



Second-growth redwood forest responses to restoration treatments

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ABSTRACT

Following 20th century logging, much of the natural coast redwood (*Sequoia sempervirens* [D. Don.] Endl.) range consists of dense second-growth stands with slow tree growth and low biodiversity. There is a landscape-scale effort in much of coastal northern California to increase tree growth rates and ecosystem biodiversity via thinning treatments, thereby hopefully accelerating the development of old-growth forest characteristics. Redwood National Park has been experimenting with thinning in these forest types since the 1970s. This study investigated short- (1 year post-thinning) and long-term (40 years post-thinning) responses of redwood physiology (water potential and stomatal conductance), redwood growth (via tree-rings), and forest biodiversity (understory plants, birds, and mammals) to restoration thinning treatments. We found that thinning second-growth redwood forests with 40% basal area reduction treatments 1) did not meaningfully influence tree water potential, 2) increased tree stomatal conductance in the short-term, 3) increased tree growth in the long-term, 4) increased understory plant diversity, and 5) did not affect bird or mammal diversity. Collectively, these findings demonstrate that thinning second-growth redwood forests has the potential to accelerate the development of old-growth characteristics. This verification of the efficacy of restoration treatments is important information for land managers, as plans are currently underway to apply these treatments at the landscape-scale. This study can provide useful baseline data to aid future assessments of long-term forest responses to contemporary restoration efforts.

1. Introduction

The iconic coast redwood (*Sequoia sempervirens* [D. Don.] Endl.) is currently restricted to a narrow natural range along the coast of northern California and southern Oregon. These foggy coastal habitats are vulnerable to climate change, as over the last century the frequency of summer fog, an important water input, has reduced (Johnstone and Dawson, 2010) and mean temperatures have increased (Koopman et al., 2014). After over 150 years of commercial logging, today less than 5% of the original old-growth redwood forest remains (Noss, 2000; Sillett and Van Pelt, 2014). There are therefore regional efforts to restore the matrix of young second-growth stands surrounding the few remaining old-growth patches to serve as habitat corridors for wildlife and act as buffers against forest edge effects (O'Hara et al., 2010).

Compared to old-growth redwood forests, second- and third-growth forests, typically established after industrial timber practices, support unnaturally high tree densities, low redwood dominance, low biodiversity, and relatively low tree vigor (Teraoka and Keyes, 2011). Old-

growth redwood forests are primary forests that have not been commercially logged. They can be characterized by a stable negative exponential size class distribution, basal area ranging from approximately 130 to 230 m² ha⁻¹, balanced mortality and recruitment rates, and a non-uniform, clumped arrangement of redwood stems (van Mantgem and Stuart, 2012). Due to this shade-tolerant forest type, stands can stagnate with exceptionally high densities of unhealthy, spindly trees with small crowns, thereby precluding the development of old forest features for decades (Veirs and Lennox, 1982; Thornburgh et al., 2000). The use of active restoration techniques in overly dense second-growth stands can therefore be helpful to accelerate natural thinning, improve forest health, and promote the development of old-growth characteristics. Prior to European settlement and fire exclusion, fire was an important part of the coastal redwood forest, with return intervals often less than 10 years (Brown and Swetnam, 1994). Likely due to Native American ignitions, these frequent fires likely limited shrub dominance in the understory to support a great diversity of understory plants and wildlife habitats (Lorimer et al. 2009). While the

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reintroduction of fire has the potential to return lands to historical conditions, prescribed burning is often not a feasible option due to numerous logistical, bureaucratic, and political barriers (Berrill et al., 2013) as well as relatively wet fuel loads in this forest type. Alternatively, forest managers can use thinning to prevent stands stagnating at high densities (Oliver and Larson, 1996; O'Hara et al., 2010) and increase forest biodiversity, the latter a fundamental guiding principal for ecologically sustainable forest management (Lindenmayer and Franklin, 2002; Carey, 2003; Larsson and Dannel, 2010). While many studies have reported on forest responses to thinning across a variety of forest types and treatment prescriptions, studies of this nature in redwood forests are comparatively limited. Generally, we expect that thinning will reduce competition for limiting resources such as water, light, nutrients, and space such that residual trees will experience less water stress and be able to support increased rates of gas exchange and growth (Covington et al., 1997; Sohn et al., 2016; van Mantgem et al., 2020).

Redwood National Park (RNP) is centrally located within redwood's range and is comprised of over 20,000 ha of second-growth forests (Sarr et al., 2004). Annexed in 1968 and 1978, these lands were predominately former industrial timberlands (Teraoka and Keyes, 2011). Since annexation, these lands have been largely unmanaged and today exhibit a high degree of even-aged trees with homogeneous stand structure and higher proportions of Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) and tanoak (*Notholithocarpus densiflorus* [Hook and Arn.] Manos, C.H. Cannon, & S. Oh) than historical reference conditions (Chittick and Keyes, 2007). In 1978, RNP began actively thinning second-growth forests in an effort to increase tree growth, redwood composition, and biodiversity. Since 1978, numerous restoration treatments have been implemented across RNP and these efforts are expanding, with current plans to thin thousands of acres of second-growth redwood forests in northern California (Burns et al., 2018).

Given the resource-intensive costs of forest restoration, it is important to monitor the efficacy of treatments to improve adaptive management efforts (Teraoka, 2012). Growth (Kerhoulas et al., 2013; King et al., 2013) and physiology (Skov et al., 2004) are two ways to evaluate and monitor forest responses to management treatments. Growth is often evaluated using tree-rings to measure basal area increments (BAI). While many investigations of forest tree responses to treatments rely on breast height diameter growth (Skov et al., 2005), this growth-based approach can take years to detect (Roberts and Harrington, 2008; Dagley et al., 2018) and can fail to detect a response if newly available carbon is allocated to fine roots, leaf area, or sugar reserves rather than to diameter growth. In complement to long-term growth-based evaluations, physiological measurements such as water potential (Ψ) and stomatal conductance of water vapor (g_s) can provide useful information about shorter-term tree responses (Skov et al., 2004). Predawn Ψ (Ψ_{pd}) can serve as a surrogate for plant-available water, representing a plant's most hydrated daily status. On the other end of the spectrum, midday Ψ (Ψ_{md}) can be used to estimate a plant's most stressed daily water status. Because plants exchange both CO_2 and H_2O through stomata, photosynthesis and transpiration are typically positively correlated. Thus, g_s measurements can serve as a proxy measurement for photosynthesis. Physiological measurements also have the potential to identify adverse initial responses to thinning such as 'thinning shock' (Harrington and Reukema, 1983), which could be useful information when formulating prescriptions and predicting short- and long-term forest responses. Despite these appeals, physiological measurements can be time consuming to conduct and require specialized equipment and skills. Thus, relatively few studies have investigated leaf-level physiological responses to restoration. Given the lack of published measurements of redwood physiology in these forest types, knowledge about redwood physiology in suppressed forests would provide useful baseline data for long-term monitoring of forest responses to treatments.

Fostering healthy understory vegetation (e.g., forbs, grasses, and shrubs) supports wildlife diversity, as these plants provide food and habitat for animals. Under closed canopies, understory vegetation is

minimal and can take decades to re-establish as it requires increased light from canopy gaps (Oliver and Larson, 1996). In forests of the Pacific Northwest, although herbaceous understory cover can initially increase following treatments, these responses are often short-lived and can frequently cause vegetation to shift towards shrub dominance (Cole et al., 2017; Goodwin et al., 2018). Furthermore, while thinning can accelerate the development of old-growth conditions capable of supporting a wide array of animals, the short-term loss of understory vegetation following thinning operations can reduce wildlife diversity (Hayes et al., 1997; Carey, 2003). However, treatments such as variable density thinning (VDT, non-uniform treatments that leave a heterogeneous mosaic of different tree densities, clumps, and gaps across the landscape) that increase stand heterogeneity seem to create suitable habitat for a variety of fauna (Carey, 2003; Verschuyt et al., 2011). As such, silvicultural treatments such as low thinning (removing smaller trees and retaining larger trees) and VDT are often used in forest restoration treatments (Carey, 2003; Teraoka and Keyes, 2011), with the use of VDT becoming increasingly widespread (Chittick and Keyes, 2007; O'Hara et al., 2010).

In this study, we examined physiological, growth, and biodiversity responses to restoration treatments applied across a chronosequence of sites in RNP that range in years-since-thinning from 40 to 1, as well as untreated sites to serve as a control. To improve our understanding of ecosystem-scale responses to restoration treatments, we investigated three questions and predictions. 1) Does treatment affect redwood physiology (Ψ and g_s), and if so, how persistent are these responses? We predicted that in response to thinning, redwood Ψ would decrease due to greater evapotranspirational water losses, redwood g_s would increase due to greater light availability, and that these responses would decrease with time-since-treatment due to the eventual closure of canopy gaps. 2) Does treatment affect tree growth (as measured by BAI), and if so, how long does this response persist? We predicted that thinning would increase growth, that this increase would be delayed a few years following treatment, and that this response would be relatively short-lived due to quick canopy reclosure in this temperate forest. And 3) does treatment affect biodiversity, and if so, how persistent are these responses? We predicted that while treatments would likely increase understory plant diversity due to increased light availability, wildlife diversity would be slow to respond due to the loss of understory vegetation resulting from thinning operations.

2. Materials and methods

2.1. Study site and design

Centrally located within redwood's range, this study occurred approximately 13 km east of Orick, CA, USA on the top of Holter Ridge in RNP (Fig. 1). This region has a Mediterranean climate with cool, wet winters and warm, typically rainless, foggy summers. Average annual temperature and precipitation at this site are 10.6 °C and 168.6 cm, respectively (NOAA, 2019: <https://www.ncdc.noaa.gov/cdo-web/datatools/normals>). The soils are classified as clay, clay loam, and silty clay loam that formed from colluvium and residuum on mountaintops and the upper third of mountainflanks (Soil Survey Staff, 2017). Historically an upland coast redwood old-growth forest (Veirs, 1986), Holter Ridge now consists of dense, second-growth stands largely established in the 1950s following clearcut logging; these stands are often dominated by Douglas-fir and support low biodiversity (Chittick and Keyes, 2007). Less common tree species at this site include western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.), tanoak, and Pacific madrone (*Arbutus menziesii* [Pursh.]). The understory vegetation is comprised mainly of evergreen huckleberry (*Vaccinium ovatum* [Pursh.]), red huckleberry (*Vaccinium parvifolium* [Sm.]), salal (*Gaultheria shallon* [Pursh.]), rhododendron (*Rhododendron macrophyllum* [D. Don]), and sword fern (*Polystichum munitum* [Kaulf.] C. Presl) (Veirs, 1986; Chittick and Keyes, 2007).

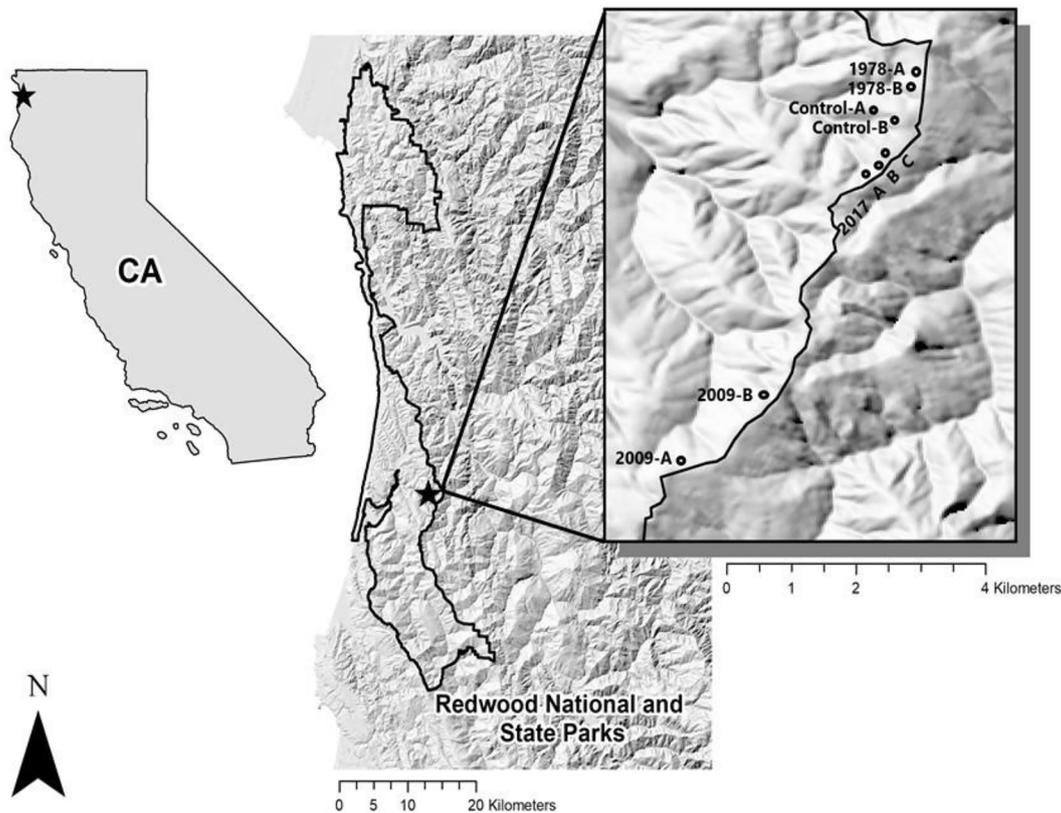


Fig. 1. Locator map of the nine 0.25 ha study plots on Holter Ridge in Redwood National Park, California. Years indicate when stands were thinned using a 40% basal area reduction treatment; control stands were untreated.

In 1978, average stand density on Holter Ridge averaged 2,400 trees ha⁻¹ with some stands having 7,400 trees ha⁻¹ (Veirs, 1986; Chittick and Keyes, 2007). For comparison, stand density in redwood-dominated old-growth stands typically ranges from 25 to 90 trees ha⁻¹, with a minor representation of Douglas-fir (typically 3–10 trees ha⁻¹) (Chittick, 2005). Due to these unnaturally high tree densities, in 1978 RNP experimentally thinned several 25-year-old second-growth stands on Holter Ridge with goals to reduce competition for residual trees, promote redwood dominance, and increase biodiversity (Veirs and Lennox, 1982). Numerous similar treatments were applied in the years that followed.

Due to this history of experimental thinning treatments, our study was able to use nine existing 0.25 ha plots that ranged in time-since-thinning from 40 years to one year and were otherwise comparable in most respects: two unthinned control plots, two plots thinned in 1978 (Veirs and Lennox, 1982), two plots thinned in 2009 (Teraoka, 2012),

and three plots thinned in 2017 (Fig. 1, Table 1). Plots thinned in 1978 were treated using a low-thinning prescription that reduced Douglas-fir numbers to 60% of redwood numbers; this treatment reduced stand basal area (BA) density by approximately 40%. Similarly, plots thinned in 2009 were also treated with a low-thinning prescription that targeted Douglas-fir removal and reduced stand BA density by approximately 40%. Plots thinned in 2017 were treated using a relatively novel VDT prescription that removed approximately 0, 25, 40, 55, and 75% of BA density, with each reduction treatment randomly applied in 0.10 ha cells across 22 ha of Holter Ridge (Fig. 2). As 2017 was the first time that a VDT prescription was used in RNP, to monitor treatment efficacy three permanent 1 ha plots were established, each with a 0.25 ha central subplot that was predominantly thinned to a 40% BA reduction, comparable to the 40% BA reduction treatments applied in 1978 and 2009. Thus, to compare tree responses to 40% BA reduction treatments across time (1978–2017), these inner 0.25 ha VDT plots were compared against

Table 1

Plot-level attributes of the nine study plots on Holter Ridge in Redwood National Park (RNP). Each plot is 0.25 ha and was treated using a low-thin prescription that targeted Douglas-fir removal. Plots were treated in 1978, 2009, and 2017, with control plots untreated. The 1978 and 2009 plots were thinned to a target basal area (BA) reduction of 40%. The 2017 plots were treated using variable density thinning (VDT) with five BA reduction treatments: 0, 25, 40, 55, and 75%. The VDT plots used in this study were predominantly thinned using a 40% BA reduction treatment. Each plot had ten study trees that were used for physiological analyses; for diameter at breast height (1.37 m, DBH) and BA, values represent mean ± SE.

Study Plot	RNP Name	Elevation (m)	Aspect	Slope (°)	Treatment Year	DBH (cm)	BA (m ² ha ⁻¹)
Control-A	Control-3	501	NE	10	n/a	29 ± 2	111 ± 10
Control-B	Control-4	504	E	14	n/a	40 ± 4	96 ± 8
1978-A	IB2-2	522	SW	10	1978	48 ± 4	62 ± 5
1978-B	IB2-4	515	SW	15	1978	44 ± 2	73 ± 7
2009-A	40L1-1	679	NNW	14	2009	37 ± 2	73 ± 8
2009-B	40L1-3	631	NNW	8	2009	42 ± 2	70 ± 9
2017-A	VDT-1	512	E	9	2017	45 ± 7	61 ± 19
2017-B	VDT-2	511	N	12	2017	52 ± 15	81 ± 8
2017-C	VDT-3	504	NE	8	2017	27 ± 4	76 ± 9

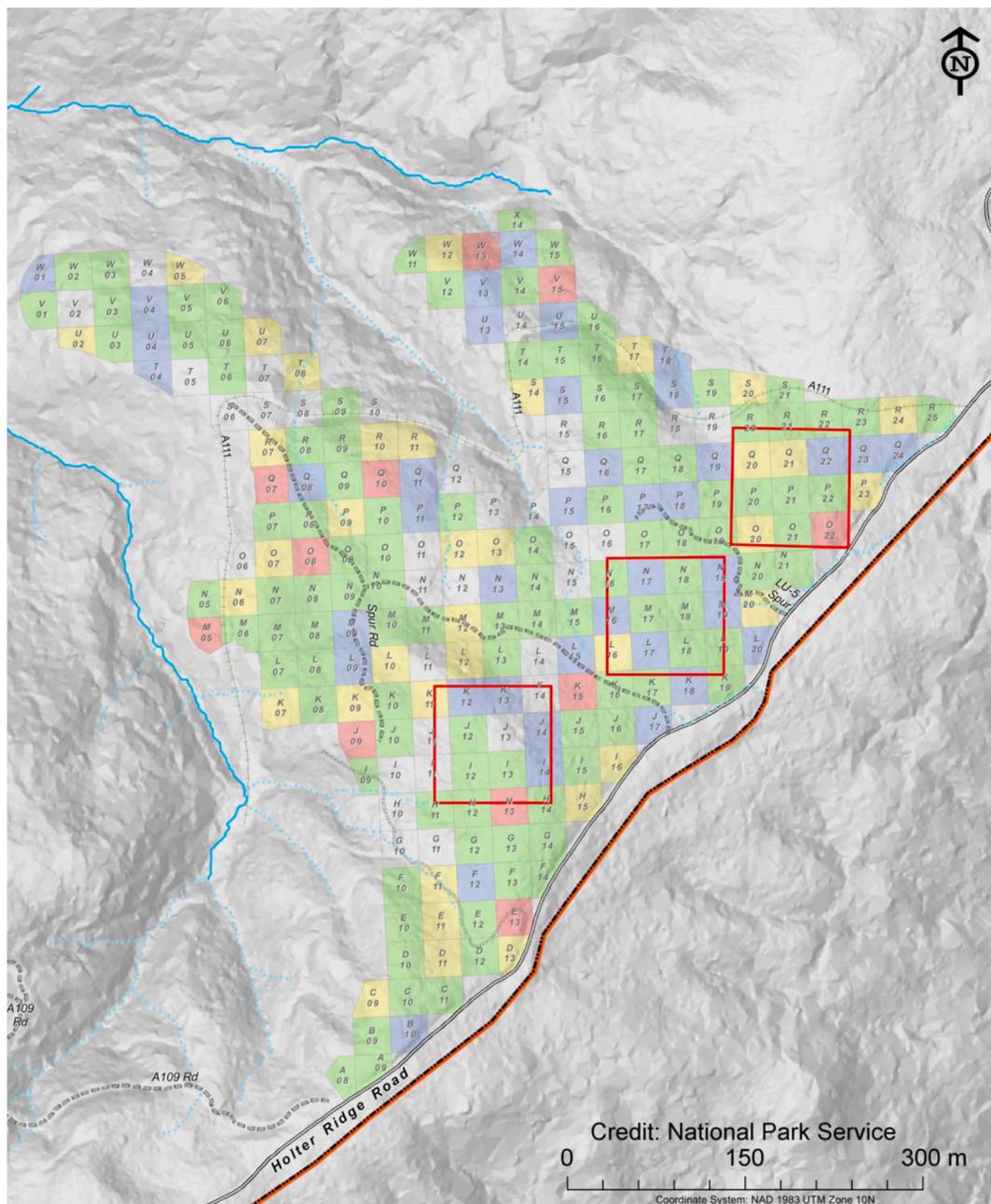


Fig. 2. The Middle Fork of Lost Man Creek variable density thinning unit map on Holter Ridge in Redwood National Park. Treatments were applied in the fall of 2017 across this 22 ha area. Each basal area (BA) reduction treatment (clear = 0%, blue = 25%, green = 40%, yellow = 55%, and red = 75%) was randomly applied to 0.10 ha subplots. Within each of the 1 ha permanent plots (red boxes), there is a 0.25 ha central plot. This study used these three central 0.25 ha plots for comparison with other stands on Holter Ridge that were thinned in 1978 and 2009. The three central plots were thinned in 2017 predominantly using the 40% BA reduction treatment. Credit: National Park Service.

the 0.25 ha plots thinned in 1978 and 2009. In all plots, Douglas-fir was targeted for removal to promote redwood dominance. Within each plot, the 10 redwood trees closest to plot center that were healthy and had a live crown base accessible via a pole pruner (no higher than 14 m) were selected as study trees for physiological and dendrochronological analyses. For each study tree, diameter at breast height (1.37 m, DBH) and local competition (as measured with an imperial prism, basal area factor 40) were recorded in 2018.

2.2. Physiological measurements

In 2018 and 2019, leaf-level physiological measurements occurred across two consecutive sunny days in July, a time of high productivity

and low precipitation input. Leaf water potential was measured using a pressure chamber (Model 600, PMS Instruments, Corvallis, OR) and g_s was measured using a leaf porometer (Model SC-1, Decagon Devices, Pullman, WA). For physiology measurements, a pole pruner was used to clip one small branch from the lower crown of each study tree at pre-dawn (Ψ_{pd}) and at midday (Ψ_{md}). Leaf Ψ_{pd} was only measured in 2018, not 2019, while leaf Ψ_{md} was measured in both 2018 and 2019. At midday, care was taken to collect the branch from a well illuminated portion of the crown. From each predawn branch, three Ψ_{pd} measurements were immediately taken from three different branchlets cut from the collected branch and averaged into a single Ψ_{pd} value for that tree. Similarly, from each midday branch, three Ψ_{md} and g_s measurements were immediately taken and averaged into single values for that tree.

In 2019, stem psychrometers (Model PSY1, ICT International, Australia) were used to continuously measure xylem Ψ during the last week of August and first week of September. For these measurements, one study tree per plot was instrumented and measured every 30 min for 17 consecutive days from August 22 to September 8; trees were chosen such that the nine study trees were comparable in size and local competition (BA density). Unfortunately, the stem psychrometers in two plots (2009-A and 2017-C) did not function properly; data from these two plots were therefore not included in our analyses or results. For each instrumented tree, on each monitoring day, the highest Ψ value occurring between 00:00–05:00 h was identified as xylem Ψ_{pd} and the lowest Ψ value occurring between 11:00 and 16:00 h was identified as xylem Ψ_{md} . Due to instrument noise, we only used a seven-day window (August 31 to September 6) for analysis of xylem Ψ .

2.3. Dendrochronological measurements

To evaluate tree growth responses to thinning treatments using dendrochronological analyses, growth was measured in trees from the control plots, plots thinned in 1978, and plots thinned in 2009. The VDT plots, thinned in 2017, were omitted from this analysis as it was deemed that insufficient time had passed since treatment (<2 years) to reliably detect a growth response.

In March 2019, two breast height increment cores (5 mm diameter) were taken at 90° angles from each other on the upslope side of each study tree used for physiological measurements ($n = 10$ trees per plot). Ten more redwood trees from each included plot were added for this growth analysis to make a total of 20 trees per plot. These additional trees were selected as the ten trees closest to plot center along randomly chosen azimuths. For all study trees used for dendrochronological analyses, DBH and BA (as measured with an imperial prism, basal area factor 40) were recorded.

Cores were mounted, sanded to 600 grit, and scanned at 2400 dpi (Epson America, Inc., Long Beach, CA) (Stokes and Smiley, 1968). Cores that were damaged or had unreadable tree-rings were excluded from analysis ($n = 16$ out of 240 cores). Attempts were made to cross-date cores using COFECHA software, but these efforts were unsuccessful, likely due to complacent growth across all plots as well as short time series (<50 years on most trees). Thus, cores were visually measured and cross-dated using WinDendro (Régent Instruments Inc., Québec, Canada) and a list of marker years. Using this method, cores were reliably cross-dated from 1960 to 2017. On each study tree, annual radial growth measurements from the two cores were averaged into a single value. These radial growth measurements were then used with tree DBH measurements and bark thickness (BT) estimates to calculate basal area increment (BAI) using the dplR statistical package with the *bai.out* function in R. To calculate an estimate of BT (in mm) for each tree, a locally-derived regression equation for coast redwoods on Holter Ridge (Lalemand, 2018) was used:

$$\text{coastredwoodBT} = 9.939 + 0.722 * \text{DBH} \quad (1)$$

where DBH is tree breast height diameter (in cm, including bark).

2.4. Biodiversity measurements

To investigate understory plant diversity, understory plants were inventoried in June (peak flowering season) of 2018 and 2019. Five circular subplots (radius = 1.78 m; 10 m²) were installed within each of the nine 0.25 ha study plots. Subplots were systematically placed within each plot: one per corner (NW, NE, SW, SE) and one directly over plot center. Within each subplot, species present, slope, aspect, and percent cover per species were recorded. Percent cover was recorded using the Daubenmire cover class scale (1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 95–100%).

Wildlife diversity was inventoried in 2018 and 2019, largely

following protocols established by California State Park wildlife biologists (Slauson, 2013). To evaluate bird abundance in each plot, three consecutive 10-minute point counts were conducted within 90 min before or after sunrise across two consecutive sunny days in June (a period of high bird song activity) (Ralph et al., 1993). All avian species were identified by sight and/or sound. In both years, mammalian diversity was quantified using camera traps (Model PH770, Enkeeo) in October, a period of high mammalian activity. Three camera traps were deployed at each plot, placed at 0°, 120°, and 240° azimuths, 10 m from plot center. Cameras were affixed to a piece of rebar 50 cm above the forest floor and set to focus on the ground 10 m away (20 m from plot center) on the same azimuth. Camera traps recorded wildlife activity on the forest floor for three weeks during each sampling period. Incidental observations of mammal scat were also recorded but not included in species diversity estimates. The use of Sherman live traps to inventory small mammal diversity was attempted in 2018, but was ultimately precluded by the presence of American black bears (*Ursus americanus*). All wildlife survey protocols were approved by the Humboldt State University IACUC, protocol: 17/18.FWR.37-A.

For each of the nine study plots, understory plants, birds, and mammals were evaluated via three diversity metrics: species richness (S), species evenness (D) calculated using the following equation:

$$D = 1 - \frac{\sum_{i=1}^S n_i(n_i - 1)}{N(N - 1)} \quad (2)$$

and the Shannon-Wiener diversity values (H') calculated using the following equation:

$$H' = - \sum_{i=1}^S \frac{n_i}{N} \ln \frac{n_i}{N} \quad (3)$$

where n_i = relative cover of each species (plants) or the number of individuals detected for each species (mammals and birds) and N = total percent cover (plants) or total number of species (mammals and birds).

2.5. Statistical analyses

Using R software version 3.5.1 (R Core Team, 2016), one-way ANOVAs were used to determine the influence of treatment (control, 1978, 2009, 2017) on tree physiology and growth. Paired *t*-tests were used to test for differences in leaf Ψ_{md} and g_s between years (2018 and 2019). Understory plant, avian, and mammalian diversities were analyzed with two-way ANOVAs using treatment and sampling year as effects. To test the assumption of equal variances among groups, Levine and Bartlett tests were used; when this assumption was violated, Welch tests were used to determine whether or not groups significantly differed. To test the assumption that data were normally distributed, Shapiro-Wilk goodness-of-fit tests were used; when this assumption was violated, Kruskal-Wallis tests were used to determine whether or not groups significantly differed. If groups significantly differed, Tukey's HSD multiple means comparisons were used to identify significant differences among groups. For all statistical analyses, an α level of 0.05 was used.

3. Results

3.1. Physiology

Across all plots used for our physiology analysis (control, 1978, and 2009, each with two replicates, and 2017 with three replicates) study trees had an average DBH of 41 ± 3 cm and BA density of 79 ± 3 m² ha⁻¹ (Table 1). Among all physiology plots, DBH was not statistically different ($p = 0.48$) but BA density was significantly higher ($p < 0.0001$) in the control as compared to the 1978, 2009, and 2017 plots.

In 2018 and 2019, water potential (Ψ) was measured on a pressure

chamber (leaf Ψ) and with stem psychrometers (xylem Ψ), respectively. In 2019, leaf Ψ_{md} was also measured in July using a pressure chamber to enable interannual comparisons. Both xylem and leaf Ψ measurements were consistently high, not dropping below -2 MPa in 2018 or 2019. Across seven days in September 2019, continuous stem psychrometer measurements showed that the 1978 and 2009 plots generally experienced the highest and lowest xylem Ψ , respectively (Fig. 3). In 2018, leaf Ψ_{pd} was significantly higher in the 2009 plots compared to all other plots ($p = 0.0002$, Fig. 4A, Table 2). In 2019, xylem Ψ_{pd} was highest in the 1978 plots compared to all other plots, although not significant ($p = 0.15$, Fig. 4A, Table 2). Due to differing methods of Ψ_{pd} collection, Ψ_{pd} between 2018 (leaf Ψ_{pd}) and 2019 (xylem Ψ_{pd}) could not be compared.

At midday, we found that the recently treated 2017 plots had the lowest Ψ_{md} and that across all plots, Ψ_{md} was lower in 2018 compared to 2019. More specifically, the 2017 plots experienced lower leaf Ψ_{md} than all other plots in 2018 ($p < 0.0001$) and in 2019 ($p < 0.0001$, Fig. 4B, Table 2). And, between years, leaf Ψ_{md} was significantly lower in 2018 than 2019 for all plots: control ($p = 0.0001$), 1978 ($p < 0.0001$), 2009 ($p < 0.0001$), and 2017 ($p = 0.01$).

In 2018, g_s was significantly higher in the 2017 plots compared to the 2009 plots ($p = 0.02$, Fig. 4C, Table 2). Similarly, in 2019, g_s was significantly higher in the 2017 plots compared to the control plots ($p = 0.01$). Compared to 2018, g_s values in 2019 were significantly higher in the 1978 ($p = 0.01$), 2009 ($p < 0.0001$), and 2017 ($p = 0.001$) plots, but not in the control plots ($p = 0.59$).

3.2. Growth

Across all plots used for growth analysis (control, 1978, and 2009, each with two replicates), there were 115 study trees (20 trees per plot minus five trees that were not cross-datable). On average, these trees had DBH 44 ± 1 cm, BA density 86 ± 3 m² ha⁻¹, and annual BAI (based on 1960–2015) 16.6 ± 0.3 cm² yr⁻¹ (Table 3). Among plots, although DBH ($p = 0.32$) and annual BAI ($p = 0.054$) did not differ significantly, BA density was significantly higher ($p < 0.0001$) in the control plots compared to the 1978 and 2009 plots. Overall, there was a general trend in all plots of increasing BAI starting around 1990 (when the stands were roughly 40 years old), with BAI generally being highest in the 1978 plots and lowest in the control plots (Fig. 5).

3.3. Biodiversity

Across all nine plots in 2018 and 2019, 24 different understory plant species were observed: 14 herbaceous plants, three ferns, four shrubs, and three trees (Table 4). Across the two sampling years, plot-level plant

species richness (S) ranged between six and 20, species evenness (D) ranged from 0.28 to 0.81, and the Shannon-Wiener diversity index (H') ranged from 0.45 to 2.29 (Table 5); neither D ($p = 0.07$) nor H' ($p = 0.054$) were significantly different among treatments. Treatment was a significant effect ($p = 0.01$) on understory S but sampling year ($p = 0.19$) was not. Compared to all other plots, understory S was significantly higher in the 2009 plots ($p = 0.003$), with these plots supporting 22 different species. Between 2018 and 2019 (1 and 2 years post-thinning) in the 2017 plots, there were notable increases in percent cover for tanoak (2 to 33%), Douglas-fir (0 to 8%), and redwood (1 to 6%) (Table 6). Understory diversity was lowest in the control plots, with these plots only supporting five different species and having ground cover dominated by forest litter (55%).

Across all nine study plots in 2018 and 2019, there were 34 avian species observed, all but one of which are federally protected under the Migratory Bird Treaty Act (Table 7). Generally, avian diversity was relatively comparable among all plots based on S, D, and H'. Across the two-year period, plot-level S ranged between 16 and 23, D ranged from 0.94 to 0.95, and H' ranged from 2.65 to 2.95 (Table 5). Among treatments, neither S ($p = 0.85$), D ($p = 0.81$), nor H' ($p = 0.78$) differed significantly. Notably, in 2019, a marbled murrelet (*Brachyramphus marmoratus*), a species federally listed under the Endangered Species Act as Threatened, was observed in the 1978 plots.

Among all study plots in 2018 and 2019, a total of 12 identifiable mammals (species or genera) were observed (Table 8). Across the two-year period, plot-level S ranged from 6 to 8, D ranged from 0.63 to 0.78, and H' ranged from 1.16 to 1.66 (Table 5). Similar to the trends observed for birds, neither S ($p = 0.28$), D ($p = 0.16$), nor H' ($p = 0.33$) differed significantly among treatments for wildlife diversity. Notably, we observed fisher (*Pekania pennanti*), a species federally listed under the Endangered Species Act as Proposed Threatened, in the 1978 and 2009 plots and Roosevelt elk (*Cervus canadensis roosevelti*) in the 2009 plots.

4. Discussion

This study's assessment of forest restoration efficacy based on tree physiology (Ψ and g_s), annual growth (BAI), and biodiversity (understory vegetation, birds, and mammals) metrics produced findings comparable with other studies (Thomas et al., 1999; Chittick and Keyes, 2007; Verschuyt et al., 2011; O'Hara et al., 2015; Sohn et al., 2016; Cole et al., 2017; Goodwin et al., 2018; Lalemand, 2018). In second-growth redwood forests, the standard approach to evaluate treatment efficacy is typically to assess breast height radial growth (Veirs, 1986; Lalemand, 2018). However, responses to treatment can take years to detect when

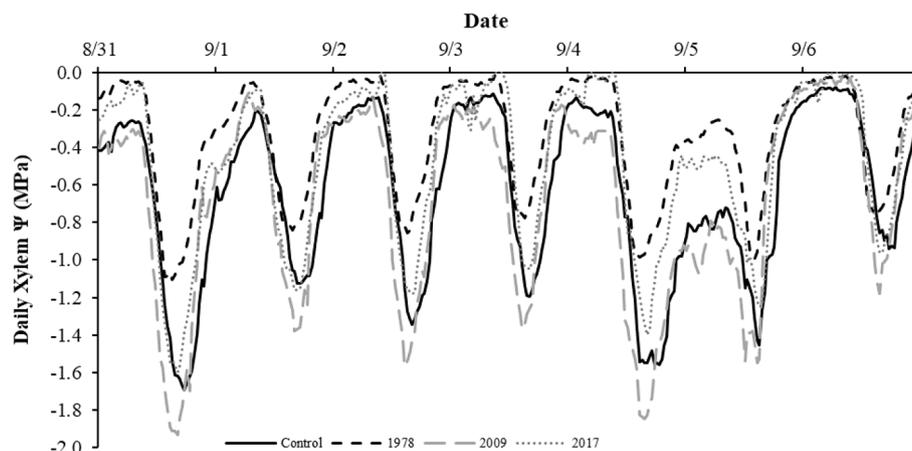


Fig. 3. Daily xylem water potential (Ψ) for redwood trees in the control (black line), 1978 (black dots), 2009 (gray line), and 2017 (gray dashes) treatment plots. Measurements were taken with a stem psychrometer every 30 min from August 31 through September 6, 2019 in Redwood National Park. The anomalous drop in Ψ on September 5 at all plots was likely due to an issue with data retrieval from the psychrometer data box on September 4.

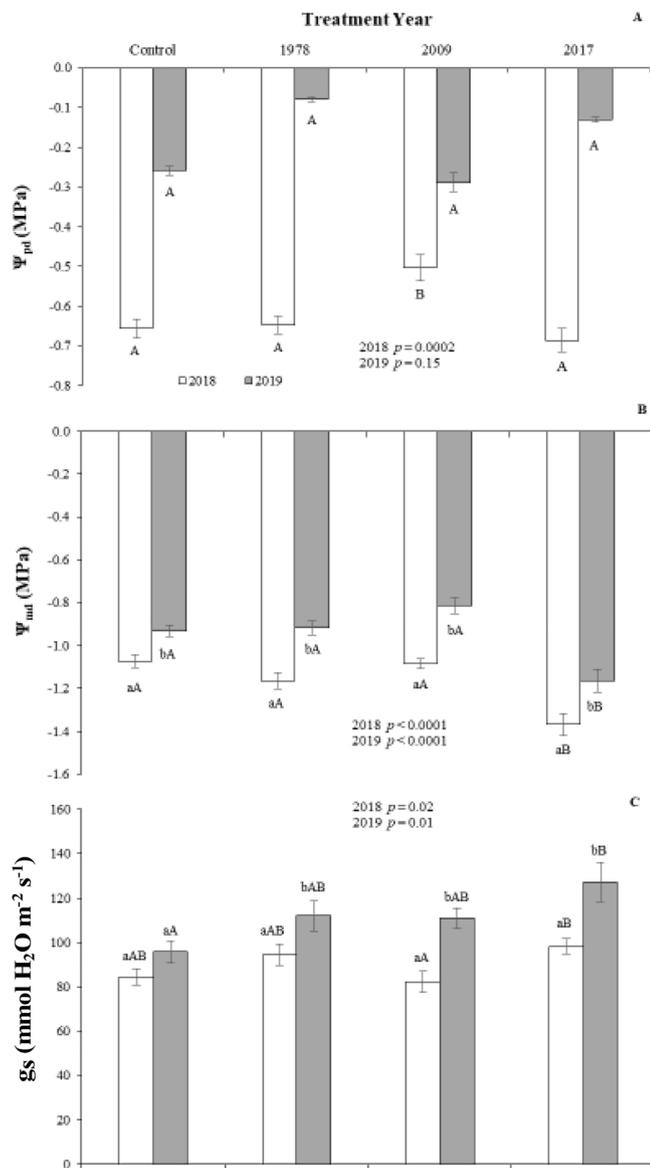


Fig. 4. Mean (\pm SE) water potential (Ψ) and stomatal conductance (g_s) for redwood trees in 2018 (white) and 2019 (gray) in Redwood National Park in control plots and plots thinned in 1978, 2009, and 2017. There were two plots for the control, 1978, and 2009 treatments and three plots for the 2017 treatments; within each plot, there were 10 trees used for physiological measurements. A) Leaf predawn water potential (Ψ_{pd}) measured in July 2018 with a pressure chamber and xylem Ψ_{pd} measured in September 2019 with stem psychrometers. B) Leaf midday water potential (Ψ_{md}) measured in July 2018 and July 2019 with a pressure chamber. C) g_s measured in July 2018 and July 2019 with a leaf porometer. For each panel, treatments within a year not sharing the same uppercase letter are significantly different. For the Ψ_{md} and g_s panels, within a treatment, years not sharing the same lowercase letter are significantly different. In each panel, p -values for one-way ANOVAs comparing treatment means within each year are provided.

relying on these growth-based metrics (Dagley et al., 2018). Thus, this study measured both physiology and growth to evaluate forest responses to treatment in both the short- and long-terms, respectively. In support of our predictions, restoration treatments on Holter Ridge in RNP elicited positive forest responses, as measured by redwood physiology, redwood growth, and plant biodiversity. Redwood physiological responses to treatment were greatest in the most recently thinned 2017 plots and were otherwise relatively homogeneous across the 1978, 2009, and control plots. Similarly, redwood growth also responded to

treatment, with the time between thinning and increased growth ranging from four to 10 years and the responses persisting for many years. Finally, treatments promoted understory plant biodiversity through increased species richness and percent cover, although this increased diversity was not detected for birds or mammals. Overall, these findings realize this study's objective to inform on the capacity of second-growth redwood forest restoration to accelerate the development of old-growth characteristics.

4.1. Physiology

Physiological responses to treatments were detectable in the 2017 plots but were relatively muted in the 1978, 2009, and control plots, demonstrating that these types of measurements can be useful to evaluate tree responses to treatments in the short-term. While in arid systems Ψ is often negatively correlated with stand density (Kolb et al., 1998) such that thinning treatments can increase Ψ in residual trees (Skov et al., 2004; Sohn et al., 2016), in the temperate redwood forest, we found that thinning did not meaningfully affect leaf Ψ_{pd} (almost all values > -0.75 MPa). This stability of Ψ_{pd} across treatments suggests that in this coastal, wet, temperate rainforest, soil water availability is ample throughout the year regardless of stand density. Corroborating this speculation of ample water availability in this forest, redwood growth on Holter Ridge was highly resistant to the recent 2012–2015 California drought (Williams et al., 2015; Lalemand, 2018). Thus, this study and others collectively suggest that in its northern range, substantial precipitation inputs of winter rain and summer fog (Litvak et al., 2011) provide sufficient water for coast redwood.

While Ψ_{pd} indicated ample soil water availability regardless of treatment history in this study, recent treatments did affect leaf Ψ_{md} . The decreased leaf Ψ_{md} measured in the 2017 plots may have resulted from increased evapotranspirational water loss due to increased light availability (Gauthier and Jacobs, 2009). By contrast, in the 1978 and 2009 plots, post-treatment times were likely sufficient to allow canopy reclosure such that light, evapotranspiration, and resulting leaf Ψ_{md} were indistinguishable from the controls. We note that although Ψ_{md} was lower in the 2017 plots, it did not reflect water limitation, as all values were consistently > -1.5 MPa.

Although leaf Ψ largely indicated that water status was invariable with treatment, Ψ_{md} in recently thinned plots being the exception, xylem Ψ suggested that treatments might quantifiably affect tree water status, even in the long-term. Among treatments, xylem Ψ was consistently lowest in the 2009 plots and highest in the 1978 plots. In the 2009 plots, it is possible that greater post-treatment light availability stimulated an increase in the leaf area to sapwood area ratio in residual trees (Simonin et al., 2006), thereby causing the measured reduction in xylem Ψ . Alternatively, because only one tree per plot was instrumented, it is also possible that the relatively consistent ranking of xylem Ψ from high to low in 1978, 2017, control, and 2009 plots, respectively, is the result of differences in microclimate, growing space, and/or physiology of the individual instrumented trees. Nevertheless, on the whole, xylem Ψ values (all > -2 MPa) generally supported leaf Ψ findings, together indicating that redwoods at this site are not water-limited.

Increased g_s in the 2017 treatments in both 2018 and 2019 indicates that thinning can enhance carbon assimilation rates in second-growth redwood forests for at least the first few years following treatment. This finding, likely due to increased light availability increasing transpiration in residual trees, showcases how thinning can rather immediately stimulate g_s . Similarly, in second-growth ponderosa pines (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) of northern Arizona, g_s often increases within one- to three-years post-thinning (Kolb et al., 1998; Skov et al., 2004). Additionally, black walnut (*Juglans nigra* L.) physiology responds to thinning via higher photosynthetic rates resulting from increased light availability just one year after treatment (Gauthier and Jacobs, 2009). While our 2017 results demonstrate that in thinned second-growth redwood forests elevated g_s in residual trees can be

Table 2

Mean (\pm SE) predawn water potential (Ψ_{pd}), midday water potential (Ψ_{md}), and stomatal conductance (g_s) for redwood trees in the control ($n = 2$) plots and plots thinned in 1978 ($n = 2$), 2009 ($n = 2$), and 2017 ($n = 3$) in Redwood National Park. All physiology measurements were based on ten trees per plot. In 2018, leaf Ψ_{pd} and Ψ_{md} measurements were made in July using a pressure chamber. In 2019, xylem Ψ_{pd} measurements were made in September using stem psychrometers and leaf Ψ_{md} measurements were made in July using a pressure chamber. In 2018 and 2019, g_s measurements were made in July using a leaf porometer. For each variable, treatments not sharing an uppercase letter are significantly different, with p -values provided. For Ψ_{md} and g_s , within each treatment, years not sharing the same lowercase letter are significantly different.

Variable	Control	1978	2009	2017	p -value
Leaf Ψ_{pd} 2018	-0.67 ± 0.03^A	-0.64 ± 0.03^A	-0.59 ± 0.05^B	-0.69 ± 0.03^A	0.0002
Xylem Ψ_{pd} 2019	-0.12 ± 0.08^A	-0.02 ± 0.02^A	-0.16 ± 0.10^A	-0.03 ± 0.00^A	0.15
Leaf Ψ_{md} 2018	-1.07 ± 0.03^{aA}	-1.16 ± 0.04^{aA}	-1.09 ± 0.02^{aA}	-1.37 ± 0.05^{aB}	<0.0001
Leaf Ψ_{md} 2019	-0.93 ± 0.03^{bA}	-0.92 ± 0.03^{bA}	-0.81 ± 0.04^{bA}	-1.16 ± 0.04^{bB}	<0.0001
g_s 2018	85 ± 4^{aAB}	94 ± 5^{aAB}	82 ± 5^{aA}	98 ± 3^{aB}	0.02
g_s 2019	96 ± 5^{aA}	112 ± 7^{bAB}	111 ± 5^{bAB}	127 ± 7^{bB}	0.01

Table 3

Mean (\pm SE) plot-level growth metrics of the six study plots used for growth analysis in Redwood National Park in 2019, including diameter at breast height (DBH), basal area density (BA), and basal area increment (BAI) for redwood growth study trees. Calculations for BAI are based on 1960 – 2015 tree-ring data. Each plot had 20 study trees that were sampled for dendrochronological analyses, although five trees were excluded because they could not be cross-dated ($n = 115$ trees).

Study Plot	DBH (cm)	BA ($m^2 ha^{-1}$)	BAI ($cm^2 yr^{-1}$)
Control-A	38 ± 3	112 ± 7	17.6 ± 0.7
Control-B	40 ± 2	101 ± 6	15.9 ± 0.6
1978-A	51 ± 3	65 ± 4	22.3 ± 0.8
1978-B	45 ± 2	76 ± 5	20.3 ± 0.8
2009-A	42 ± 4	75 ± 6	19.9 ± 1.2
2009-B	43 ± 3	82 ± 6	20.5 ± 0.8
All Plots	44 ± 1	86 ± 3	16.6 ± 0.3

expected in the short-term, our 2009 results suggest that in the longer-term g_s will likely decrease to pre-treatment rates as the canopy recloses. We also note that interannually, across all plots, Ψ_{md} and g_s were lower in 2018 compared to 2019, and that these trends were likely climate-driven, as 2018 was drier (Palmer Drought Severity Index [PDSI] = -2.77) than 2019 (PDSI = -1.23) at this site (WRCC, 2020: wrcc.dri.edu). This finding indicates that even though redwood temperate forests do not appear to be water-limited, they are nevertheless responsive to climate and highlights the need to better understand potential influences of climate shift on this geographically limited forest type with remarkable carbon storage capacity (Sillert et al., 2020).

Overall, these physiology measurements collectively demonstrate

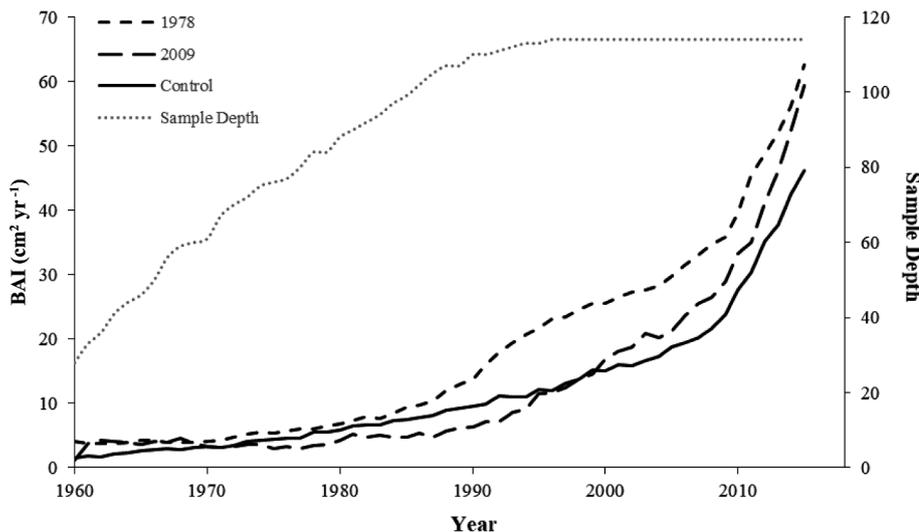


Fig. 5. Mean annual growth, as measured by basal area increment (BAI), for redwood trees in each treatment (control = black solid line, 1978 treatment = small black dashes, and 2009 treatment = large black dashes) across 55 years (1960–2015) in Redwood National Park. For each treatment, there were two replicate plots; each plot had 20 trees used for dendrochronological analysis, with five trees excluded because they could not be cross-dated ($n = 115$ trees). Tree sample depth (gray dots) is shown on the right vertical axis.

that this redwood forest is not water-limited and that increased light availability following thinning therefore has the potential to increase tree productivity until canopy re-closure again limits light. Continued monitoring of Ψ and g_s in the 2017 plots over the next five to seven years would provide useful information about how long enhanced gas exchange persists following thinning in this forest type. Given current projections for regional climate change and widespread efforts to restore second-growth redwood forests in northern California (Burns et al., 2018), these physiological measurements can serve as useful baseline data to help land managers tailor thinning treatments for desired short- and long-term responses and monitor forest responses to treatment and climate over time. For example, the knowledge that leaf Ψ_{md} is reduced immediately following thinning could help minimize negative responses to treatment such as ‘thinning shock’ (Harrington and Reukema, 1983), particularly in a future with projected increases in mean annual temperatures and decreased summer fog (Johnstone and Dawson, 2010).

4.2. Growth

Given that increased leaf-level gas exchange is a typical short-term response to reductions in stand density for multiple forest types, it reasons that growth should also increase following thinning treatments. In second-growth redwood forests, it can take from four (Dagley et al., 2018), to five (Roberts and Harrington, 2008), to 10 years post-treatment (O’Hara et al., 2010) for growth rates to increase in response to thinning. The longevity of this type of ‘release effect’ response is variable across species and locations, varying from 4 (O’Hara et al., 2010) to 10 (Kerhoulas et al. 2013) to 20 (Latham and Tappeiner, 2002) years following treatment. In agreement with many investigations

Table 4

List of vascular plants observed across the nine study plots in Redwood National Park in June 2018 and 2019 in control plots ($n = 2$) and plots thinned in 1978 ($n = 2$), 2009 ($n = 2$), and 2017 ($n = 3$). "X" Denotes presence.

Species	Common Name	Control	1978	2009	2017
<i>Achlys triphylla</i>	Deer's foot			X	
<i>Agrostis</i> spp.	Grass			X	
<i>Asarum caudatum</i>	Western wild ginger			X	
<i>Berberis nervosa</i>	Little Oregon-grape	X		X	X
<i>Claytonia sibirica</i>	Spring beauty			X	X
<i>Corallorhiza maculata</i>	Spotted coralroot			X	
<i>Galium aparine</i>	Cleavers grass			X	X
<i>Gaultheria shallon</i>	Salal	X	X	X	X
<i>Iris douglasiana</i>	Douglas' iris			X	
<i>Lilium bolanderi</i>	Bolander's lily		X	X	X
<i>Listera cordata</i>	Heart-leaf twayblade			X	X
<i>Notholithocarpus densiflorus</i>	Tanoak	X	X	X	X
<i>Polypodium glycyrrhiza</i>	Licorice fern			X	
<i>Polystichum munitum</i>	Sword fern		X	X	X
<i>Pseudotsuga menziesii</i>	Douglas-fir			X	X
<i>Pteridium aquilinum</i>	Bracken fern		X	X	
<i>Rhododendron macrophyllum</i>	Pacific rhododendron	X			X
<i>Rubus ursinus</i>	California blackberry		X	X	
<i>Sequoia sempervirens</i>	Coast redwood			X	X
<i>Trichostema ovatum</i>	San Joaquin blue curls			X	
<i>Trientalis latifolia</i>	Pacific starflower			X	X
<i>Vaccinium ovatum</i>	Evergreen huckleberry	X	X	X	X
<i>Vaccinium parvifolium</i>	Red huckleberry		X		X
<i>Viola glabella</i>	Stream violet			X	X

of forest responses to thinning, our study found that treatment increased growth; this can be seen in the 1978 and 2009 treatments as delayed departures from the controls (Fig. 5). Notably, these increases in growth have persisted through 2015 in both the 1978 and 2009 treatments, suggesting that the benefits of thinning can be impressively long-lived in this system. This finding that restoration treatments can elicit substantial and persistent increases in tree growth is particularly important, given recent work demonstrating the remarkable capacity of second-growth redwood forests to sequester and store carbon (Disney et al., 2020; Sillett et al., 2020). Additionally, the widespread and extensive plans to restore thousands of acres of second-growth redwood forests in northern California (Burns et al., 2018) make this study's confirmation of treatment efficacy notably timely and applicable to current regional management objectives.

As typically occurs in many forest systems, there was a delay between treatment and a release in growth at this site. General reasons for the common lag between treatment and increased breast height growth are variable, most notably including thinning shock (Harrington and Reukema, 1983) and the fact that newly available photosynthate from increased leaf-level carbon uptake might first be allocated to numerous competing sinks other than breast height diameter growth (Lagergren et al., 2019). Examples of alternative carbon sinks following treatment

include increased leaf area to take advantage of greater light availability (McDowell et al., 2003) and increased structural roots for improved stability under more severe wind exposure (Thornburgh et al., 2000). For redwoods, because this species can prolifically sprout in response to thinning disturbance (O'Hara et al., 2015), increased photosynthate after treatment may have been allocated to basal sprout production rather than diameter growth until the canopy sufficiently closed to suppress sprouting. Trees in the 1978 and 2009 plots experienced a growth-based departure from the control about 10 and four years post-treatment, respectively (Fig. 5). This difference in lag time between treatment and release could relate to tree age, as the single cohort of trees in the 1978 plots were approximately 25-years-old at the time of treatment and the single cohort of trees in the 2009 plots were approximately 45-years-old when thinned (Veirs and Lennox, 1982; Teraoka and Keyes, 2011). In 1978, only 25 years after clear-cutting, it is possible that thinning did not increase a limiting resource, as trees were not yet light-limited, hence the ten-year delayed response.

Our detection of persistently increased growth and no adverse physiological effects in stands treated with 40% BA reductions compared to control stands suggests that perhaps heavier BA reductions could be used in this forest type. Pre-treatment, these stands had tree densities of approximately 2,400 trees per hectare (TPH), dramatically

Table 5

Species richness, species evenness, and Shannon-Wiener diversity index for plants, birds, and mammals in 2018 and 2019 among the control plots ($n = 2$) and plots treated in 1978 ($n = 2$), 2009 ($n = 2$), and 2017 ($n = 3$) in Redwood National Park. In both years, understory plant surveys were conducted in June, bird point count surveys were conducted in June, and mammals were inventoried for three weeks in October using trail cameras.

Diversity Metric	Taxon	2018				2019			
		Control	1978	2009	2017	Control	1978	2009	2017
Species Richness	Plants	5	6	17	11	5	6	20	15
Species Evenness	Plants	0.28	0.68	0.81	0.48	0.28	0.68	0.72	0.72
Shannon-Wiener Diversity Index	Plants	0.45	1.22	2.29	1.14	0.45	1.22	2.15	1.96
Species Richness	Birds	17	16	17	16	16	23	17	19
Species Evenness	Birds	0.94	0.94	0.94	0.94	0.94	0.95	0.94	0.94
Shannon-Wiener Diversity Index	Birds	2.66	2.65	2.68	2.69	2.71	2.95	2.68	2.74
Species Richness	Mammals	7	6	6	6	6	7	10	7
Species Evenness	Mammals	0.76	0.72	0.73	0.73	0.76	0.78	0.70	0.78
Shannon-Wiener Diversity Index	Mammals	1.47	1.40	1.16	1.44	1.49	1.66	1.66	1.63

Table 6

Change in percent cover (based on Daubenmire cover classes) of understory vegetation in the variable density thinning plots (treated in 2017; $n = 3$) in Redwood National Park between 2018 (1 year post-treatment) and 2019 (2 years post-treatment).

Species	Common Name	Change in Cover (%)
<i>Berberis nervosa</i>	Little Oregon-grape	0
<i>Claytonia sibirica</i>	Spring beauty	-1
<i>Galium aparine</i>	Cleavers grass	5
<i>Gaultheria shallon</i>	Salal	3
<i>Lilium bolanderi</i>	Bolander's lily	-1
<i>Listera cordata</i>	Heart-leaf twayblade	7
<i>Notholithocarpus densiflorus</i>	Tanoak	31
<i>Polystichum munitum</i>	Sword fern	-1
<i>Pseudotsuga menziesii</i>	Douglas-fir	8
<i>Rhododendron macrophyllum</i>	Rhododendron	0
<i>Sequoia sempervirens</i>	Coast redwood	5
<i>Trientalis latifolia</i>	Pacific starflower	2
<i>Vaccinium ovatum</i>	Evergreen huckleberry	1
<i>Vaccinium parvifolium</i>	Red huckleberry	1
<i>Viola glabella</i>	Stream violet	3

high compared to the historical old-growth reference conditions of 25 to 90 TPH (Chittick, 2005). Previous work in 40- to 50-year-old second-growth redwood forests suggests that to foster the greatest increase in growth, BA reductions ranging from 50 to 75% should be used (O'Hara et al., 2015). Thus, these physiology- and growth-based analyses as well as multiple other studies on second-growth redwood forests all suggest that heavy basal area reductions, or possibly silvicultural methods other than low thinning, are needed to elicit a large release in residual trees. We note however that following aggressive thinning treatments, there is

Table 7

List of avian species observed in Redwood National Park in June of 2018 and 2019 in control plots ($n = 2$) and plots thinned in 1978 ($n = 2$), 2009 ($n = 2$), and 2017 ($n = 3$) using point count surveys. X Denotes presence and * denotes species federally listed under the Endangered Species Act as Threatened.

Scientific Name	Common Name	Control	1978	2009	2017
<i>Bombycilla cedrorum</i>	Ceder waxwing		X		
<i>Brachyramphus marmoratus</i> *	Marbled murrelet		X		
<i>Calypte anna</i>	Anna's hummingbird	X			
<i>Cardellina pusilla</i>	Wilson's warbler	X	X	X	X
<i>Catharus guttatus</i>	Hermit thrush	X	X	X	X
<i>Catharus ustulatus</i>	Swainson's thrush		X		X
<i>Certhia americana</i>	Brown creeper	X	X	X	X
<i>Chaetura vauxi</i>	Vaux's swift				X
<i>Chamaea fasciata</i>	Wrentit				X
<i>Contopus cooperi</i>	Olive-sided flycatcher				X
<i>Corvus brachyrhynchos</i>	American crow			X	
<i>Corvus corax</i>	Common raven	X		X	X
<i>Cyanocitta stelleri</i>	Steller's jay	X	X	X	X
<i>Dryobates villosus</i>	Hairy woodpecker	X	X	X	
<i>Dryocopus pileatus</i>	Pileated woodpecker	X	X	X	X
<i>Empidonax difficilis</i>	Pacific-slope flycatcher	X	X	X	X
<i>Regulus satrapa</i>	Golden-crowned kinglet	X	X	X	X
<i>Ixoreus naevius</i>	Varied thrush	X	X	X	X
<i>Junco hyemalis</i>	Dark-eyed junco	X	X	X	X
<i>Oreortyx pictus</i>	Mountain quail		X		
<i>Patagioenas fasciata</i>	Band-tailed pigeon	X	X	X	X
<i>Pheucticus melanocephalus</i>	Black-headed grosbeak	X			
<i>Piranga ludoviciana</i>	Western tanager			X	X
<i>Poecile rufescens</i>	Chestnut-backed chickadee	X	X	X	X
<i>Selasphorus sasin</i>	Allen's hummingbird		X		
<i>Setophaga coronata</i>	Yellow-rumped warbler	X	X	X	X
<i>Setophaga occidentalis/nigrescens</i>	Hermit/Black-throated gray warbler	X	X	X	X
<i>Sialia mexicana</i>	Western bluebird		X	X	
<i>Sitta canadensis</i>	Red-breasted nuthatch	X	X	X	X
<i>Sphyrapicus ruber</i>	Red-breasted sapsucker		X		
<i>Troglodytes hiemalis</i>	Winter wren	X	X	X	X
<i>Turdus migratorius</i>	American robin		X		X
<i>Vireo huttoni</i>	Hutton's vireo	X	X	X	X
<i>Zenaidura macroura</i>	Mourning dove			X	

also the increased risk of insect, wind, and bear damage to residual trees (O'Hara et al., 2010).

4.3. Biodiversity

While common objectives for restoration treatments include increasing vigor in residual trees, increasing biodiversity is another important goal. This is particularly true in second-growth redwood forests where impenetrably dense thickets of suppressed trees stalled in the stem exclusion phase of stand development can blanket extensive swaths of the landscape. Previous work in redwood forests (Chittick, 2005; Chittick and Keyes, 2007) and in mixed-conifer forests of the Sierra Nevada Mountains (Goodwin et al., 2018) and Oregon (Cole et al., 2017) has shown that thinning treatments can help spur a shift towards understory reinitiation with increased plant diversity (Oliver and Larson, 1996). However, in these studies, initial increases in understory plant diversity were often followed by shrub dominance and a corresponding decrease in herbaceous cover. In RNP, this shift from understory herbaceous dominance to shrub dominance can occur within three years of a clearcut (Muldavin et al., 1981; Chittick, 2005), suggesting that heavy thinnings should be avoided, if maximizing understory plant diversity is a high priority of treatment. On the other end of the spectrum, low-intensity restoration treatments (e.g., the 40% BA reductions implemented on Holter Ridge) can also foster the development of large shrub thickets capable of persisting after canopy closure (Thomas et al., 1999; Chittick, 2005; Teraoka, 2012).

Similar to previous work, the 40% BA reduction treatments that we studied in RNP promoted the development of understory vegetation, as measured by increased species richness, species evenness, Shannon-Wiener diversity indices, and percent cover compared to control plots.

Table 8

List of mammals observed in Redwood National Park in October of 2018 and 2019 in control plots ($n = 2$) and plots thinned in 1978 ($n = 2$), 2009 ($n = 2$), and 2017 ($n = 3$) using camera traps. X Denotes presence and * denotes species federally listed under the Endangered Species Act as Proposed Threatened.

Species	Common Name	Control	1978	2009	2017
<i>Cervus canadensis</i> ssp. <i>roosevelti</i>	Roosevelt elk			X	
<i>Glaucomys oregonensis</i>	Humboldt's flying squirrel	X	X	X	X
<i>Neotamias</i> sp.	Chipmunk species	X	X	X	X
<i>Mustela</i> sp.	Weasel			X	
<i>Procyon lotor</i>	Raccoon	X			
<i>Sorex</i> sp.	Shrew species	X	X	X	
<i>Odocoileus hemionus</i>	Black-tail deer	X	X	X	X
<i>Pekania pennanti</i> *	Fisher		X	X	
<i>Peromyscus maniculatus</i>	Deer mouse	X	X	X	X
<i>Sciurus griseus</i>	Western gray squirrel	X	X	X	X
<i>Tamiasciurus douglasii</i>	Douglas squirrel	X	X	X	X
<i>Ursus americanus</i>	American black bear	X	X	X	X

In the 2017 plots, understory herbaceous cover dramatically increased from 2018 to 2019, as did all other biodiversity metrics, indicating a positive short-term response to treatments. We also note that in the 2017 plots, there was a 5% and 8% increase in redwood and Douglas-fir seedling percent cover, respectively, between the first and second post-treatment years, suggesting that the recent treatment stimulated forest regeneration. This stimulation of redwood seedling regeneration is noteworthy, as this species typically relies on asexual sprouting as the primary mode of reproduction (Noss, 2000). Overall, the 2009 and 2017 plots supported markedly higher plant species richness compared to the 1978 and control plots, which were dominated by evergreen huckleberry and overstory litter, respectively. We expect that plant community structure in the 2009 and 2017 plots will likely follow this trajectory towards shrub dominance near the time of canopy re-closure due to decreased light availability, as plant communities in the Pacific Northwest often revert to pre-thinning conditions after 20–55 years (Halpern and Spies, 1995; Jules et al., 2008). Thus, because in many forest types this initial pulse of understory plant diversity following thinning seems to diminish relatively quickly due to increasing shrub dominance, if promoting the development of understory vegetation is a management objective, then multiple treatment entries to keep the upper canopy open for light availability may be needed to stall shrub dominance (Hayes et al., 1997).

Research in diverse western forest types has reported positive effects of thinning treatments on avian communities (Verschuyl et al., 2011; Slauson, 2013). Similarly, in old-growth forests of central Europe, bird diversity was significantly higher in gaps compared to closed-canopy stands (Przepióra et al., 2020), suggesting that thinning treatments that create gaps would also in theory increase bird diversity. However, there was no detectable influence of restoration on birds in this study, as evidenced by relatively homogeneous species richness and diversity across all plots. This trend may continue until old-growth features such as large trees, large diameter branches, and multiple canopy layers are present to create habitats suitable for a wider array of avian life. Based on the diversity of birds detected in this study, it seems that Holter Ridge stands are developing these characteristics. For example, the federally threatened marbled murrelet (Hayes et al., 1997), a species dependent on large diameter branches for viable nesting platforms, was observed in the 1978 plots. And, in addition to the commonly-observed mixed-conifer-dependent bird species, the chestnut-backed chickadee (*Poecile rufescens*), a species dependent on hardwoods (Hayes et al., 1997), likely tanoak in this study, was recorded in all plots during both sampling years. The presence of this chickadee confirms the existence of suitable habitat and forage for hardwood-dependent avian species at this site and verifies tanoak as a functionally meaningful component of this redwood forest. Additional evidence that these stands are on track to support rich bird diversity, the Pacific-slope flycatcher (*Empidonax difficilis*), a species typically less abundant in treated stands (Hagar et al., 1996; Hayes

et al., 1997), was observed in all study plots, suggesting that despite treatments, suitable habitats and forage existed. Thus, while thinning treatments can quicken growth in residual trees and increase herbaceous plant diversity, it seems that these treatments are slow to quantifiably boost bird diversity. Nevertheless, the treated and untreated second-growth stands on Holter Ridge do appear to support a rich mixture of bird species.

Similar to bird diversity, mammal diversity was also relatively homogeneous across all plots, suggesting that mammals may be slow to respond to changes in forest structure in the wake of thinning treatments. In other forest types such as hardwood and mixed pine-oak forests of West Virginia (Muzika et al., 2004), ponderosa pine forests of the Southwestern U.S. (Converse et al., 2006), and mixed-conifer forests of Washington (Carey, 2003), thinning generally has a positive influence on small mammal abundance. Although mammal species detections suggest low diversity across Holter Ridge, sensitive species such as the fisher, Roosevelt elk, and the Humboldt's flying squirrel (*Glaucomys oregonensis*) were observed in the 2009 plots. The latter species is typically associated with old-growth forests and is an important prey species for the northern spotted owl (*Strix occidentalis* ssp. *caurina*), a threatened species (Carey, 1991). Nevertheless, as wildlife diversity can be positively correlated with understory vegetation complexity in eastern Canadian boreal forests (Desrochers and Major, 2013) and Pacific Northwest forests (Hayes et al., 1997; Thysell and Carey, 2001), the biodiversity of birds and mammals in these second-growth redwood stands could be slow to recover if understory shrub dominance persists.

Thus, although old-growth features such as nesting cavities and large branches to support birds and arboreal rodents are necessary to support high levels of wildlife diversity, it appears that second-growth redwood forests can support a diverse collection of bird and mammal species. However, despite the presence of sensitive species, the Holter Ridge 40-year chronosequence suggests that although treatments can accelerate old-growth features beneficial for wildlife habitat (Noss, 2000; O'Hara et al., 2017), animals can be slow to respond to these changes. Compellingly, crown manipulations in second-growth redwood trees, while time-consuming and requiring specialized training to implement, may be an effective way to accelerate the development of wildlife habitat in developing canopies (Sillett et al., 2018). Although our study did not detect a significant positive effect of thinning on wildlife diversity, a study (Slauson, 2013) focused on bird and mammal diversity did detect significantly higher diversity in treated stands compared to control stands in RNP. We note that our assessment of biodiversity did not include cryptogams, insects, structural forest features, or a focus on the detection of indicator species. In many boreal forests of Europe and Scandinavia, biodiversity is remarkably high for insects and fungi (Nilsson et al., 2001); thus, by not including these taxa in our assessment, we clearly underestimated biodiversity in this temperate redwood forest. Further, it is possible that our 0.25 ha plots were too spatially

limited to effectively detect bird and mammal diversity. Alternatively, our failure to detect a significant treatment effect on wildlife could suggest that heavier thinning treatments might be warranted in this forest type, if increasing biodiversity is a primary management objective.

5. Conclusions

In forests of the Pacific Northwest, restoration treatments can open the canopy to accelerate the development of old-growth forest features (McComb et al., 1993; Carey and Curtis, 1996; Hayes et al., 1997). Because redwoods are fast-growing, long-lived, and rot-resistant, they can store large amounts of carbon for millennia in standing live trees, downed coarse woody debris, and lasting wood products. Thus, post-thinning enhanced growth in this forest type has important societal implications for resource management goals. In European forests, long-term carbon-related climate benefits can be comparable between even-aged (single cohorts that are cyclically clear-cut and re-planted) and uneven-aged (trees are selectively harvested so that there are multiple cohorts continuously on the landscape) management (Lundmark et al., 2016). The persistent post-treatment ecological benefits reported in this study support the use of selective thinning treatments, as they effectively maximize carbon sequestration and support diverse and presumably more resilient ecosystems. Managers at RNP are currently focused on accelerating the development of these features in dense second-growth forests using thinning as a tool for restoration. Results from this study verify that restoration treatments in this forest type can improve growth conditions for residual trees in both the short- and long-term. This work also demonstrates the usefulness of physiological measurements for short-term assessments of treatment efficacy when increases in growth are often delayed numerous post-treatment years.

Given the complexity of redwood ecosystems, managers must balance forest, watershed, and landscape management as well as logistical, social, and bureaucratic challenges to achieve their objectives. For a multitude of reasons, including the widespread need for thinning across much of the redwood range, managers are often limited to one-time single-entry treatments. Additionally, multiple-entry, low-severity thinning treatments would be expensive and time consuming to plan, prepare, and execute, as each thinning cycle could potentially require its own series of consultations with regulatory agencies, fish and wildlife surveys, and possibly Environmental Assessments. Moreover, because RNP is concurrently thinning and removing logging roads whenever possible and equipment and contractor costs plus labor-intensive methods such as lop-and-scatter slash treatments can be prohibitively expensive, stand access for future treatments would likely be limited.

Thus, given that most stands will likely only be able to be thinned once in this region in the foreseeable future, our findings suggest that higher basal area reductions will yield more persistent canopy gaps to increase gas exchange and growth in residual trees and support rich plant and animal communities. Correspondingly, our findings also indicate that trees in second-growth redwood forests have access to ample water and are unlikely to experience marked water stress due to increased evapotranspiration following thinning. While redwood has a limited range, we speculate that the ecosystem responses to thinning treatments measured at this location in northern California would likely be similar across this species' range. Given that comparable responses to treatments have been observed in other vegetation types in the western U.S., these findings are likely applicable to many temperate forests around the world. Future investigations of long-term tree growth and biodiversity responses to thinnings in other forest types and locations would help verify the ability of restoration treatments to accelerate the development of old-growth features in second-growth forests.

CRedit authorship contribution statement

Kevin R. Soland: Conceptualization, Methodology, Formal analysis,

Investigation, Writing - original draft, Visualization. Lucy P. Kerhoulas: Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. Nicholas J. Kerhoulas: Conceptualization, Methodology, Investigation, Writing - original draft, Project administration, Funding acquisition. J.R. Teraoka: Conceptualization, Methodology, Funding acquisition.

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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