneficial effect of oak competition on drought resistance could relate to subsurface resource sharing by neighboring trees, as some oaks grow in a multistem habit with a shared root system. In addition, drought impacts may be minimized at an intermediate level of shade for drought-tolerant species (Holmgren et al., 2012). Compared to Douglas-fir, understory light is abundant under an Oregon white oak canopy, as evidenced by the rich understory communities that these ecosystems support (Devine et al., 2007; Livingston et al., 2016; Thysell and Carey, 2001). Thus, it is possible that shading associated with higher oak competition might be advantageous during drought through reduced heating and evapotranspirational demand on crowded Oregon white oak trees while still providing adequate light for growth. However, further investigation is required to determine the mechanisms producing this uncommonly found relationship.

4.2. Competition and climate

Competition had a greater effect on radial growth than climate in both Oregon white oak and Douglas-fir. This is consistent with other climate-competition studies (e.g., Go´mez-Aparicio et al. 2011; S´anchez-Salguero et al. 2015; Zhang et al. 2015; Carnwath et al., 2016). Excluding DBH, intraspecific competition was the most influential factor on radial growth for both species, indicating that growth was most affected by the presence of conspecific neighbors competing for resources of the same type or within the same subsurface strata (Tilman, 1982). Oak competition was not an important predictor for Douglas-fir growth, which is not surprising given this conifer's ability to rapidly grow through the canopies of Oregon white oak (Hunter and Barbour, 2001).

We also found several relationships between climate variables and radial growth. Oregon white oak growth benefited the most from winter (November-January) and late summer (July-August) precipitation. This association of Oregon white oak growth with winter and summer precipitation may relate to deep roots and arbuscular and ectotrophic mycorrhizal associations that have been documented in other California oaks, enabling trees to take advantage of both deep water reserves and rare summer rain events (Allen, 2015). Our results show a negative interaction between Douglas-fir competition and July-August precipitation on oak growth. This interaction likely reflects increased competition from Douglas-fir for this ephemeral soil moisture or, as previously shown in encroached oak woodland habitats (Devine and Harrington, 2007), greater interception of precipitation by Douglas-fir encroachers.

Oregon white oak growth had a negative relationship with maximum summer temperature. It is possible that higher temperatures cause xylem tension to cross a critical threshold leading to widespread loss of transport capacity, and therefore reduced radial growth (Hacke et al., 2006; Johnson et al., 2012; McDowell et al., 2008). Oregon white oak appears to regulate stomatal conductance in accordance with losses in transport capacity (Hahm et al., 2018; Johnson et al., 2009), so it is possible that the highest temperatures are also affecting growth due to reductions in photosynthesis from stomatal closure. Our study is not able to determine the physiological mechanisms associated with the observed growth trends, but if growth trends were reflective of reduced carbon assimilation from conservative stomatal regulation, we might expect to see a negative association with maximum temperature over a longer period rather than an association with the magnitude of maximum temperatures during summer.

In contrast to maximum summer temperatures, late spring (April-June) and early fall (September) maximum temperatures were positively associated with growth in Oregon white oak. These positive relationships may simply reflect an extended growing season with warmer temperatures. However, warmer spring temperatures, earlier onset of vessel enlargement, and longer vessel enlargement period result in larger vessels in other oak species (Kudo et al., 2014; P´erez-de-Lis et al., 2016). Thus, improved hydraulic capacity resulting from larger vessels could partially explain the positive relationship found between spring maximum temperatures and growth in this ring-porous species. Importantly, we found a negative interaction of spring (April-June) maximum temperature and Douglas-fir competition on Oregon white oak growth. This is a developmentally important window of time, as in 2017 and 2018 we observed that Oregon white oak broke bud in April, leafed out in May, and only had mature leaves by June. We speculate that reduced spring temperatures due to Douglas-fir shading may limit oak growth by delaying bud break and the onset of cambial activity, altering the structure and chemical composition of developing leaves, or reducing the size of developing vessels.

For Douglas-fir, we found a positive association between growth and late spring (May-June) precipitation, possibly reflecting water limitation during the subsequent recurrently dry growing season in this climate (Littell et al., 2008). We also found a negative relationship between Douglas-fir growth and June-July maximum temperature (Littell et al., 2008). These relationships may indicate high variability in stomatal regulation during this period compared to later in the summer when stomatal regulation may vary less with temperature due to constant water stress (Beedlow et al., 2013).

4.3. Climate change and management implications

Trees with declining growth trends, whether from high competition, climate, or from some other factor, are more vulnerable to mortality (Cailleret et al., 2017; DeSoto et al., 2020; Pedersen, 1998). Similar to other angiosperms trees, drought-related oak mortality may be associated with drought resistance (DeSoto et al., 2020), but we found the ability of Oregon white oak to resist drought was compromised by Douglas-fir encroachment. Research conducted on the northern edge of Oregon white oak's range comparing Oregon white oak and Douglas-fir growth sensitivity to PDSI under varying competitive environments corroborates our conclusion that although Oregon white oak may be more resistant to drought than Douglas-fir encroachers, this ecosystem is especially threatened by expected shifts in climate variability when coupled with Douglas-fir competition (Gedalof and Franks, 2019). It is important to note that Douglas-fir is also a fairly drought-tolerant species and on average maintained greater radial growth than Oregon white oak regardless of its lower drought resistance. For gymnosperms such as Douglas-fir, mortality is associated with extended growth declines, while for angiosperms, especially *Quercus*, mortality is more likely after short-term growth declines (Cailleret et al., 2017). Thus, drought-affected Douglas-fir may persist with low growth for an extended time period before dying, suggesting that in the short term, encroached Oregon white oak will have compromised drought resistance, facilitating replacement by Douglas-fir. Over the long-term however, the drought sensitivity of Douglas-fir suggests that it may be less suited to future climate conditions.

In California, climate models project increased climate volatility with increases in both extreme drought events and extreme wet events into the mid to late 21st Century (Swain et al., 2018). In our study, Oregon white oak and Douglas-fir of northwestern California were sensitive to precipitation and temperature. However, Douglas-fir was more sensitive to growing-season precipitation (May-June) and Oregon white oak was more sensitive to winter precipitation (November-January). Therefore, enhanced precipitation seasonality (i.e. enhanced winter and reduced summer precipitation; Swain et al., 2018) would likely negatively impact growth in Douglas-fir more than Oregon white oak. Projected increases in temperature are more certain than precipitation projections and are expected to play an important role in future drought events (Diffenbaugh et al., 2015; Williams et al., 2015). Although temperature increases will likely affect both species, our results showed maximum summer temperature negatively influenced oak growth while temperature during the growing season and at the onset of summer drought negatively influenced Douglas-fir growth and that Douglas-fir drought resistance declined over an extended drought period. Oregon white oak may therefore be sensitive to severe drought and Douglas-fir sensitive to prolonged drought, including sustained increases in temperature. We also found oak growth was positively related to both spring and fall temperatures, suggesting that projected temperature increases (>2 °C by the end of the 21st century for the study region; Grantham 2018) may benefit Oregon white oak.

Forest dynamics in this and other ecosystems continue to be driven more by competition than climate (also see Zhang et al., 2015), but the combination of both can lead to increased mortality, especially during extreme drought (Bradford and Bell, 2017; Young et al., 2017). The presence of Douglas-fir encroachment threatens Oregon white oak woodlands in multiple ways. In the Pacific West, reduction of Douglas-fir density will enhance the ability of Oregon white oak to resist future drought events and adjust to future climate conditions. These results present a strong case for the need to release Oregon white oak by controlling Douglas-fir in areas that were historically oak woodlands with diverse understory species, wildlife, and important traditional ecological values and services.

CRediT authorship contribution statement

Jill J. Beckmann: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Rosemary L. Sherriff:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition. **Lucy P. Kerhoulas:** Conceptualization, Writing - review & editing, Funding acquisition. **Jeffrey M. Kane:** Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119543.

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