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Forest restoration thinning accelerates development of old-growth characteristics in the coastal Pacific Northwest, USA

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Abstract

A century of industrial-scale management has transformed vast swaths of forest land across the Pacific Northwest (PNW), USA, from ancient forests with complex structure and diverse habitats to young forests with simple structure and dominated by few species. Consequently, there have been calls to restore ecosystem integrity and resilience. Here, we apply data from a watershed-scale experiment to determine if restoration treatments have achieved our management goal of accelerating the development of old-growth forest characteristics. We provide empirical evidence of how restoration treatments have affected key old-growth forest indicators resulting in larger trees, more complex vertical and horizontal forest structure, reduced stand density, and increased understory plant richness. Our study also demonstrates that some restoration indicators responded in counter-intuitive ways contingent on interactions between stand age and restoration treatment. Through this work, we learned two important lessons: (1) more time and monitoring may be needed to fully understand the effects of restoration treatments and (2) a “one and done” approach of implementing restoration treatments may not achieve a full suite of old-growth characteristics. Moreover, long-term management for wildlife habitat and climate resilience will likely require an adaptive approach, with ongoing monitoring continually informing and adjusting management practices.

KEYWORDS

adaptive management, ecological climate adaptation, ecological indicators, ecological monitoring, forest structure, late-successional forests, natural resource management

1 | INTRODUCTION

Temperate coastal forests of the Pacific Northwest (PNW) provide a myriad of benefits and services including timber, wildlife habitat, recreation, carbon storage, water regulation, and cultural and spiritual values (Brandt et al., 2014; Case et al., 2020). These forests are heavily influenced by their close proximity to the Pacific Ocean, resulting in relatively moderate temperatures, high amounts of precipitation, and long fire return intervals

(Agee, 1993; Franklin & Dyrness, 1973). As such, temperate forests along the PNW coast are some of the most productive forests in the world and because of their longevity, they have the potential to store large amounts of carbon for centuries (Smithwick et al., 2002). However, a century of industrial-scale, production-oriented management has transformed many ecologically diverse forests into intensively managed forests typically dominated by a single species, such as Douglas-fir (*Pseudotsuga menziesii*) (DeMeo et al., 2018; Spies et al., 1994). Consequently, the vast majority of non-federal forestland within the current PNW landscape is now characterized by young, structurally simple forests (Spies et al., 2010; Strittholt et al., 2006).

Forests characterized by simple structure and low diversity are likely at higher risk to stressors like climate change and climate-induced disturbances, such as wildfire, insects, and diseases when compared to older, more complex, diverse forests (Halofsky et al., 2018; Millar et al., 2007). Warmer temperatures (Vose et al., 2017) and potentially longer, drier summers (May et al., 2018) may lead to decreased tree growth and productivity, and slower carbon sequestration rates in some water-limited PNW forests (Case et al., 2021). Climate change also threatens critical wildlife habitat in old-growth PNW forests (Spies et al., 2018). We define old-growth as forests over 200 years old with multiple overstory species, a wide range of tree sizes, relatively low tree density, high vertical complexity with multiple layers, a deep, multilayered canopy, high horizontal complexity with large quantities of down woody debris and snags, and a well-developed understory (Franklin, 1981; Franklin & Van Pelt, 2004).

There have been calls to restore PNW forests by increasing their ecological integrity and resilience (Franklin & Johnson, 2012; Spies et al., 2010). Here, we focus on a restoration goal of recreating the forest stand structure and ecological function characterized by the once ubiquitous old-growth forests of the region. Common management objectives include increasing tree species diversity, decreasing tree density, and accelerating the development of forest structural characteristics (Franklin & Johnson, 2012). We explore how meeting these objectives can also enhance wildlife habitat, particularly for endangered and threatened species, and may increase forest resilience to climate change (Halofsky et al., 2018). For instance, increasing species diversity, particularly of deciduous hardwood species, can increase resilience to climate change (Johnstone et al., 2004; Swank et al., 1988), and reducing tree density may reduce the effects of drought (Sohn et al., 2016) and other stressors, such as insects and diseases, as the climate continues to warm (Gillette et al., 2014; Kolb et al., 2016). Forest restoration thinning can also accelerate the development of forest structure in young, simplified monocultures to more closely resemble old-growth ecosystems, in comparison to doing nothing (Bauhus et al., 2009; Carey, 2003) and may provide more diversity of wildlife habitats (Franklin et al., 2002; Hunter Jr, 1990). For example, some species require unique nesting and foraging habitats characterized by complex vertical, horizontal, and canopy structures (Franklin & Van Pelt, 2004; North et al., 1999).

There is a clear ecological need to restore PNW forests and accelerate the development of young, structurally simple forests (Franklin & Johnson, 2012). However, there are relatively few studies that have attempted to evaluate the efficacy of restoration in accelerating the development of old-growth characteristics and even fewer that explore how those effects can have implications to wildlife habitat and climate change resilience (see Crouzeilles et al., 2016; Dodson et al., 2012; Willis et al., 2018). Here, we quantify the effects of ecological forest restoration treatments on tree growth, forest structure, regeneration, plant diversity, and organic soil layer depth by analyzing a suite of empirical data collected from two time periods. Although there is no one metric or indicator that can solely define restoration success, forest structure is a recognized surrogate for other functions (e.g., productivity) and organisms that are difficult to measure directly, such as cavity-dwelling animals (Franklin et al., 2002). Therefore, we build upon other approaches (e.g., Gatica-Saavedra et al., 2017) and apply a "multiple lines of evidence" approach to evaluate how restoration treatments have affected forest structure and other ecological attributes. Our assumption was that restoration treatments accelerated the development of old-growth forest indicators. We demonstrate these restoration effects by quantifying the changes in (1) adult tree growth, (2) vertical and horizontal forest structure, (3) tree regeneration, (4) plant diversity and abundance, and (5) soil organic layer depth.

2 | METHODS

2.1 | Study site

Our study site is located at Ellsworth Creek Preserve, hereafter referred to as Ellsworth, situated in the Willapa Hills region of southwestern Washington, USA (Figure 1). This experimental forest was acquired by The Nature Conservancy (TNC) in the early 2000s and covers approximately 2300 ha. Elevation in the preserve ranges from 0 to 365 m and the region has a mild, maritime climate characterized by cool, wet winters and warm, dry summers. Ellsworth is largely characterized by

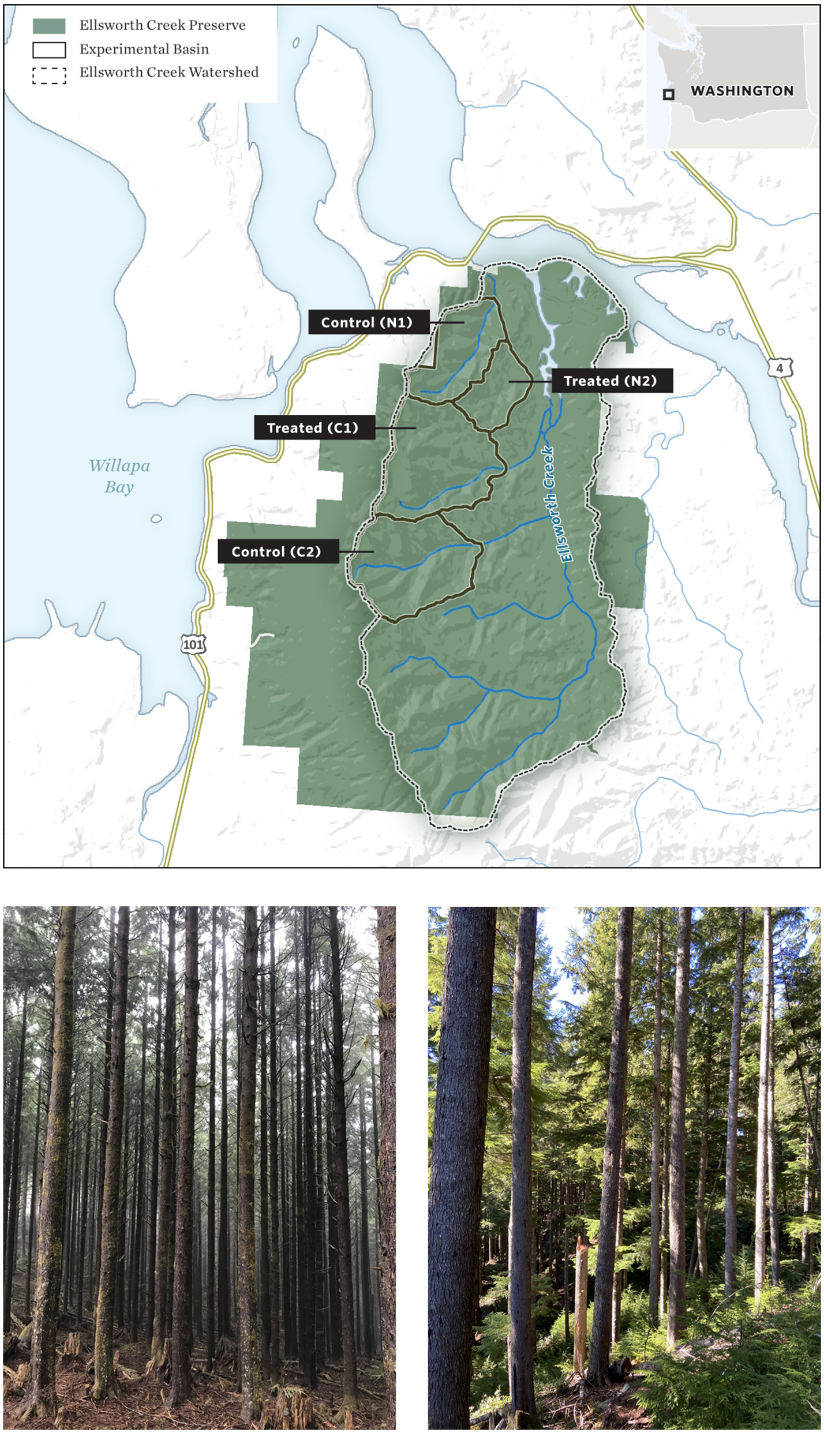

FIGURE 1 Top: Ellsworth Creek Preserve, located in southwestern Washington, USA. The four focal experimental sub-basins included in this study are highlighted—two control sub-basins (C2 and N1) and two treated sub-basins (C1 and N2). Bottom: photographs illustrating typical forest structure, density, and composition associated with control plots (left) and treated plots (right) within the study site. Note the differences in understory, mid-canopy structure, tree density, and the uniformity of tree sizes.

second-growth forests dominated by a mix of western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), Douglas-fir (*P. menziesii*), and red alder (*Alnus rubra*). These forests were previously managed for timber production and typically range in age from 20 to 80 years old. Most of the forest stands have relatively simple forest structure and many are in the competitive exclusion stage of stand development—a common result of stands systematically planted after clear-cut harvesting (Franklin et al., 2002; Oliver & Larson, 1996).

2.2 | Experimental design

With support of a science advisory committee largely composed of academic and management agency representatives, TNC designed and implemented a watershed-scale experiment with the goal of evaluating the effectiveness of restoration efforts at Ellsworth. Restoration pathways—control and treated—were replicated across the study area using an unbalanced, randomized blocked design. The control pathway are areas in which forest stands are left to develop without management intervention whereas, the treated pathway is areas where forest restoration treatments were implemented to promote management objectives, including increased forest growth, lower tree density, increased species diversity and abundance, and the accelerated development of forest structural complexity. We focused our analysis on forest structure and vegetation plots within two treated sub-basins (C1 and N2) and two control sub-basins (C2 and N1), all of which were measured in 2007 (pre-) and 2020 (post-treatment) (see Figure 1 photographs for typical forest stand structure, composition, and tree density).

2.3 | Restoration treatments

TNC applied two general types of restoration treatments in the treated sub-basins between 2009 and 2013; (1) commercial thinning (implemented in mature stands, 60–71 years old) and (2) pre-commercial thinning (implemented in young stands, 15–30 years old). There were no treated stands between the ages of 31 and 59 years. We refer to both commercial thinning and pre-commercial thinning as restoration treatments, with the difference in stand age indicating which silvicultural treatment type was implemented. That is to say, older stands received commercial thinning and younger stands received pre-commercial thinning.

Although dominant tree species abundance and composition varied across the forest stands, in general, species were thinned in the following order due to their relative abundance within the study area: western hemlock, Douglas-fir, Sitka spruce, western redcedar, and red alder. For example, western hemlock was typically removed at the highest rate because it is the most abundant species within the study area. In areas that were previously planted with Douglas-fir and heavily infected with Swiss needle cast, caused by the fungal pathogen *Nothophaeocryptopus gaeumannii*, we adjusted the order and removed infected Douglas-fir first. We also avoided cutting hardwoods, tree saplings and seedlings, and minimized the disturbance and removal of the understory and shrub layers whenever possible.

Commercial thinning treatments followed a variable density thinning with "skips and gaps" silvicultural design, focused on promoting structural heterogeneity and species diversity (Churchill et al., 2013; Harrington, 2009). The overall objective of the commercial thinning was to remove approximately 52.5–69.9 $m^3\ ha^{-1}$ (9000–12,000 board feet per acre). Consequently, these treated stands were thinned to a target basal area ranging from 37 to 46 $m^2\ ha^{-1}$, with a lower diameter limit of 15 cm diameter at breast height (DBH) and upper limit of 48 cm DBH—that is, no trees less than 15 cm or greater than 48 cm DBH were cut. Basal area is a measure of tree density in a specific area of land and is commonly used for silvicultural prescriptions in mature stands. Horizontal structural heterogeneity was promoted by retaining small clumps of trees and avoiding even spacing. Skips—areas that were intentionally not cut—and gaps—areas that were cut—were dispersed throughout the treatment stands. Gaps ranged in size from 0.05 to 0.60 ha with a target within gap basal area of 18 $m^2\ ha^{-1}$. Skips ranged in size from 0.01 to 0.40 ha and were strategically placed around small riparian zones or other features including unique species assemblages, snags, and rock outcrops.

Pre-commercial thinning treatments were implemented in the younger forest stands (15–30 years old) with a target density that ranged from 444 to 790 trees per hectare, and we focused on removing unhealthy or overtopped trees. Tree density targets are generally used in young stands where tree volume is not relevant. We used

TABLE 1 Ecological characteristics and indicators used to evaluate the effects of restoration treatments (adapted from Gatica-Saavedra et al., 2017).

Ecological characteristics	Indicators
Forest growth	Live tree diameter Live tree height Basal area of live trees Relative growth of live trees
Vertical and horizontal structure	Basal area of large woody debris Tree mortality Presence of dead trees (snags) Ratio of small to large diameter trees Abundance of large diameter trees Canopy cover* Dwarf mistletoe presence and infection severity
Regeneration	Abundance of seedlings and saplings*
Plant diversity	Species richness* Percent cover of understory plants* Life form percent cover*
Soil organic layer	Depth of organic soil layer*

Note: Indicators were measured throughout the entire 0.1 ha plot unless identified by asterisks (*), then they were sampled within four 0.002 ha subplots.

a modified variable density approach with skips that were dispersed throughout the treatment stands, ranged in size from 0.01 to 0.40 ha, and were located to purposely protect sensitive areas and unique species assemblages.

2.4 | Data description

We analyzed vegetation data from 60 circular 0.1 ha permanent plots across two time periods—2007 and 2020. Thirty-one plots were in control sub-basins (16 young plots and 15 mature plots) and 29 plots were in treated sub-basins (13 young and 16 mature plots). Although the original plot location was randomly determined, we selected our 60 plots by identifying similar characteristics between control and treated plots (e.g., similar stand ages, pre-treatment species composition, aspect, slope, and elevation). We also avoided treated plots that were located within the "skip" treatments and retained treated plots that were in the "gap" treatments. Our data included metrics of overstory, understory, vertical and horizontal structures, forest health, regeneration, and soil organic layer measurements (see Supporting Information, protocol adapted from Cissel et al., 2006). We identified characteristics and indicators that have been used for assessing the effects of ecological forest restoration (Table 1), including tree diameter, tree height, tree basal area, and tree relative growth to assess changes in forest growth. Trees were defined as being greater than or equal to 14.5 cm DBH. We also quantified indices of forest structure, including tree mortality, changes in large woody debris basal area, the abundance of dead trees (snags), ratio of small to large diameter trees, presence of large diameter trees, presence and infection severity of dwarf mistletoe (parasitic plants, *Arceuthobium* spp.), and overstory canopy cover, using a convex densiometer (see Supporting Information). To assess changes in tree regeneration, we examined the abundance of tree seedlings (trees that were less than 1.37 m in height) and saplings (trees that are 1.37 m or greater in height and less than 14.5 cm DBH) across the two survey years. We also quantified differences in understory vascular plant species richness and the percent cover of understory vascular plants and general life forms, such as forbs, grasses, moss, hardwood trees, and conifer trees (see Supporting Information for details). Lastly, we measured the depth of the organic soil layer as an indicator of soil organic matter mass—a factor often associated with surface-soil carbon stores, cation exchange capacity, and nutrient retention. Some of these indicators were measured across the entire 0.1 ha plot, while others were sampled within four 0.002 ha sub-plots, each located 9 m (slope-corrected) from plot center in the four cardinal directions of plot center (see Table 1 and Table S1 for details).

2.5 | Analysis and statistical approach

Recognizing that forest restoration treatments can have different effects depending on the average age of the forest stand, we analyzed the changes of indicators among two age class categories—young (15–30) and mature (40–71) for both control and treated plots (also see Chamberlain et al., 2021). Although our mature treated plots ranged from 60 to 71 years old, they were comparable to mature control plots, which ranged from 40 to 71 years old. We used the following categorical predictor variables: stand age (young, mature), treatment (control, treated), and their interaction for our statistical models. Analyses were conducted in R, version 4.1.2 (R Core Team, 2021) and we used the lme4 package (Bates et al., 2015) to fit mixed effects models, the multcomp package (Hothorn et al., 2008) for post hoc tests, and the vegan package (Oksanen et al., 2022) for the multivariate analyses.

2.5.1 | Forest growth

We fit linear mixed-effects models with response variables (with Gamma error distributions) for the following: (1) adult tree DBH in 2007 and 2020, (2) change in tree diameter between 2007 and 2020, (3) tree height in 2007 and 2020, and (4) change in tree height between 2007 and 2020. We fit linear mixed-effects models with response variables (with Gaussian error distributions) for the change in tree relative basal area (basal area increment) between 2007 and 2020 and tree relative growth from 2007 to 2020. We compared the same individual tree when quantifying changes between 2007 and 2020. However, we did not include trees that were alive in 2007 and dead in 2020 or trees that were not measured in 2007 but were large enough to be measured in 2020. To calculate relative growth, we divided the basal area increment from 2007 to 2020 by the basal area in 2007 for each individual tree. For all models, predictors were stand age, treatment, and their interaction and we included "plot" as an intercept-only random effect to account for non-independence of trees within the same plot.

2.5.2 | Vertical and horizontal structure

We examined changes in vertical and horizontal structure by quantifying adult tree mortality, change in the abundance of snags and large woody debris, presence and infection severity of dwarf mistletoe, canopy cover, and the ratio of small to large trees (see Supporting Information for details). For all models, predictor variables were stand age, treatment, and their interaction. Mortality was determined if a tree was alive in 2007 and dead in 2020 (harvested trees were excluded from this analysis) and a snag was determined as a dead tree still standing (see Supporting Information). To quantify treatment and stand age effects on mortality, we fit a generalized linear model with a Bernoulli response variable for mortality, and plot was included as an intercept-only random effect. To understand how treatment and stand age affect the abundance of snags, we fit a generalized linear model with change in abundance of snags within a plot from 2007 to 2020 as the response variable (with a Poisson distribution). To quantify effects on large woody debris, we fit two types of models. First, to evaluate treatment and age effects on abundance of large woody debris, we fit a linear model with 2020 basal area of large woody debris (m^2) as the response variable (with Gamma error distribution). Second, to evaluate whether treatments have altered abundance of large woody debris, we fit a linear model with change in basal area of large woody debris (m^2) within plots between the two time periods (2007 and 2020). To quantify treatment effects on the ratio of small to large trees, number of large trees, canopy cover, and change in canopy cover between 2007 and 2020, we fit linear models with the ratio, counts of large trees, and plot canopy cover estimates from 2020, as well as the change in average canopy cover from 2007 to 2020, respectively, as response variables (all with Gaussian error distributions). We also examined whether experimental stands differed prior to treatment, by fitting models to 2007 survey data.

2.5.3 | Regeneration

To quantify differences in seedling and sapling counts, we fit generalized linear models to 2007 and, separately, to 2020 survey data with Poisson-distributed response variables to quantify differences. We also fit linear mixed-effects models with response variables of change in seedling and sapling counts (modeled with Gaussian errors to accommodate both negative and positive change) within plots from 2007 to 2020. Plot was included as an intercept-only random effect and predictors were stand age, treatment, and their interaction for all models.

2.5.4 | Plant diversity and abundance

To understand treatment effects on understory plant diversity we examined species richness and percent cover of understory vascular plants and general life-form types. For understory plant species richness, we fit a mixed-effects model with a response variable of number of species observed in 2020 (plot was included as an intercept-only random effect).

For both understory and life-form percent cover, we first calculated plot level values by averaging percent cover data collected at each sub-plot within the plot. We then used two-way permutational multivariate analysis of variance (perMANOVA; Anderson, 2001) to identify (a) multivariate differences in understory percent cover for 2020 and (b) change in life form percent cover between the two sample periods (2007 and 2020) based on age class (young or mature) and treatment type (control or treated). We followed these analyses with a test for multivariate homogeneity of group dispersions (Anderson, 2006). For the understory percent cover, we also used principal coordinates analysis (PCoA) to examine similarities and differences among the treatment, age class, and key species. Key species are defined as species that have significant loadings on the first two principal components that contribute to the PCoA. We then compared percent cover for each species between treatment-types within each age group.

2.5.5 | Soil organic layer

To quantify effects on the organic soil layer, as well as changes between 2007 and 2020, we fit three linear mixed-effect models: one with 2007 measurements of organic soil layer depth averaged across the four measurements within each of four sub-plots per plot (to test for pre-treatment differences), one with 2020 measurements, and one with change in average depth of organic soil layer as response variables (plot was included as an intercept-only random effect). Response variables were modeled with Gaussian errors.

3 | RESULTS

Our analysis showed distinct changes that occurred across treatments and between 2007 and 2020 for a number of restoration indicators. Moreover, our results demonstrate that forest restoration treatments had significant effects on some, but not all, of our restoration indicators. The largest effects were found among forest structure characteristics and regeneration indices. We were not able to detect significant changes for some indices, such as the abundance or large woody debris, presence and infection severity of dwarf mistletoe, and depth of soil organic layer. Though we did find pre-treatment differences in effects of stand age on restoration indicators, we found no significant trends across treatment groups prior to thinning (i.e., in 2007, Tables S1, S2, S3, S5, and S8),

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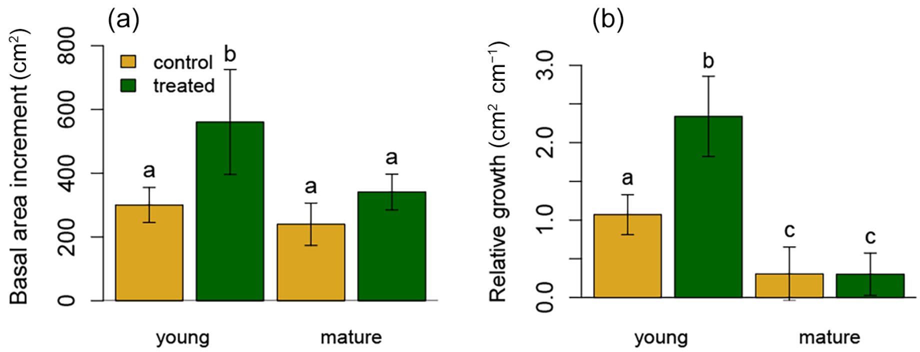

FIGURE 2 Changes in tree growth. Tree growth was higher with restoration thinning ("treated"), as measured by basal area increment (a) as well as by relative growth (b) from 2007 to 2020, particularly for young stands. Bars represent estimates from linear mixed-effects models; error bars show 95% confidence intervals (also see Table S1). Different letters indicate that estimates are significantly different ($p < .05$ for post hoc Tukey multiple comparisons of means test).

with the exception of mistletoe abundance (Table S2), seedling abundance (Table S3), and understory percent cover (Table S5).

3.1 | Tree growth

From 2007 to 2020, tree basal area increased more, and relative growth was greater in treated plots compared to control plots of young stands (Figure 2, Table S1). Thinned young stand basal area increment was 261 cm^2 greater ($p < .05$ based on post hoc tests) and relative growth was 1.26 greater ($p < .05$) compared to basal area increment in control young stands (Figure 2). Differences across treatment groups were not significant for mature stands ($p > .05$ based on post hoc tests). Similarly, tree diameter increased 5.8 cm more in thinned versus control treatments for young stands ($p < .05$ based on post hoc tests), but differences across treatments were not significant for mature stands (Figure S1, Table S1). Tree height increased by 1.4 m more in young, treated compared to young, control stands ($p < .05$ based on post hoc tests); there was no significant difference between mature, control and mature, treated plots (Figure S2, Table S1).

3.2 | Vertical and horizontal structure

Large woody debris was most abundant in the mature age class compared with young age class but did not differ statistically across treatment types (Figure 3a, Table S2). Mature, control plots had nearly three times as much large woody debris basal area as compared to young, control plots; however, the change in large woody debris basal area between 2007 and 2020 was not significant (Figure 3b, Table S2).

Tree mortality between 2007 and 2020 was more than twice as high in treated plots (0.43 for young and 0.15 for mature) compared to control plots (0.03 for young and 0.04 for mature, Figure 3c). Surprisingly, this increased mortality did not translate into a greater presence of standing dead trees (i.e., snags) within treated plots, perhaps because many of the dead trees fell over on to the ground. Changes in snag abundance from 2007 to 2020 were generally not significant, though mature thinned stands did experience significantly less change in snag abundance than young control stands (Figure 3d).

The ratio of small to large diameter trees varied by age class category, with lower ratios in mature age classes (Figure S3). The total counts of large diameter trees differed strongly across treatment and age class. Mature, treated plots had the greatest number of large diameter trees in 2020, followed by mature, control; young, control; and lastly young, treated plots (Figure S3, Table S2). The substantial abundance of large diameter trees found within young, control plots was likely driven by the presence of legacy trees—old trees that were spared during previous harvests.

Mature, treated plots had a significantly lower canopy cover (by more than 10%) when compared to mature, control plots (80% vs. 91% canopy cover, respectively) (Figure 3e). However, young, control and young, treated plots had similar canopy cover indicating that young, treated plots responded much differently to thinning than mature, treated plots. We observed a relatively high amount of canopy cover and a positive change in canopy cover in young, treated plots (Figure 3f), even though a substantial number of trees were removed during the thinning treatments.

We found that pre-treatment differences in mistletoe abundance existed across treatment groups (Table S2) and age; post hoc tests indicated that the young control stands had significantly more mistletoe abundance than

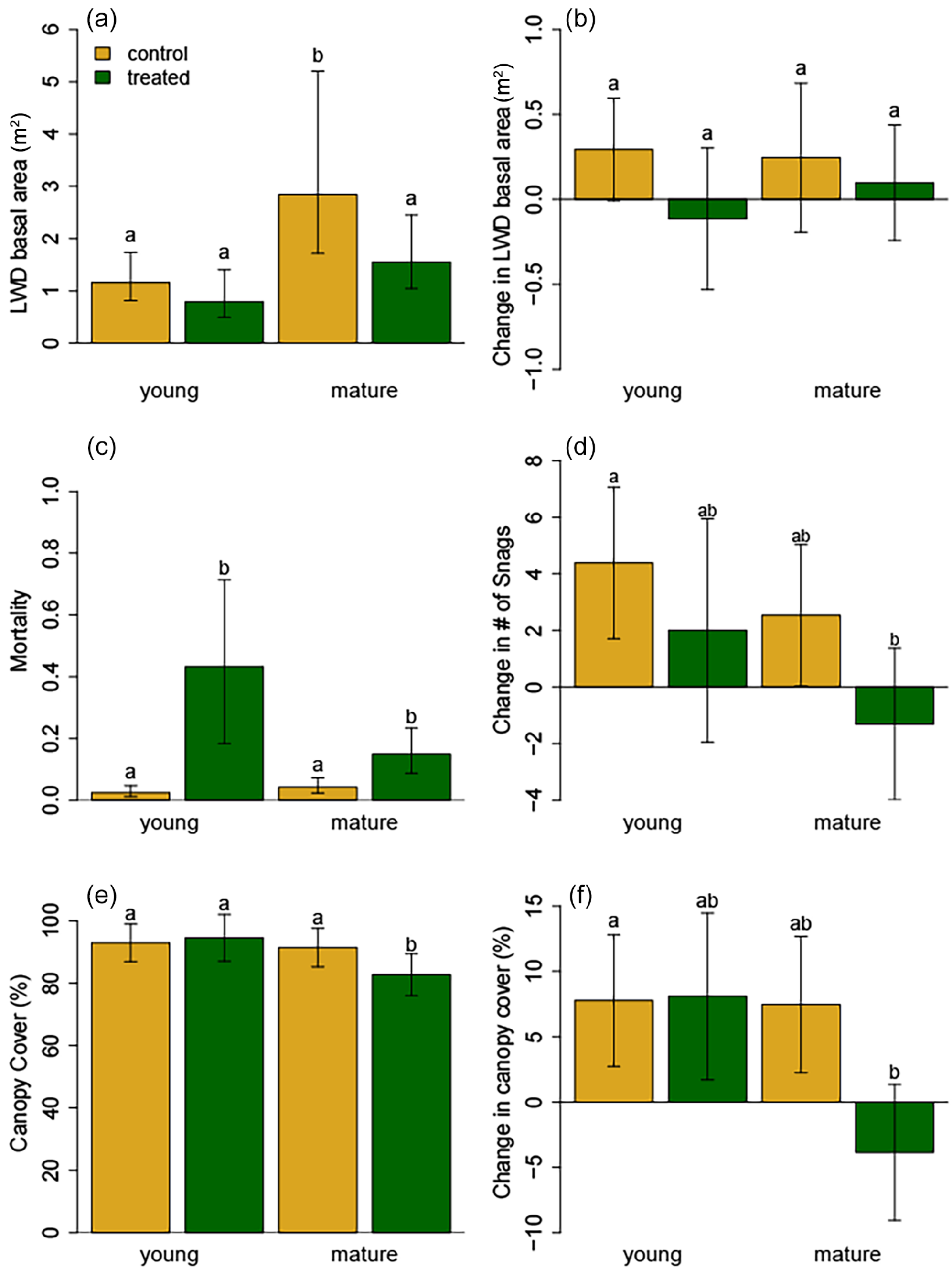

FIGURE 3 Changes in vertical and horizontal structure. Large woody debris (LWD) basal area was most abundant in mature stands and is not statistically different between treatment types (a). Changes in LWD basal area from 2007 to 2020 were not significant and 95% uncertainty intervals overlapped zero for all treatments and age classes (b). Mortality was higher in treated plots, especially those in young stands (c), and the number of standing dead trees (snags) increased in control plots from 2007 to 2020 but did not change considerably in treated plots (d). Canopy cover percent in 2020 (e) and change in canopy cover percent from 2007 to 2020 (f). Canopy cover percent in 2020 was more than 10% lower in mature, treated plots compared to mature, control plots (79.7% vs. 94.2%). There was not a substantial change in canopy cover within mature, treated plots from 2007 to 2020 (i.e., uncertainty intervals overlap with zero); whereas canopy cover increased for young, treated and all control plots during this time period (b) (also see Table S2). Bars represent estimates from models and error bars show 95% confidence intervals (also see Table S2). Different letters indicate that estimates are significantly different ($p < .05$ for post hoc Tukey multiple comparisons of means test).

other treatment combinations, even before thinning was conducted. Although the abundance of mistletoe increased with stand age in 2020 (Figure S4A), we did not detect a significant change in mistletoe presence between 2007 and 2020 across treatment or age categories (Figure S4B, Table S2).

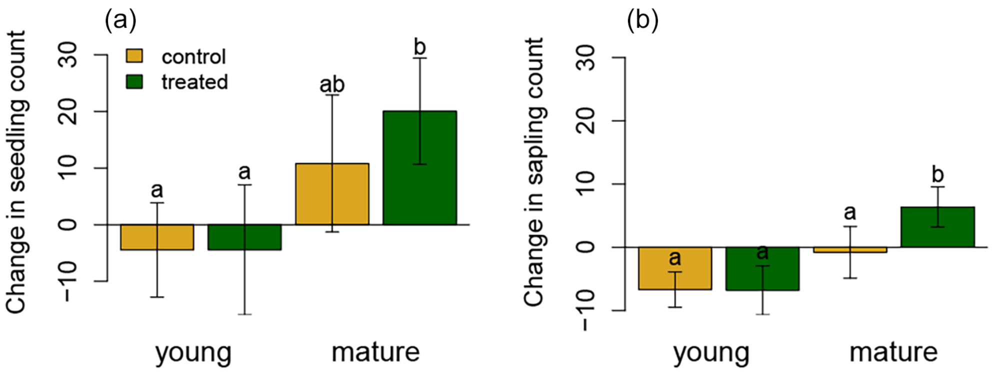

FIGURE 4 Regeneration responses as measured by the change in seedling count (a) and sapling count (b) between 2007 and 2020. Bars represent estimates from generalized linear models and error bars show 95% confidence intervals (also see Table S3, Figure S5).

3.3 | Regeneration

Restoration treatments had a positive effect on the abundance of saplings but had no significant effect on seedling abundance (Figure 4a,b). Sapling counts were highest in mature, thinned plots (Figure 4b, post hoc tests indicate counts were higher in this group compared to all other groups) and these same plots had the largest change between 2007 and 2020. Sapling counts increased by 20 saplings per plot on average in mature, thinned plots, which was significantly greater than changes in all other groups based on post hoc tests. Seedling abundance was higher in mature plots (averaging 24 seedlings per plot in treated stands and 12 seedlings per plot in control stands. Mature plots also experienced the largest increase in seedlings from 2007 to 2020, but differences were not significant across treatments (Figure 4a, Table S3). We found that stand age alone was not a significant predictor of proportional change in seedling and sapling abundance, though interactive effects of age and treatment were significant for saplings (Table S3, Figure S5).

3.4 | Understory plant composition and cover

Overall, there were 6 species of overstory trees and 280 understory species identified within the study area. We found greater understory species richness in young, treated and both mature plots compared to young, control plots for 2020 data (Figure S6, Table S4). Our multivariate analysis highlighted that understory community group centroids—the median in ordination space—were significantly different from one another based on two-way perMANOVA for 999 permutations (Figure 5a, Table S5). However, the interaction between age and treatment type was not significant. We found no significant differences in group dispersions for treatment; however, there was a difference in dispersion for age. Specifically, there was a higher dispersion among young plots compared to mature. We also found that treated plots were generally characterized by higher percent cover of key species, including lady fern (*Athyrium filix-femina*, ATFI), deer fern (*Blechnum spicant*, BLSP), salal (*Gaultheria shallon*, GASH), mock azalea (*Menziesia ferruginea*, MEFE), western sword fern (*Polystichum munitum*, POMU), salmonberry (*Rubus spectabilis*, RUSP), and huckleberry (*Vaccinium* spp., VACCI) (Table S6).

Overall, we observed two general groupings of key species based on our multivariate analysis that were not correlated with one another. The first group was composed of salal (GASH), huckleberries (VACCI), and mock azalea (MEFE) and were negatively loaded on the first PCoA axis. The second group was composed of deer fern (BLSP), lady fern (ATFI), western sword fern (POMU), and salmonberry (RUSP) and were negatively loaded on the second PCoA axis (Figure 5b). This second group also had higher average percent cover in treated plots compared to control plots (Figure 5c,d).

The change in life-form cover between 2007 and 2020 was significantly different across stand age (Table S7). The difference between group centroids in treated versus control plots was marginally significant and the interaction between age and treatment type was not significant (Figure 5e). Group dispersions for treatment were also not significantly different, but there was a significant difference across age classes and young plots, which had a greater dispersion than mature plots (Figure 5e). The ordination space for difference in life-form community composition (Figure 5f) is not as clearly grouped by treatment as the ordination at the species level (Figure 5b). However, mature, treated plots tended to be characterized by larger increases in saplings (both conifer and hardwood), shrubs, and conifer seedlings (Figure 5f).

3.5 | Soil organic layer

Our results show that treatment and age class did not significantly affect the depth of the organic soil layer (Figure S7, Table S8). However, we observed an increase in the depth of the organic soil layer between 2007 and 2020 for all plots (Figure S7).

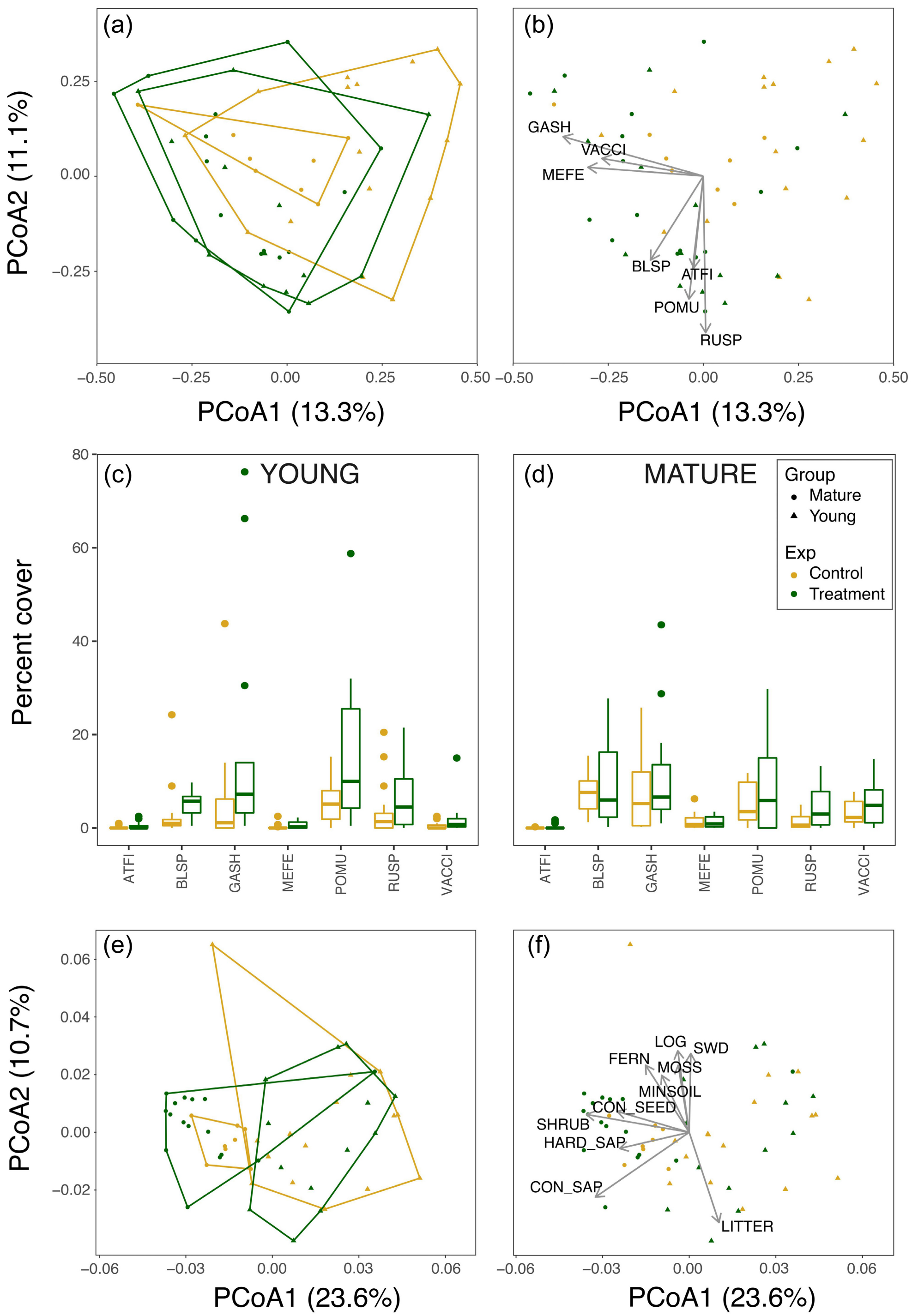

FIGURE 5 Principal coordinates analysis (PCoA) of understory cover for 2020 data (a). Convex hulls represent plots that are in young, control (yellow triangles); mature, control (yellow circles); young, treated (green triangles); and mature, treated (green circles). Understory species with statistically significant ($p < .01$) loadings on the first two PCoA axes are shown in (b). Percent cover of key understory species is shown for young plots (c) and mature plots (d). Significant differences between control and treated plots are indicated by * where $p < .05$ (also see Tables S5 and S6 for more information and species names). The change in lifeform cover between 2007 and 2020 is shown in (e). Lifeform categories that had a statistically significant ($p < .01$) loading on the first two PCoA axes are shown in (f) and include change in percent cover of SWD (small woody debris), LITTER, MOSS, LOG, FERN, MINSOIL (mineral soil), CON_SEED (conifer seedling), SHRUB, HARD_SAP (hardwood sapling), and CON_SAP (conifer sapling).

4 | DISCUSSION

Our findings suggest that forest thinning may be accelerating the development of some old-growth characteristics that are relevant for restoration. These results add to the body of literature describing short-term effects of restoration treatments and indicate that some, but not all, focal indicators show a measurable impact from restoration thinning. Here, we explore these findings and demonstrate the implications on wildlife habitat and climate change resilience, two important management objectives.

4.1 | Restoring old-growth forest characteristics

Our results show that restoration thinning has affected several important old-growth forest indicators, supporting research conducted in other areas and ecosystems (e.g., Davis et al., 2007; Garman et al., 2003; Willis et al., 2018). Key growth metrics, such as live tree basal area and relative growth rate of live trees showed substantial increases within treated plots compared to control plots, consistent with other studies (Curtis et al., 1997; Li, 1923). Our findings also support research demonstrating that younger forest stands have a faster and larger growth response to thinning treatments than older, mature stands (Bradford & Palik, 2009; Reukema, 1975). Our results show positive effects of treatments on basal area and relative growth, which were greater in young versus mature stands. However, we were not able to quantify the degree of this accelerated growth and how much time would be needed to develop old-growth characteristics (Reilly & Spies, 2015). Nevertheless, our results complement studies that demonstrate how thinning can be effective at accelerating both tree growth and the development of structural complexity associated with old-growth forests (Chamberlain et al., 2021; Dodson et al., 2012; O'Hara et al., 2010).

Not all forest restoration indicators responded in ways that are consistent with old-growth forest characteristics. We found that some indicators are contingent on the combined effect of stand age and the type of silvicultural treatment that was applied. For example, thinning treatments initially opened up the overstory canopy in young and mature plots; however, the canopy cover in the young, treated plots filled after thinning, likely due to the increase in light, newly available growing space, and the fast growth response of the remaining live trees (Bailey & Tappeiner, 1998). Young, treated plots had comparable canopy cover to the young, control plots in 2020, despite the fact that a substantial portion of the overstory trees were removed between 2009 and 2013. The canopy cover response was quite different in mature, treated plots that received variable-density thinning, where trees have not responded as much and in 2020 still had much lower canopy cover. Thinning not only lowered the canopy cover but also led to more variable and potentially more complex canopy cover in mature, treated plots when compared to the mature, control plots. These variable conditions resemble the characteristics found in coastal old-growth PNW forests and support findings from other recent studies (Chamberlain et al., 2021; Dodson et al., 2012).

Regeneration also responded in divergent ways. Sapling counts were lower in young stands in 2020 compared to 2007, potentially due to the process of natural self-thinning (Reilly & Spies, 2015). Tree seedling abundance is commonly higher in older forests (O'Brien et al., 2012), potentially due to increases in seed production with tree maturity (Viglas et al., 2013) or due to better microsite conditions that promote seedling survival (Gray & Spies, 1997). We also found more seedlings and saplings in mature plots and a significantly greater increase in sapling counts in mature, treated plots, suggesting that these saplings capitalized on the increased light after thinning treatments were implemented.

4.2 | Improving wildlife habitat

Although we did not directly quantify changes in wildlife presence or abundance, our analyses demonstrate that indicators of wildlife habitat may have also been affected. For instance, our thinning treatments have led to increased plant growth, cover, and forest structural development, which are associated with increased wildlife habitat for a diversity of species (Hayes et al., 2003; Neill & Puettmann, 2013). Our restoration treatments increased the richness of understory plant composition, growth of residual trees, and tree regeneration, all of which can provide important wildlife habitat (Bauhus et al., 2009; Spies et al., 2018). Snags, which can benefit a diversity of species, are another critical component of wildlife habitat (Harmon et al., 2004; Neitro et al., 1985), especially for nesting and hunting by the endangered Northern spotted owl (*Strix occidentalis caurina*) and cavity dwelling species (Spies et al., 2018). Interestingly, the average number of snags did not change significantly across plot types, even though tree mortality was higher in mature, treated plots. Although seemingly contradictory, a possible explanation is that many of the trees that died in treated plots fell to the ground within 7–11 years since treatment implementation, perhaps from windthrow; however, our large woody debris analysis did not detect this.

A critical component of wildlife habitat for canopy nesting species, such as Marbled murrelet (*Brachyramphus marmoratus*), is the presence of dwarf mistletoe. This native parasite can negatively affect tree growth and seed production and can lead to severe damage to conifers (Shaw et al., 2008). However, dwarf mistletoe can also help create more nesting opportunities for species like the Marbled murrelet, by developing suitable structural platforms within the forest canopy (Hamer & Nelson, 1995). Although we found that dwarf mistletoe presence and infection severity was higher in older and treated plots, the change in mistletoe did not vary significantly across treatment or age categories. More time may be needed to further evaluate the long-term effect of our treatments may have on various aspects of wildlife habitat.

4.3 | Enhancing climate change resilience

Our results have implications for managing climate change resilience and climate adaptation strategies. For example, some of our restoration effects align with general strategies of restoring habitat and ecosystem functions and processes, which are expected to increase ecosystem resilience (Lawler, 2009; Peterson et al., 2011). Our thinning treatments reduced stand density, which can lessen the competition between residual trees for water, nutrients, and light and increase the growth and vigor of the remaining trees. Less competitive conditions may increase the ability of some forests to cope with future disturbances, such as summer droughts and insect and disease infestations (Anderegg & HilleRisLambers, 2016; Kolb et al., 2016; Sohn et al., 2016). However, some thinning treatments can have less of an effect on the prolonged response to drought (Castagneri et al., 2002). Our treatments also created small patches of early successional habitat and enhanced structural complexity, which may increase resilience to climate-induced disturbances including wildfire, drought, insects, and diseases (Donato et al., 2020; Seidl et al., 2014).

More diverse forests may have a better chance of keeping pace with a changing climate and responding after disturbances (Dymond et al., 2014; Halofsky et al., 2018). Our restoration treatments increased natural tree regeneration and understory vascular plant richness, complimenting other studies (Thysell & Carey, 2001). Increased species diversity has been identified as a method to increase community resilience (Tilman, 1999) and can provide additional habitat and forage opportunities for a diversity of species (Stein et al., 2013). A diversity of habitats and food may become increasingly important as animal species move in response to warming temperatures and changes in moisture regimes (Littlefield et al., 2019; Pradhan et al., 2023).

4.4 | A need for more time and monitoring

In several cases, the differences we quantified across treatments or age classes were not significant at conventional levels (i.e., 0.05), suggesting that there was no effect or that more time may be required for the full suite of treatment effects on ecosystem functions and processes to be observable (Crouzeilles et al., 2016). Indeed, long time frames are required for processes of forest succession and ecosystem development (Franklin et al., 2002). The combination of restoration treatment and stand age at the time when treatments are implemented will also likely affect how forests develop over time (Dodson et al., 2012; Reilly & Spies, 2015). The differences that we detected between young and mature age classes suggest that there may be unique trajectories of forest development determined by the combination of stand age and the type of silvicultural treatments that are applied. Climate change also impacts vegetation dynamics, growth, mortality, and regeneration and therefore, long-term monitoring (i.e., dendrochronology, climate monitoring, tree-water relationships, and insect and disease monitoring), and subsequent analyses are needed to determine the successional pathway and assess whether restoration objectives are continually being met (Reilly & Spies, 2015). Future research could also integrate our empirical results with modeling studies to further assess and prioritize restoration treatment effects aimed at accelerating old-growth forest characteristics, enhancing wildlife habitat, and increasing climate change resilience (e.g., Pradhan et al., 2023). Further, our results could be combined with other research studies in a meta-analysis to better understand the multiple spatial, temporal, and population effects of restoration treatments.

Our study highlights the complexities of restoring old-growth forest habitat and suggests that a “one and done” approach of implementing restoration treatments may not achieve a full suite of goals. Nonetheless, it is encouraging that our results demonstrate the effect that restoration treatments have on the accelerated development of some old-growth characteristics, thereby adding to the breadth of knowledge on old-growth restoration. We also recognize that subsequent treatments and more time are needed before those characteristics resemble reference old-growth conditions (Dodson et al., 2012; Puettmann et al., 2016). Targeted treatments aimed at the creation of specific indicators, such as snags and large woody debris could be prioritized in areas that have been identified as lacking those features. Although there would be economic cost associated with implementing these treatments, they would undoubtedly speed up the development of some old-growth characteristics in locations that have low structural complexity. Clearly, there is a need for more interdisciplinary research on how to effectively restore old-growth forests and safeguard the benefits and services they provide, particularly given increasing stressors, such as climate change.

AUTHOR CONTRIBUTIONS

Michael J. Case conceived and designed the research; Michael J. Case, Ailene K. Ettinger, and Kavya Pradhan analyzed the data; Michael J. Case, Ailene K. Ettinger, and Kavya Pradhan wrote and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors confirm that there are no conflicts of interest or significant financial support that could have influenced this work. The manuscript has been read and approved by all named authors.

DATA AVAILABILITY STATEMENT

The data and analysis code for reproducing all results and figures are available on the public repository, Knowledge Network for Biocomplexity (KNB) (Ettinger et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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