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RESEARCH ARTICLE

Restoration thinning enhances growth and diversity in mixed redwood/Douglas-fir stands in northern California, U.S.A.

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We examined early responses to different forest restoration thinning treatments to evaluate their efficacy in accelerating tree growth rates, changing species composition, and enhancing structural diversity while minimizing stem damage by black bears and reducing slash depth. Treatments were conducted in 15–25-year-old mixed redwood/Douglas-fir stands and consisted of high-density, low-density, and localized release thinning, as well as a control. Four years post-treatment, data collected from 60 large plots in 20 stands spread across the Mill Creek and Rock Creek watersheds in Del Norte County, California, indicated that spatial variability created from thinning treatments was reflected in diameter growth. Trees having no crown competition had on average a 33% greater basal area increment than trees surrounded by neighboring trees. Thinning treatments enhanced redwood representation by preferentially removing other species, but also promoted rapid growth which increased incidences of bear damage. Approximately 25% of redwood trees sustained bear damage in thinned stands. The localized release thinning created a mosaic of circles flanked by unthinned patches within which trees grew slowly. Localized release created more heterogeneity in tree size but did not generate significantly greater fuel bed depths, result in more bear damage, or represent any sacrifice in understory light or plant abundance and species diversity than a more conventional approach to thinning.

Key words: black bear damage, old-growth, precommercial thinning, *Pseudotsuga menziesii*, *Sequoia sempervirens*, variable-density thinning

Implications for Practice

- Managers have options to choose different variable-density thinning methods that foster development of old-growth forest conditions by favoring desired species and enhancing tree growth and variability within stands.
- Understory vegetation cover and diversity increased swiftly following thinning despite heavy slash. Repeat treatments will be needed to forestall rapid declines in understory light as overstory trees respond to thinning.
- Rapid ocular assessment of crown competition gave data correlating strongly with tree growth. Therefore, enhanced variability in tree growth rates could be achieved by prescribing thinning to release individual trees from competition on one, two, three, or four sides, randomly or systematically.
- Thinning prescriptions that are unfamiliar to contractors will require landowner supervision or tree marking to meet tree spacing goals.

Introduction

In northern California's redwood region, state and federal agencies have taken ownership of many private industrial timberlands. Prior to change in ownership, most stands were managed for timber production and consisted of young, well-stocked even-aged stands. Species composition may have been altered by planting or seeding, shifting from historical conditions where coast redwood (*Sequoia sempervirens*) was the dominant species to coast Douglas-fir (*Pseudotsuga menziesii*) dominance. Other stands regenerated naturally with an overabundance of tanoak (*Notholithocarpus densiflorus*). Thus, public agencies have been actively managing these young forests with restoration objectives of encouraging the development of old-growth forest structures, enhancing structural diversity, and shifting species composition (O'Hara et al. 2010; Teraoka & Keyes 2011; O'Hara et al. 2017). In California where catastrophic wildfires are common, restoration thinning

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or partial harvesting also serve to lower the risk of wildfires by managing vegetation to modifying/reducing hazardous fuels.

Old-growth forests are known to have a wide range of tree sizes, large live trees, large snags, and multiple canopy layers (Lorimer et al. 2009). Several studies have defined reference conditions in old-growth forests within the redwood region (Dagley 2008; Dagley & Berrill 2012; van Mantgem & Stuart 2012; Berrill et al. 2013). Within a redwood forest type and even between alluvial flat and upland forest types, old-growth stands have similar structural characteristics that can serve as key reference conditions in restoration efforts. For example, old-growth redwood stands found on alluvial flats had 118–148 stems/ha of trees >15 cm diameter at breast height (dbh), and an upper canopy density of 45–74 stems/ha (Dagley & Berrill 2012). The spatial pattern for trees was most often random with some clumping at small scales (Dagley 2008). Species composition was mostly redwood with a few small hardwoods. For upland old-growth redwood forests, stem density ranged from 171–216 stems/ha with an upper canopy density of 48–61 stems/ha (Berrill et al. 2013). Species composition for these upland redwood sites was a mix of conifers (redwood, coast Douglas-fir, grand fir [*Abies grandis*]) and hardwoods (tanoak and California bay [*Umbellularia californica*]), but redwood still dominated in terms of density and basal area (BA). Another study in upland redwood forests (van Mantgem & Stuart 2012) found a similar spatial pattern to that found by Dagley (2008) on alluvial flats.

Management of young redwood stands typically includes some form of thinning to reduce stand density and increase tree growth rates (Oliver et al. 1994; O'Hara et al. 2010; Teraoka & Keyes 2011; OHara et al. 2015). Thinning in stands managed for timber production tends to favor the best individuals and create homogeneity in tree size, reduced species diversity in mixed stands, and a uniform spatial pattern of residual tree locations (Smith et al. 1997). Variable-density thinning (VDT), a type of thinning that reduces stand density at varying intensities, mitigates these problems (Carey 2003; Pukkala et al. 2011). Thinning to different densities throughout a stand not only allows us to mimic the spatial patchiness found in old-growth forests but also allows for the retention of trees in all crown classes or species diversity in mixed stands, thus enhancing heterogeneity. Additionally, residual trees are expected to grow at different rates according to their local environment, further enhancing tree-size variability into the future (Roberts & Harrington 2008; Dodson et al. 2012; Berrill & O'Hara 2014).

A potential disadvantage to thinning in young stands in north coastal California is widespread damage from black bears (*Ursus americanus*) (Giusti 1988; Hosack & Fulgham 1998; O'Hara et al. 2010; Perry et al. 2016). Bears strip off large pieces of bark and eat the inner bark, phloem, cambium, and outer sapwood, wounding all or part of a stem's circumference. Damage to trees typically occurs in the spring and is often concentrated near logging roads, skid trails, or other openings (Giusti 1988; Perry et al. 2016). Damage is also often concentrated on the more vigorous trees (Kimball et al. 2008; Berrill et al. 2017). Some bear damage may benefit restoration by creating basal cavities, snags, and other decadent features. However, losing too many rapidly growing trees could alter a stand's trajectory by changing species composition and unnecessarily delaying the development of large upper canopy trees in accordance with the reference condition (Dagley & Berrill 2012; van Mantgem & Stuart 2012; Berrill et al. 2013).

Our objectives were to compare the effectiveness of different approaches to thinning at promoting redwood dominance, redwood tree growth, and stand structural complexity. We also compared incidences of bear damage and depth of slash following each thinning treatment and over the same time period in unthinned control stands. Specifically, we sought to answer the following questions: (1) "what were the outcomes of each thinning treatment, in terms of tree species composition, structural diversity, canopy cover, understory vegetation, and fuel load?" and (2) "what was the response, in terms of tree growth and probability of bear damage, among individual tree species over four years following each thinning treatment across a range of sites and stands?"

Individual hypotheses to be tested were as follows:

(1) The localized release (LR) treatment will not shift species composition in favor of redwood as much as the low-density (LD) or high-density (HD) thinning.
(2) LR treatment will enhance structural tree-size diversity most.
(3) Understory vegetation will be most abundant in terms of percent cover in areas of high understory light and low canopy cover following LD thinning. In accordance with the highest spatial variability in understory light and canopy cover derived from hemispherical image analysis, understory vegetation will be most diverse following LR.
(4) The layer of cut wood left on the ground after thinning will be deepest following LD thinning, shallowest following HD, and intermediate in depth and most variable spatially after LR.
(5) Diameter growth will be greatest overall following LD thinning and most variable after LR.
(6) Bear damage will be restricted to redwood and Douglas-fir, and highly variable among stands, with the most damage occurring after LD thinning. Bears will target the fastest-growing individuals irrespective of tree size, and favor redwood over Douglas-fir.

Methods

Three thinning prescriptions were tested across a broad geographic area in the Mill Creek addition (MCA) of Del Norte Coast Redwoods State Park, just south of Crescent City, in Del Norte County, California (41°44′N, 124°05′W) (Fig. 1). A Mediterranean climate brings dry summers with warm days and mild winters. August is the warmest month with an average high of 19°C and an average low of 11°C. The coolest month, December, averages a high of 12°C and a low of 4°C. Average precipitation is 1,810 mm, with the wettest months being November to March (https://www.usclimatedata.com). Soils are well-drained and include loam, gravelly loam, and gravelly silt loam from the Coppercreek, Slidecreek, and Wiregrass series, respectively (NRCS 2008).

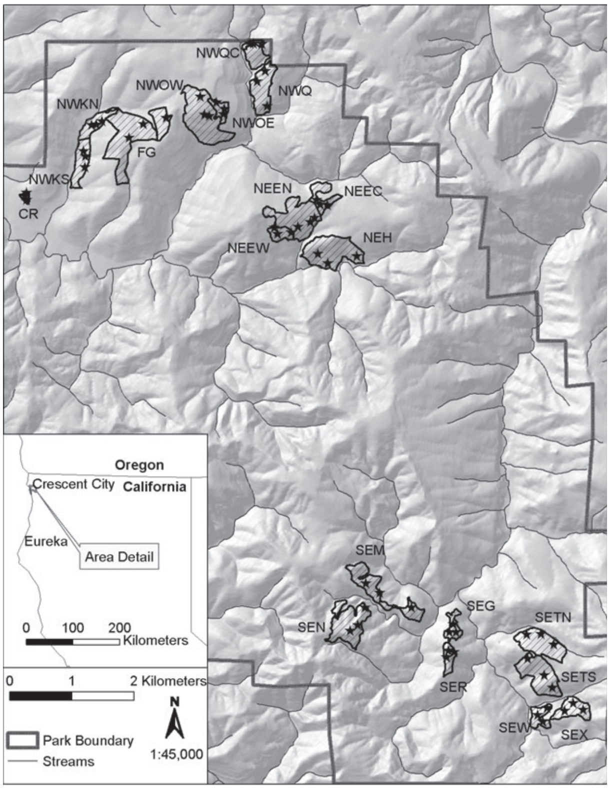

Figure 1. Stand ($n = 20$) and plot ($n = 60$) location map within the Mill Creek addition of Del Norte Coast Redwoods State Park, Crescent City, California.

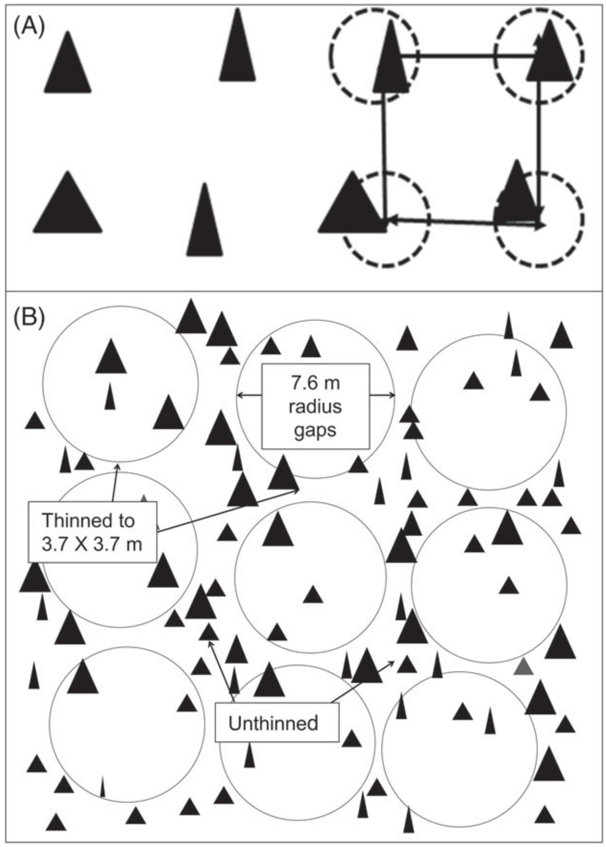

Figure 2. Schematic diagram of thinning protocols (adapted from O'Hara et al. 2012). (A) Thinning to spacing of 6.4 × 6.4 m or 4.9 × 4.9 m with circles representing a 1.2-m allowance for selecting the best tree. (B) Localized release treatment where three trees were retained within 7.6-m radius gaps. Between two circles, trees were thinned to a 3.7 × 3.7-m spacing while areas between three and four circular gaps remained unthinned.

The MCA includes two watersheds (Mill Creek and Rock Creek) and is primarily composed of young, HD forests dominated by Douglas-fir regenerating after conifer harvesting (at times followed by aerial seeding of Douglas-fir). Other conifers include redwood, and in much smaller numbers grand fir, western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Port Orford cedar (*Chamaecyparis lawsoniana*). Naturally regenerating hardwoods are tanoak, California bay, bigleaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). The even-aged stands prior to treatment were entering the stem exclusion stage of stand development (Oliver & Larson 1996), and had approximately 1,300 stems/ha averaging 15 cm dbh of which two-thirds were Douglas-fir (O'Hara et al. 2012). Common understory plants include evergreen huckleberry (*Vaccinium ovatum*), salal (*Gaultheria shallon*), and western sword fern (*Polystichum munitum*).

The study was conducted in five areas of the MCA (Fig. 1), hereafter referred to as blocks. Within each block, four stands ranging from 15 to 25 years in age were identified for the study, and one of the four thinning prescriptions was randomly assigned to each stand: LD, HD, LR, and no-thin control (C). Thinning treatments sought to reduce tree densities, shift species composition toward redwood, and preserve tree species diversity. The LD and HD prescriptions defined average spacing of retention trees (6.4 × 6.4 m and 4.9 × 4.9 m, respectively) but were designed to introduce more spatial variability than a traditional thinning by allowing a 1.2-m offset to choose the best tree (Fig. 2). The "best" tree was chosen based on size and species with dominant redwoods being the most desirable followed by less common conifers, Douglas-firs, and tanoaks, respectively. LR was designed to create more spatial variability by creating 7.6-m radius circular gaps in which the three tallest trees would be retained inside the gap. In between gaps, space for a row of trees was left and thinned to a 3.7 × 3.7-m spacing, while areas between three and four circular gaps remained unthinned (Fig. 2). Thinning contractors were told to treat multiple stems originating from a single redwood stump as a single tree for spacing purposes, and not to thin within the sprout clump.

Three permanent plots were established in each stand soon after treatment (within 1 year of the treatment date). All plots were then remeasured 4 years after establishment. Each permanent plot within each stand was 0.242 ha in size in thinned stands and 0.081 ha in unthinned control stands (Fig. S1, Supporting Information). For each plot, we recorded slope and aspect. All trees over 7.6 cm dbh were measured for dbh and instances of health issues or damage recorded (bear damage was recorded separately). For each tree, an ocular estimate was used for crown ratio (percent of total tree's height that was occupied by tree crown). Crown competition was assessed and assigned a value between 0 and 4, which represented the number of sides the subject tree's crown came in contact with a neighboring tree crown. Tree heights were recorded for a large subset of trees (>50%) covering the range of diameters within each plot. Understory vegetation was sampled in 0.01 ha subplots (Fig. S1). Understory species were identified and their percent cover recorded. In instances where vegetation was overlapping, percent cover for the 0.01 ha area could exceed 100. On cloudy days or at dusk, hemispherical photos were taken 1.37 m aboveground at the interior of each subplot corner, and were analyzed using gap light analyzer giving percent canopy openness, percent above canopy light (PACL), and leaf area index. Depth of the layer of cut wood (hereafter referred to as slash depth) was measured at 0.3 m intervals along a 10 m length transect bisecting each plot (Fig. S1).

Data Analysis

All analyses were performed in SAS version 9.3 (SAS Institute Inc. 2011). Mean density, dbh, height, BA, stand density index (SDI), site index, and species composition were calculated for each plot and averaged for each stand and treatment. SDI was calculated by summing individual tree SDI because the dbh data were not normally distributed: $SDI = \sum(0.04\text{dbh}_i)^a$, where $\text{dbh}_i = \text{dbh}$ in centimeter of the ith tree in the plot, and $a = 1.605$ (Shaw 2000). Site index using a base age of 50 was calculated for each plot using plot age and heights of the dominant undamaged Douglas-fir trees in each plot (Krumland & Eng 2005). The proportion of redwood and Douglas-fir by stand BA was calculated for each plot. A 4-year periodic annual BA increment (BAI) and diameter increment (DBHI) were calculated and represented individual tree growth.

We used mixed-effects regression analysis to study relationships among response variables (i.e. individual tree growth, understory vegetation cover, slash depth) and candidate explanatory variables (i.e. treatment, stand density, site index, species composition, understory light, topographic variables). Using logistic mixed-effects regression we modeled the probability of tree injury from bears as a function of the same suite of candidate explanatory variables. We compared the coefficient of variation (CV) in dbh and height to evaluate treatment effects on structural heterogeneity.

Models were fit using PROC GLIMMIX in SAS. The class variables "block," "stand," "plot," and/or "subplot" entered the models as random effects to account for nesting when needed. Model selection was based on likelihood ratio tests comparing the full model against reduced models in terms of model chi-square at the 0.05 significance level. Residuals were evaluated for all models to ensure the assumptions of normality, equal variance, and independence were met. Square root transformations were applied where needed. Aspect was cosine transformed to a continuous value ranging from 0 to 2, with a value of 2 representing a southern aspect of 202.5° and a value of 0 representing a northern aspect of 22.5°. When treatment was included as an explanatory variable in a model, a post hoc Tukey–Kramer test was performed to identify significant differences between treatments.

Results

Stand Structure

Post-thinning densities of trees greater than 7.6 cm dbh were higher than anticipated, presumably due to some redwood sprout clumps being entirely retained and contractors deviating from the prescription (Table 1, Fig. 3). As expected, LR, LD, and HD treatments were significantly lower in density, BA, and SDI compared to the unthinned controls. Trees in unthinned control stands were significantly smaller on average in dbh and height than thinned stands ($p < 0.05$). Structural diversity in terms of tree-size variability was generally greater in the thinned plots as compared to the unthinned controls (Table 1). Mortality was low for all treatments over the 4-year study period (<0.82% per year).

Among 17 tree species present in sample plots, Douglas-fir, redwood, and tanoak were most common (Table S1). Thinned stands had significantly more redwood than unthinned control stands when comparing proportion of BA by species, but redwood dominance was not attained posttreatment. Redwood represented only 29% of stand BA in unthinned control stands, 37% after HD, 44% after LR, and 46% of stand BA after LD. Douglas-fir represented 66% of stand BA in unthinned control stands, 60% after HD, 50% after LR, and 48% of stand BA after LD.

The LD and HD treatment prescriptions both specified the same approach to thinning (i.e. thin to a specific spacing; cut smaller trees), but they were designed to result in lower and higher densities, respectively. However, we did not detect significant differences in density, species composition, or tree size ($p > 0.18$) between the LD and HD treatments. Therefore we decided to combine the data for LD and HD treatments into one group, hereafter referred to as the low thinning (LT) treatment.

Mixed-effects regression analysis of CV for dbh and height at the initial posttreatment measurement indicated that there were differences due to treatment and species composition. Tree-size variability was lower in areas with more Douglas-fir and in the unthinned controls. However, a post hoc Tukey–Kramer test showed no significant differences in CV for dbh or height ($p > 0.06$) between any of the treatments immediately after treatment. Four years after treatment, the mixed-effects analysis of CV for dbh and height revealed a thinning treatment effect. The Tukey–Kramer test found significant differences in CV for dbh between all treatments and ranked LR > LT > C. For height, CV was significantly different only between the LR and control treatments, with rankings similar to that for dbh.

Structural attributes characteristic of old-growth forests were also found in our plots. Four years after treatment, the LT treatment had higher frequencies of standing dead (i.e. snags) and dead down trees (i.e. coarse woody debris [CWD]) (Table S2). Control plots had more instances of forked tops and broken tops, suggesting that LR and LT thinning treatments led to the

Table 1. Summary data by treatment taken after thinning and 4 years later including density, metric stand density index (SDI), basal area, average dbh, dbh of the top (largest-diameter) 50 trees/ha, height, and height of the top 50 trees/ha with standard deviations in parentheses. LR = localized release; LD = low density; HD = high density; C = control.

		Treatment			
Measure	*Year*	*LR*	*LD*	*HD*	*C*
Density (stems/ha)	1	686.5 (344.1)	566.4 (213.2)	586.7 (222.3)	1, 322.9 (366.6)
	5	613.0 (345.2)	528.0 (223.5)	542.0 (207.7)	1, 297.3 (376.2)
SDI	1	369.8 (239.5)	312.8 (177.4)	354.7 (203.6)	599.2 (328.3)
	5	431.2 (280.9)	393.1 (228.2)	453.2 (259.2)	737.1 (413.4)
BA (m^2/ha)	1	17.3 (0.1)	14.6 (0.1)	16.8 (0.1)	25.5 (0.2)
	5	21.4 (0.1)	19.6 (0.1)	23.1 (0.1)	34.2 (0.2)
dbh (cm)	1	16.8 (5.9)	16.9 (5.9)	17.5 (5.9)	14.8 (4.9)
	5	17.7 (9.4)	19.1 (8.6)	19.9 (8.9)	16.7 (6.1)
Dominant dbh (cm)	1	22.4 (7.0)	21.0 (5.4)	23.1 (6.8)	23.1 (5.2)
	5	26.7 (7.3)	25.6 (5.9)	27.7 (7.3)	26.5 (6.1)
Height (m)	1	11.1 (3.2)	11.1 (2.9)	11.5 (2.7)	10.6 (2.3)
	5	13.6 (5.3)	13.8 (3.5)	14.1 (3.3)	13.2 (2.9)
Dominant height (m)	1	12.8 (3.0)	12.7 (2.8)	13.3 (3.5)	13.2 (2.5)
	5	16.0 (3.0)	16.0 (2.7)	16.5 (3.5)	15.8 (3.0)

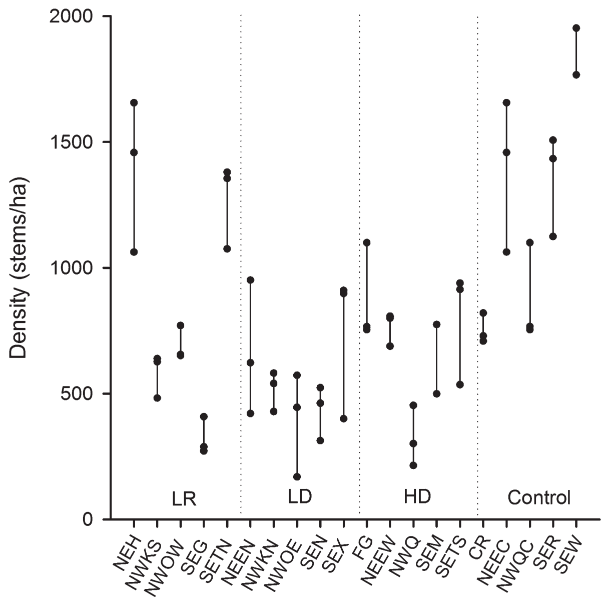

Figure 3. Density of trees >7.6 cm dbh by treatment for each plot (●) within each stand (n = 20). LR = localized release; LD = low density; HD = high density.

removal of some trees with these features. However, the various structural attributes were all present in most plots.

Tree Diameter Growth

Our analysis revealed differences in radial growth (in terms of BAI) among redwood, Douglas-fir, and tanoak, which together represented 99% of the trees (n = 8,277) in all plots. Trees with damaged tops, bear damage, and/or missing or estimated dbh data were excluded, leaving 2,036 tree records for redwood, 3,277 for Douglas-fir, and 748 tree records for tanoak. Mixed-effects analysis of tree BAI indicated that the larger conifers grew much more rapidly than smaller conifers in these even-aged stands (Table S3). Douglas-fir grew more rapidly than redwood (Fig. 4). Compared to the LT treatment, redwood grew relatively well and Douglas-fir relatively poorly after LR, where many Douglas-fir were left crowded while clumps of redwood stump sprouts were preferentially released from competition within the circular gaps. Douglas-fir remaining after LT grew most rapidly. For example, for a tree of average size, BAI was 33.5, 29.4, and 20.5 cm^2/year for redwood and 34.0, 37.3, and 24.8 cm^2/year for Douglas-fir in the LR, LT, and C treatments, respectively. Modeled predictions of growth revealed that, on average, smaller tanoak outgrew smaller Douglas-fir in the control stands, and outgrew smaller redwood irrespective of treatment. After accounting for the effects of tree size, crown ratio, and neighbor competition, trees in younger stands were growing more quickly than in older stands. Trees with higher crown ratio exhibited more rapid growth, as did trees that were not in direct contact with neighboring tree crowns on one or more sides. A post hoc Tukey–Kramer test showed significant differences in growth of redwood among all treatments with growth ranking LR > LT > C. Douglas-fir radial growth was fastest in the LT treatment, and close to being significantly greater than the LR treatment (p = 0.07). For tanoak, no significant differences in BAI were detected among treatments.

Average tree BAI of the 50 top (largest-diameter) redwood/ha and 50 top Douglas-fir/ha, presumably an important part of the future restored old forest overstory, ranked LR > LT > C for redwood and LT > LR > C for Douglas-fir (Table S5). This was consistent with the growth data for all tree sizes, where in relative terms, LR favored redwood while restricting Douglas-fir growth. Our mixed-effects model analysis of tree BAI among the top redwood and Douglas-fir gave similar predictions of radial growth to that of the BAI models for all undamaged trees; however crown ratio was replaced by aspect in the model (Table S5). For redwood and Douglas-fir, growth, on average, was greater for trees located on southern aspects than on other

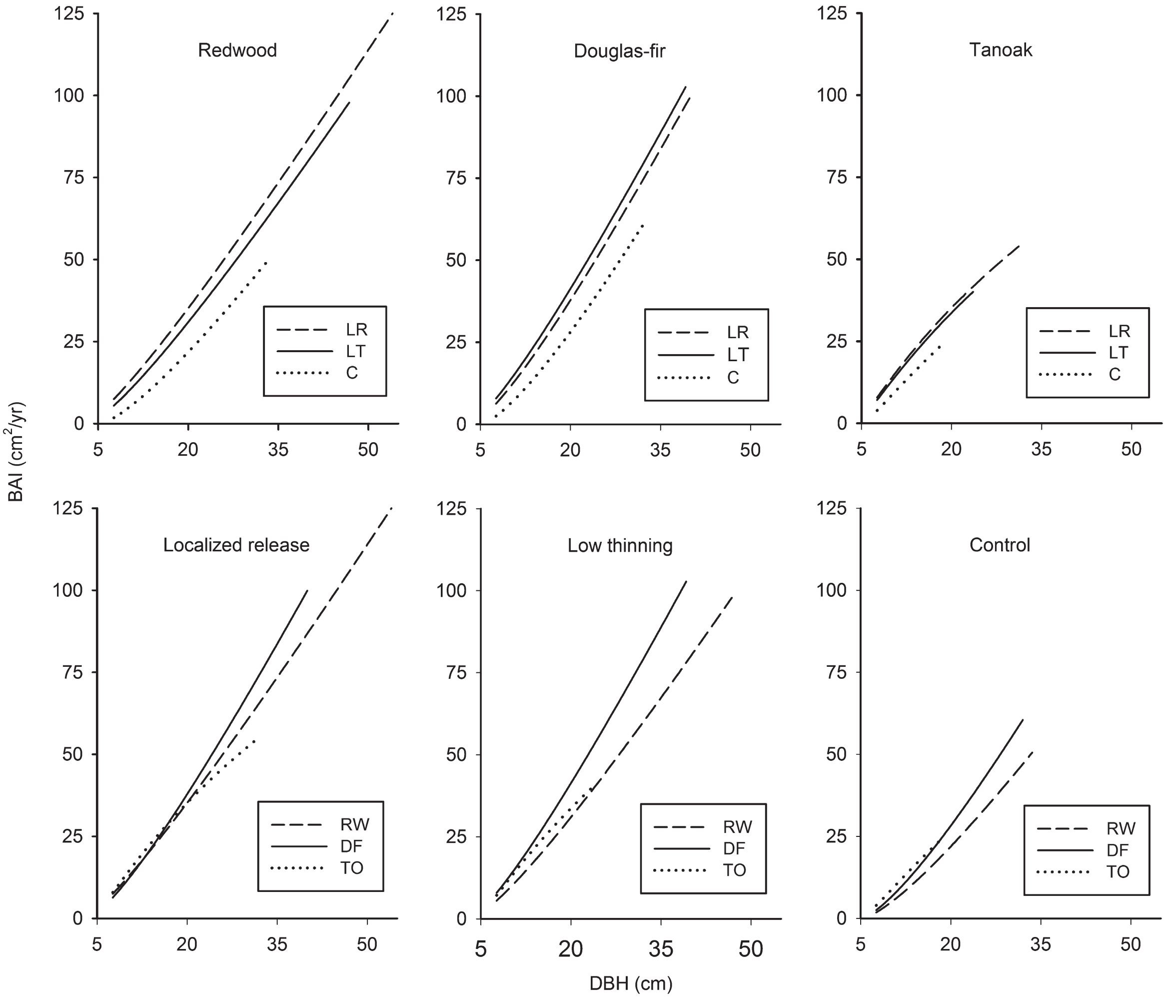

Figure 4. Expected (average) basal area increment (BAI; cm^2/yr) across a range of tree diameters (dbh) for redwood, Douglas-fir, and tanoak for three different treatments. LR = localized release; LT = low thinning; C = control.

aspects. Overall, the average BAI for redwood was 20 and 15% greater in the LR and LT treatments, respectively, than in the unthinned controls (Fig. S2). For Douglas-fir, the average BAI was 17 and 20% greater in the LR and LT treatments, respectively, than in the unthinned controls. A post hoc Tukey–Kramer test showed that for redwood and Douglas-fir, growth did not differ significantly between the LR and LT treatments but was significantly faster than in the unthinned controls ($p \leq 0.01$).

Understory Vegetation and Light

We found 45 different understory plant species throughout all subplots. In year 1, plant species diversity was similar among treatments with 18, 19, and 18 species found in the LR, LT, and C treatments, respectively. Despite the relatively high number of plant species found, most species were rare. Species richness within subplots was low irrespective of treatment (< 2; Table 2). Subplots were dominated by western swordfern, and salal, and to a lesser extent bracken fern (*Pteridium aquilinum* var. *pubescens*) in thinned subplots.

There were no significant differences in species richness and Shannon's diversity index between the LR and LT treatments at the first or second measurement following thinning. Both thinning treatments had significantly higher richness and diversity than the unthinned control at the second measurement ($p < 0.05$; Table 2). Four years after treatment, we found 14, 19, and 8 understory plant species in the LR, LT, and C treatments, respectively. Richness within subplots remained low, and there was a significant decline over the 4-year period in C ($p < 0.01$; Table 2). Western swordfern and salal remained common throughout all treatments, and bracken fern remained common in thinned subplots. Pacific blackberry (*Rubus ursinus*), a rare species found at the first measurement became more common at the second measurement within thinned subplots.

Percent herbaceous cover was highly variable in all treatments and at both measurements. Cover in the LT treatment was significantly lower than C immediately following treatment ($p = 0.03$). Four years after treatment, cover was reduced by

Table 2. Sample size (n subplots) and subplot mean (SD) of understory vegetation species richness, Shannon's diversity index, cover, canopy openness, leaf area index (LAI), and percentage of above-canopy light (PACL) by treatment for measurement event in year 1 and year 5 in each subplot.

		Treatment					
	Year	n	*Localized release*	n	*Low thinning*	n	*Control*
Species richness	1	60	1.4 (1.1)	113	1.3 (1.2)	56	1.9 (1.4)
	5	64	2.3 (1.3)	120	2.1 (1.5)	60	1.3 (1.1)
Shannon's diversity index	1	60	0.2 (0.2)	112	0.2 (0.2)	56	0.3 (0.3)
	5	64	0.3 (0.2)	120	0.3 (0.2)	60	0.2 (0.2)
Cover (%)	1	60	12.7 (20.6)	113	8.7 (13.5)	56	13.4 (16.8)
	5	64	14.2 (13.4)	120	12.8 (15.2)	60	6.8 (10.1)
Canopy openness (%)	1	64	28.5 (17.9)	112	32.8 (18.6)	48	16.2 (14.4)
	5	60	19.1 (12.5)	116	19.3 (12.8)	60	8.6 (2.7)
LAI (5-ring 0–75°)	1	64	1.6 (0.8)	112	1.4 (1.0)	48	2.4 (1.3)
	5	60	2.1 (0.8)	116	2.1 (0.9)	60	2.8 (0.6)
PACL (%)	1	64	36.0 (23.4)	112	39.1 (22.8)	48	20 (19.3)
	5	60	24.0 (18.7)	116	25.4 (18.4)	60	11.1 (5.1)

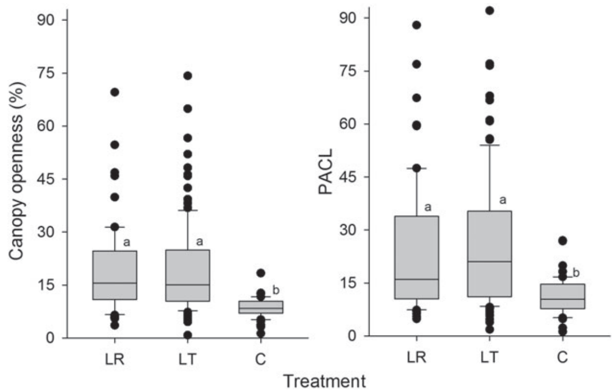

Figure 5. Boxplots of percent canopy openness and percentage of above-canopy light (PACL) for each treatment 4 years after thinning. The center line represents the median, the lower and upper edges of the box are the 25th and 75th percentiles, and the dots are extreme values. LR = localized release; LT = low thinning; C = control. Different letters indicate significant differences among treatments ($p < 0.05$).

50% in the C, and significantly lower than the LT and LR treatments ($p \leq 0.01$).

Percent canopy openness and PACL in thinned plots were close to twice that found in control plots at the first measurement period (Table 2). Canopy closure (i.e. declining canopy openness) proceeded rapidly after the LR and LT treatments and after 4 years was close to canopy openness values found in the control at the first measurement.

We expected there to be higher spatial variability in understory light and canopy cover after the LR treatment. However, we found high variability in canopy openness and understory light in both the LR and LT thinning treatments (Fig. 5). For example, percent canopy openness ranged from 1 to 74% throughout the LT treatment.

Bear Damage

Little to no bear damage was noticed while overseeing the thinning operation and so we assume all bear damage occurred after treatment. Approximately one-third of bear damage was recorded in the first measurement, when monitoring plots were installed, within 1 year of treatment. Additional damage was noted during the second assessment 4 years later. Among 3,230 redwood trees in all plots sampling all treatments, 25.3 and 26.5% were damaged after LT and LR thinning treatments, respectively, whereas only 8.2% were damaged in unthinned control plots over the same period. Mortality was low with only 5.3% of bear damaged redwood trees recorded as dead by the second assessment. Among the 4,177 Douglas-fir trees in all plots, bear damage was almost half that of redwood with 12.8 and 16.3% damaged after LR and LT treatments, respectively, and very few damaged in unthinned stands (1.1%). Bears mainly damaged redwood and Douglas-fir; damage was only noted for 19 other conifer trees (five species) and one tanoak in the sample of 8,366 trees in 60 plots across all treatments.

Logistic regressions consistently predicted greater probability of occurrence of bear damage for redwood than Douglas-fir. Separate models for each species and combined models including both species were tested. One model including both species (root-mean-square error [RMSE] = 0.279) fit the data better than separate species models (RMSE = 0.282). The logistic regression model indicated that trees with faster DBHI were more likely to be damaged (Fig. 6). Models including crown ratio or crown competition did not perform as well as the simpler model with species and DBHI (Table S6).

Slash Depth

Differences in slash (fuel bed) depth were not significant among thinning treatments immediately after treatment ($p = 0.14$). The LR treatment generated the deepest fuel beds, averaging 0.98 m (Fig. S3). Slash depths declined at a faster rate over the 4-year study period for the LT treatment (30 and 24% decline in the LT and LR treatments, respectively), which contributed to significant differences in slash depth between thinning treatments at the second measurement ($p = 0.05$). Despite apparent differences in spatial pattern between thinning treatments, CV in slash depths were not significantly different between thinning

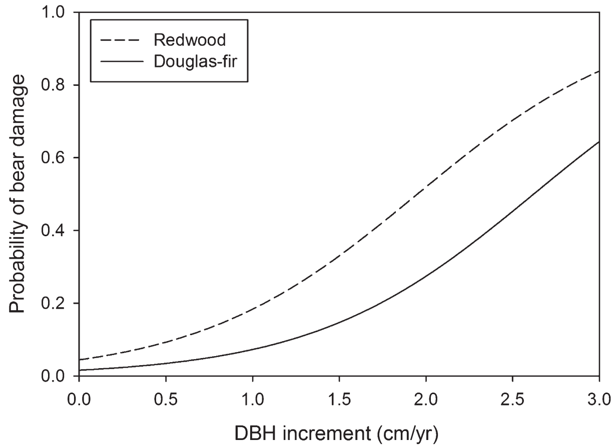

Figure 6. Modeled probability of bear damage for redwood and Douglas-fir in response to varying levels of dbh increment (cm/year).

treatments ($p \geq 0.24$). Mortality within unthinned control plots was contributing very little fuel load, with an average slash depth of 0.12 m.

Discussion

LR at Mill Creek increased redwood abundance and resulted in a favorable combination of rapid redwood tree growth and enhanced structural tree-size diversity compared to unthinned controls. We expect sustained differences in growth rates among trees retained within the circular gaps, on the edge of gaps, and inside unthinned patches, leading to greater tree-size diversity over time. However, posttreatment densities were higher than target densities in all thinning treatments and will result in shorter treatment longevity. Posttreatment densities in the LD and HD treatments were similar to each other. In the LR treatment, we intended the circular gaps to be installed side by side. Instead, they were installed in a more random fashion leaving more unthinned area between gaps. Training and supervision of contractors who may be more accustomed to industrial thinning methods should help meet retention goals. Density retention goals were not met in the thinning treatments in part because of our desire to leave redwood sprout clumps intact.

Thinning can have positive and negative effects on understory plant species richness and abundance. Increases in plant species diversity following thinning have been linked to increases in light availability (Harrington & Edwards 1999), while decreases have been attributed to increased dominance by a few species (Alaback & Herman 1988) or harvesting practices (Nagai & Yoshida 2006). We found increased richness and cover in response to thinning treatments within subplots (100 m^2 area), consistent with other studies in this region (Thysell & Carey 2001; Aukema & Carey 2008; Ares et al. 2009, 2010). Interestingly, Ares et al. (2009, 2010) found much greater richness and cover of understory vegetation after extraction of cut trees than our study where cut trees were left to form an intermittent and variable layer of slash.

Crown closure proceeds rapidly in young redwood stands bringing heavy shade to the understory and loss of biodiversity (O'Hara et al. 2007; O'Hara & Berrill 2010). Canopy closure (i.e. declining canopy openness) proceeded rapidly in all treatments over the 4-year period. In the LR and LT treatments, canopy openness values had returned to similar canopy openness values found in the control at the first measurement. Therefore, we should expect cover, species richness, and Shannon's diversity index to continue to decline. Recommendations for future restoration activities should include heavier cutting and cutting patches of varying sizes, including large openings needed to create persistent gaps in the forest canopy. Canopy gaps of all sizes up to 1,272 m^2 were measured in old-growth redwood stands (Dagley & Berrill 2012).

Thinning to release suppressed redwood and promote the development of large overstory trees as found in old-growth stands predisposes these trees to bear damage (Mason & Adams 1989; Hosack & Fulgham 1998; Perry et al. 2016). Bear damage is undesirable in most managed forests but may be advantageous in restoration. Damage to the lower bole may lead to large basal cavities which are common in old-growth redwood trees (Dagley & Berrill 2012). Bear-damaged trees may die sooner and become snags, and eventually fall to become CWD. Large snags and CWD are characteristic of old-growth forests but less common in young forests (Spies et al. 1988; Carey & Johnson 1995). It is unfortunate that bears preferentially damage redwood which is often underrepresented or suppressed and the focus of restoration activities in this region (O'Hara et al. 2010). Additionally, faster growing young trees are more likely to sustain damage (Mason & Adams 1989; Nelson 1989; Schmidt & Gourley 1992; Berrill et al. 2017). In this study, 100% of the fastest growing redwoods (DBHI >2.8 cm/year) were damaged by bears. Nevertheless, many trees did not sustain bear damage and showed significantly higher rates of growth for trees in thinned stands than in unthinned controls.

Approximately one quarter of redwood trees sustained bear damage after thinning, of which 5.3% died in the short term as a result of excessive damage. It is unknown how many of the bear-damaged trees will die; however, restoration thinning prescriptions could call for retention of extra trees to compensate for expected mortality and still maintain enough overstory trees to meet reference conditions for alluvial flat redwood forests (Dagley 2008; Dagley & Berrill 2012) or upland redwood/Douglas-fir/tanoak forests (van Mantgem & Stuart 2012; Berrill et al. 2013). Alternatively, restoration thinning prescriptions could be delayed until stands are older or have attained larger tree sizes. A study in Douglas-fir forests in Oregon showed that bear damage was most often noted on trees 15–45 years old (Maser 1967). A study with redwood in northern California found trees 10–50 cm dbh to be most susceptible to bear damage, and redwood over other species (Russell et al. 2001). Our finding that diameter growth response to thinning was greater in young stands and that bears preferentially damage faster growing trees also supports the idea of delaying thinning until trees are larger and older.

Variable slash accumulation averaging up to a meter depth, including thick patches and areas without slash, were found within thinned stands. Similarly, a study in a redwood/Douglas-fir forest at Headwaters Forest Reserve reported an average fuel height of 0.84 m (range 0.04–3.04 m) and 0.19 m (range 0.02–0.71 m) in thinned and unthinned stands, respectively (Glebocki 2015). In our study, fuel beds were decreasing in depth by 24–30% over the 4 years since treatment, with LT (i.e. thinning from below) exhibiting the greatest decrease; possibly due to smaller trees being cut and decaying and breaking down more quickly. These stands were older than stands that O'Hara et al. (2010) studied at Mill Creek where slash depths had declined to approximately 50–66% over 4 years where smaller younger trees were cut and presumably decayed more quickly. This suggests that a benefit of early thinning may be a relatively shorter-term fire hazard due to the more rapid decomposition of smaller fuels.

Local competition has been shown to influence individual tree growth, and may be particularly important in projecting growth and yield in diverse stands (Roberts & Harrington 2008; Berrill & Dagley 2012; Berrill et al. 2013; van Mantgem & Das 2014; Kuehne et al. 2015). Most promising appears to be the use of spatially explicit models that utilize stem-mapped data to examine the competitive environment of each tree. These models have the additional benefit of being able to determine impacts on growth from different neighboring species. For example, van Mantgem and Das (2014) showed that western hemlock and tanoak more negatively affected redwood growth than Douglas-fir, suggesting that the preferential removal of species other than Douglas-fir may be warranted unless these species would then be underrepresented in the restored stand. Stem-mapped data also helps us relocate trees with missing tags at repeat measurements, but collecting these data represents an additional expense for researchers. Our crown competition code, an easily assessed qualitative measure of neighbor competition for each individual tree, was a strong predictor of growth in our study. Growth declined sharply when more crown extent abutted neighbor trees. Holding all other variables constant, trees with near neighbors on all four sides of their crown grew on average 33% slower than trees without neighboring tree crowns in the immediate vicinity. This is consistent with results from a study in 40–60-year-old Douglas-fir stands where they found tree diameter growth to be 40% greater for trees located on the edge of gaps (Dodson et al. 2012).

Results from our study indicated that thinning in young stands (age 15–25 years) enhanced tree growth, redwood composition, and tree-size variability within stands. However, Douglas-fir remained the dominant species in thinned and unthinned stands. Total stem densities after thinning were approximately three times higher than those reported for upland old-growth forests. Large snags and large CWD, which are important for certain wildlife and characteristic of old-growth forests, were absent. Taken collectively, these findings suggest that thinning in young stands can enhance or accelerate the development of some characteristics associated with old-growth forests, but that additional restoration treatments will be needed to further reduce densities, furnish large CWD and understory light to support a diverse understory, and maintain tree growth and vigor into the future.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Density of trees >7.6 cm dbh for each species.
Table S2. Density and range of values among stands having structural attributes common to old-growth forests.
Table S3. Generalized linear mixed-effects models of basal area increment.
Table S4. Summary data for basal area increment.
Table S5. Generalized linear mixed-effects models of basal area increment for the largest 50 stems/ha.
Table S6. Candidate logistic regression models of bear damage.
Figure S1. Schematic diagram of permanent monitoring plots.
Figure S2. Adjusted least squares means of average basal area increment.
Figure S3. Adjusted least square means of slash depth.

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