

Medium-term effects of active management on the structure of mature Douglas-fir (*Pseudotsuga menziesii*) stands

NEIL WILLIAMS † AND MATTHEW POWERS

Department of Forest Engineering, Resources and Management, Oregon State University, Corvallis, Oregon 97331 USA

Citation: Williams, N., and M. Powers. 2019. Medium-term effects of active management on the structure of mature Douglas-fir (*Pseudotsuga menziesii*) stands. *Ecosphere* 10(8):e02830. 10.1002/ecs2.2830

Abstract. We developed an observational study to (1) examine differences in the structure of mature Douglas-fir stands representing thinned, structural retention harvest and unmanaged conditions, and (2) assess the extent to which active management in mature stands expedites development of old-growth structure, relative to two old-growth indices. Time since treatment averaged 38 and 22 yr in thinned and retention harvest conditions, respectively, and stand age ranged from 106 to 193 yr when sampled. Differences in stand structure were apparent between all three management conditions, with attributes associated with stumps, live tree diameter diversity, understory vegetation, and vertical foliage structure being the strongest individual drivers of these differences. Mean old-growth index scores were lower than expected of true old-growth for each of the management conditions examined here, but were not significantly different between thinned and unmanaged stands. Our results suggest thinning in mature stands may promote certain elements of old-growth structure, including foliage height diversity, but also indicate the need for provisions against the depletion of dead wood resources. Stumps are an understudied dead wood structure, and in actively managed mature stands, our results imply that stumps may provide a degree of functional substitution where down log availability is low.

Key words: complexity; foliage height diversity; mature; old-growth; retention harvest; stand structure; stumps; thinning.

Received 10 April 2019; revised 16 June 2019; accepted 20 June 2019. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** neil.williams@oregonstate.edu

INTRODUCTION

Structural heterogeneity is a cornerstone of contemporary multi-objective forest management (Franklin et al. 2018) that has become an important target in its own right (Franklin et al. 1986, USDA and USDI 1994). Forests composed of a range of tree species and size classes facilitate long-term wood production through risk diversification, while also providing flexibility against the unknowns presented by global change (Puettmann et al. 2009, O'Hara 2014). At the same time, a diverse physical structure increases the breadth of micro-environments for occupancy by species with distinct habitat requirements, thereby favoring a diverse forest

fauna (Carey et al. 1999, Ishii et al. 2004). Maintenance of native forest biodiversity is, in turn, an advantage when engaging with a public that places greater emphasis on species conservation, as an objective of forest management, than in the past (Sharik et al. 2010).

Enhancing structural diversity is particularly relevant to mid-successional forests, which are characteristically less complex than their early- and late-successional counterparts (Spies and Franklin 1991, Franklin et al. 2002). Structural legacies like snags, dead wood, and residual live trees, common to early successional systems developing after natural disturbances, are often scarce or heavily decayed by the onset of the mature phase of stand development (Spies et al.

1988). Stands entering maturity may also display relatively simplified structure in the live understory and overstory, particularly when the pioneer cohort is shade intolerant and resources are not sufficiently limited to prevent young stands achieving canopy closure. In the understory, shrub and herb cover, species richness, and biomass typically decline as a corollary of the establishment of canopy cover, and the associated changes in understory resource availability (Jules et al. 2008, Reich et al. 2012, Schmiedinger et al. 2012). Meanwhile, competition among overstory trees—a process that initially drives heterogeneity through crown differentiation—progressively eliminates less-competitive trees and may ultimately result in natural stands with a relatively homogenous main canopy, in which foliage is concentrated in large, increasingly regularly spaced, dominant, and codominant trees (Oliver and Larson 1990, North et al. 2004, Ashton and Kely 2018).

As a result of these changes, mature stands often retain few of the structures responsible for heterogeneity in early successional landscapes originating via natural disturbance and have not yet developed many of the characteristics associated with complexity in old-growth forests (Franklin et al. 2002, 2005, Keeton et al. 2007). Shade-tolerant understory and mid-canopy trees are a prominent feature of many old-growth forests, contributing to the stem size diversity and multi-layered canopy that are also associated with these systems (Spies and Franklin 1991, Van Pelt and Franklin 2000, Janowiak et al. 2008). The dead wood pool is a similarly important element of old-growth structure (Ziegler 2000, Franklin et al. 2005) and, in addition to comprising large snags and logs, often exhibits greater decay class diversity than in younger forests (Gibb et al. 2005, Burrascano et al. 2008). Although the rate at which individual mature stands accumulate these old-growth characteristics varies considerably (Acker et al. 1998), observations from a variety of temperate systems reinforce the notion that mature stands, on average, possess lower structural diversity than old-growth stands (Keeton et al. 2010, Burrascano et al. 2013, Freund et al. 2015).

Stands displaying overstory characteristics associated with maturity are now more abundant than old-growth in many temperate regions (Oswalt et al. 2014, Davis et al. 2015), but are

commonly managed using the same passive—that is, no active management treatments—strategies. In some settings, policy or social constraints discourage active management in older forests (Thomas et al. 2006). However, blanket restrictions of this nature are inconsistent with the widely held desire to engender old-growth-like complexity, given the potential ability of certain forms of active management to shorten the timeframes needed to develop key elements of old-growth structure in stands previously lacking in such components (Carey and Curtis 1996, Latta and Montgomery 2004, Andrews et al. 2005). Moreover, following protracted and widespread anthropogenic disruption of natural disturbance regimes, the extent to which passive management will result in contemporary mature stands developing similar conditions to those found in current old-growth forests is open to question (Keeton et al. 2012, Sensenig et al. 2013). Management over extended rotations (those matching or exceeding the biological rotation length for a given forest type) with one or more thinnings is among the active management strategies proposed as an alternative or complement to reserve-based management (Curtis 1995, Gronewold et al. 2010). By promoting growth of a shade-tolerant understory, and crown depth among overstory trees, reductions in stand density should expedite the development of vertical complexity (Bailey and Tappeiner 1998, Chan et al. 2006) and are also consistent with production of the large overstory trees characteristic of old-growth structure (Latham and Tappeiner 2002). There are, however, concerns that conventional commercial thinning may have a negative effect on the development of other elements of old-growth structure, notably dead wood (Cline et al. 1980, Debeljak 2006). Moreover, there have been few comprehensive analyses of the effect of thinning in mature stands on overall forest structure, including live and dead vegetation in the understory and overstory.

Whereas thinning has been proposed as a means of shifting the structure of the current stand toward old-growth conditions, even-aged regeneration harvest with (live or dead) structural retention may greatly reduce the time required for the subsequent stand to develop late-successional structural complexity (Franklin et al. 1997). Such approaches may also promote

the development of stands in which overstory trees exhibit a wide range of ages and size classes—a condition observed in many old-growth stands (Tappeiner et al. 1997, Poage and Tappeiner 2002, Sensenig et al. 2013). Management techniques designed to replicate this age and size class diversity using structural retention during final harvest have been widely adopted throughout the temperate and boreal zones over the past decades (Gustafsson et al. 2012). However, despite this applied interest, there have been few analyses of the medium-term impacts of retention harvest on aggregate stand structure. Instead, existing research has typically focused on a subset of structural elements or has been limited to the first decade following treatment application (Maguire et al. 2007, Curzon et al. 2017, Crotteau et al. 2018). Although valuable, these analyses provide limited information on the longer-term structural development trade-offs involved in the application of retention harvesting in mature stands.

To understand the implications of alternative approaches to the development of structural complexity, we assessed current forest structure, two to five decades following treatment, in mature stands (*sensu* Williams and Powers 2019; here assumed to be those with overstory dominants aged 80–199 yr) managed using commercial thinning over extended rotations (as defined above), structural retention harvest, and an unmanaged condition involving no intentional overstory density reduction. We focused on the moist, temperate forests of western Oregon, a region in which mature stands are a major component of the total forested area (Oswalt et al. 2014, Davis et al. 2015) and restoration of structurally complex old-growth forest remains a primary goal of forest policy on public lands (USDA and USDI 1994). Expediting the structural development process in structurally simplified mature stands is one possible means of contributing toward this goal. Thus, management options for enhancing structural complexity in mature stands are highly relevant, and a number of indices have been developed to assist in the evaluation of forest structure, relative to the desired old-growth condition (Acker et al. 1998, Franklin et al. 2005). In addition to describing the current structure of stands in our three management conditions, we also sought to

evaluate their relative progress toward old-growth conditions, as measured by two such indices for forests in this region.

Our specific objectives were to:

1. Describe the structure, and its variability, of mature stands managed using active and passive (defined above) approaches. Of particular interest are whether:
 - 1.1. Active management results in a distinct structural profile, several decades following harvest, relative to passive management; and
 - 1.2. If so, which structural attributes are most important in differentiating between stands managed using active and passive approaches?
2. Determine whether active management expedites the development of late-successional structure in mature, Douglas-fir-dominated forests. Of particular interest is whether:
 - 2.1. Management of mature stands using thinning (during maturity) engenders a structure more comparable with old-growth conditions than passive management.

METHODS

Study sites and experimental design

In the Pacific Northwest region of the USA, moist, temperate forests are a dominant ecosystem type at low to moderate elevations west of the Cascade Range crest. Gradients in climate are an important driver of broad changes in forest structure and composition across this region (Berner et al. 2017), with variability in edaphic and physiographic conditions thought to influence forest composition, in particular, at finer spatial scales (Ohmann and Spies 1998). In efforts to isolate the influence of management on forest structure and composition (henceforth simply “forest structure,” unless noted to the contrary), we (1) restricted sampling to forests in the Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Grand Fir (*Abies grandis* (Dougl. ex D. Don)

Lindl.) plant Zones (McCain and Diaz 2002), within the Coast Ranges and Western Cascades physiographic provinces of western Oregon (Franklin and Dyrness 1988), and (2) employed a randomized complete block study design, with blocking based on Landtype association (Ecoshare 2016) and geographic proximity (described further below). Mean monthly temperatures at our study sites ranged from a low of -3°C in January to a maximum of 28°C in August, with annual averages over the past thirty years of $8\text{--}11^{\circ}\text{C}$ (PRISM Climate Group 2018). Mean annual precipitation over this period of time was 1400 mm at our driest study site and 2730 mm at the wettest, with the majority of this occurring between October and April. Soils in the Coast Ranges are commonly sandstone- or basalt-derived Inceptisols, while Andisols originating from mafic andesite and associated pyroclastic sequences predominate in the Western Cascades. In spite of this variation, soils in both provinces are typically deep to moderately deep, well-drained and mildly acidic, often supporting considerable organic matter accumulation.

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the dominant overstory component of forests throughout much of the study region, with its late-successional associates, western hemlock, and grand fir, occupying mid- to lower-canopy positions in most mature stands. Shade-tolerant western redcedar (*Thuja plicata* Donn ex D. Don) is locally abundant on mesic sites, while mid-tolerant incense cedar (*Calocedrus decurrens* Torr.) and intolerant sugar pine (*Pinus lambertiana* Dougl.) occur on drier sites. Bigleaf maple (*Acer macrophyllum* Pursh.), golden chinkapin (*Castanopsis chrysophylla* (Dougl. Ex Hook.)), Pacific madrone (*Arbutus menziesii* Pursh), and red alder (*Alnus rubra* Bong.) are the principal hardwood tree species but are typically minor components in terms of stand basal area and stem density. Composition of the shrub and herbaceous layers is also heavily influenced by site moisture regime. Major shrub species at study sites include beaked hazel (*Corylus cornuta* Marshall), vine maple (*Acer circinatum* Pursh.), salal (*Gaultheria shallon* Pursh.), dwarf Oregon grape (*Mahonia nervosa* (Pursh.) Nutt.), and *Vaccinium* spp. Meanwhile, sword fern (*Polystichum munitum* (Kaufl.)), bracken fern (*Pteridium aquilinum* (L.) Kuhn), Oregon oxalis (*Oxalis oregana*

Nutt.), vanilla leaf (*Achlys triphylla* (Sm.) DC), and Pacific twinflower (*Linnaea borealis* ssp. *longiflora* (Torr.) Hult) are frequently encountered herbaceous species.

Although ecological definitions of the various phases of stand development are based on differences in forest structure, age-based criteria were used here as an initial screen to identify potentially suitable mature stands representing our active and passive management conditions. In so doing, we made the necessary simplifying assumption of stand development proceeding in a relatively linear pathway following stand-replacing disturbance. Under such models, the mature interval loosely corresponds to stands in which overstory dominants are aged 80–199 yr (Spies and Franklin 1988). For consistency with the requirements of a companion study, we further restricted our sampling to stands in which active management, if any, occurred before 2001. Consequently, the operational definition of the mature interval used in site selection—which took place from mid-2016 to mid-2017—was stands with a dominant overstory age of 97–199 yr at the time of sampling. Preliminary screening indicated that stands in this age range were primarily located on federal land, with a lesser amount on state land.

Stands conforming to the above age criteria and representing the following three management approaches (henceforth also referred to as management condition classes) were identified using GIS databases of state and federal agencies, and of Oregon State University's McDonald-Dunn Research Forest, and by discussion with management personnel.

1. Unmanaged, that is, no history of intentional overstory density reduction. Basal area at the time of sampling for this condition ranged from 57.6 to 107.6 m^2/ha (mean 76.1 m^2/ha).
2. Thinning, that is, extended rotation (in this instance 100–199 yr), even-aged management with a single thinning, and overstory retention of 50–85% of pre-treatment basal area. Basal area at the time of sampling for this condition ranged from 22.2 to 127.9 m^2/ha (mean 70.0 m^2/ha).
3. Structural retention harvest (retention harvest), that is, even-aged regeneration harvest with overstory retention of 15–30% of pre-

treatment basal area (live + dead). Basal area at the time of sampling for this condition ranged from 18.2 to 54.5 m²/ha (mean 32.2 m²/ha).

Structural characteristics representative of those expected prior to data collection, for each of these management conditions, are displayed in pictures in Fig. 1. In most cases, overstory

density reduction in our retention harvest management condition was originally implemented as the shelterwood cut in stands managed using a shelterwood system. As a consequence of subsequent changes in the social and policy environment in the Pacific Northwest, residual overstory trees—live and dead—in these stands are now intended to be retained permanently, subject to natural mortality and treefall. The effect is



Fig. 1. Structural characteristics representative of those expected prior to data collection, for our unmanaged management condition (top), thinned management condition (lower left), and retention harvest management condition (lower right).

analogous to the impact of final harvest in stands managed using a variable retention harvest system (applied intentionally in stand S09-M04; Tables 1, 2). However, it is important to note that the conventional shelterwood origin of most of our retention harvest stands resulted in the retention of predominantly live trees, while modern variable retention harvest practices also advocate the retention of snags and down logs (Lindenmayer and Franklin 2002, Gustafsson et al. 2010, Lindenmayer et al. 2012). Both structural retention harvesting and the use of extended rotations with thinning are now advocated for managing stands for advanced structural complexity and the maintenance of biodiversity in managed landscapes (Curtis 1995, Bauhus et al. 2009, Franklin et al. 2018). In this sense, our study provides an opportunity to consider the potential consequences of management for structural complexity over a longer time horizon than many

manipulative experiments designed expressly for this purpose, despite the differences between historical and modern treatment practices noted above.

The following hierarchical selection criteria were then used to identify stands representing management conditions (1)–(3), above, and to assign stands to treatment blocks.

Management history.—Among actively managed stands (i.e., our commercial thinning and retention harvest conditions), we focused on those in which overstory density reduction was approximately evenly distributed throughout stands. The principal effect was to exclude stands managed using variable density thinning, and variable retention harvest treatments incorporating significant levels of aggregated retention or large gap creation. Excluding these treatments was necessary in order to reliably capture the potential effect of overstory density reduction on

Table 1. Location, stand structure, and site characteristics for 24 mature stands in western Oregon representing unmanaged, thinned, and retention harvest management conditions.

Stand ID	Block	Location	Stand age (yr)	Years since harvest	Elevation (m)	Slope (%)	Dominant aspect
Unmanaged							
S01-M01	1	Alsea	137	NA	230	40	W
S02-M01	2	Idleyld Park	156	NA	659	20	S
S03-M01	3	Breitenbush	123	NA	701	55	S
S04-M01	4	Belknap Springs	145	NA	967	5	N
S05-M01	5	Elkhorn	157	NA	511	50	S
S06-M01	6	Table Rock	131	NA	610	10	N
S09-M01	7	Idleyld Park	157	NA	350	20	N
S10-M01	8	Cougar Reservoir	193	NA	941	10	S
Thinned							
S01-M02	1	Alsea	127	46	571	45	NW
S02-M02	2	Idleyld Park	106	26	760	25	W
S03-M02	3	Breitenbush	123	40	924	20	S
S04-M02	4	Carpenter Mountain	187	37	785	40	NW
S05-M02	5	Elkhorn	157	45	414	15	NW
S06-M02	6	Table Rock	137	44	664	35	E
S09-M02	7	Idleyld Park	117	33	676	35	E
S10-M02	8	Cougar Reservoir	193	31	1052	30	SW
Retention harvest							
S01-M04	1	Corvallis	107	17	298	15	S
S02-M04	2	Idleyld Park	106	17	539	55	SW
S03-M04	3	Marion Forks	166	19	11,222	5	N
S04-M04	4	Belknap Springs	145	28	966	5	N
S05-M04	5	Elkhorn	134	34	609	65	N
S06-M04	6	Table Rock	131	17	641	30	N
S09-M04	7	Idleyld Park	117	17	469	10	E
S10-M04	8	Cougar Reservoir	193	26	11,088	35	S

Table 2. Additional site characteristics for 24 mature stands in western Oregon representing unmanaged, thinned, and retention harvest management conditions.

Stand ID	MAP (mm)†	MAT (°C)†	Area (ha)	Percent conifer‡	Basal area§ (m ² /ha)	SDI ⁽³⁾
Unmanaged						
S01-M01	1726	11	125	81	70.3	823
S02-M01	2097	11	160	96	57.6	778
S03-M01	1772	8	33	99	77.4	1151
S04-M01	2217	9	54	100	80.4	1181
S05-M01	2118	9	53	100	68.7	942
S06-M01	1868	9	16	99	76.2	825
S09-M01	1395	11	54	93	77.4	922
S10-M01	2730	9	40	100	107.6	1429
Thinned						
S01-M02	2279	11	72	100	127.9	1696
S02-M02	2147	11	12	97	43.2	613
S03-M02	1836	9	40	99	28.5	465
S04-M02	2080	9	23	100	73.4	927
S05-M02	1918	10	67	99	72.9	1040
S06-M02	2359	9	58	100	69.4	939
S09-M02	1655	11	34	97	62.1	803
S10-M02	2733	8	15	100	82.7	1045
Retention harvest						
S01-M04	1422	11	26	98	25.5	365
S02-M04	1618	11	38	87	22.2	347
S03-M04	2157	8	17	100	35.7	473
S04-M04	2233	9	27	99	18.2	328
S05-M04	2075	10	22	94	44.8	877
S06-M04	1886	9	58	97	23.1	359
S09-M04	1400	11	13	97	33	502
S10-M04	2732	8	23	100	54.5	714

† MAP, mean annual precipitation, and MAT, mean annual temperature.

‡ By basal area.

§ In stems ≥ 5 cm dbh.

stand structure, during sampling, given available study resources.

Landtype Association and geographic proximity, used for blocking.—Landtype Associations (LTAs) are geospatial units of similar climatic, geologic, edaphic, and geomorphic conditions. The 2016 database of LTAs for the Pacific Northwest (Eco-share) was used to group potential stands by LTA. Complete treatment blocks were then constructed by randomly selecting one stand per management condition from LTAs in which at least two of our three management conditions were present. Where multiple polygons representing a given LTA existed and included potential sample stands, preference was given to stands located in a single LTA polygon unless doing so greatly increased the distance between potential sample stands. For LTAs in which only two management conditions were present,

blocks were completed by including a stand from the missing management condition in a nearby LTA with similar physiographic and/or climatic characteristics. To the extent possible, we attempted to control for overstory age across management conditions within blocks, while retaining an element of randomization in stand selection.

Using this procedure, eight complete blocks were delineated (i.e., $N = 24$), with the constituent stands all located on land managed by either the Oregon Bureau of Land Management, the Willamette National Forest, or the Oregon State University's McDonald-Dunn Research Forest. The mean age of these stands was 144 yr at the time of sampling (minimum of 106, maximum of 193 yr, Table 1). Among actively managed stands, time since treatment ranged from 17 to 46 yr and was, uncontrollably, greater (F -test

$P = 0.0015$) in our commercial thinning management condition (mean 38 yr, range: 26–46) than retention harvest stands (mean 22 yr, range: 17–34). These stands span a wide range of basal area (18.2–127.9 m²/ha, among stems ≥ 5 cm diameter at breast height at the time of sampling), with the vast majority of this being Douglas-fir. Similarly, stand density index (SDI; Long and Daniel 1990) among stands in the final sample varied from 328 to 1696 (Table 2).

Data collection

Data were collected in the summers of 2016 and 2017 using standard forest inventory protocols, supplemented with additional procedures for estimating vertical foliage distribution. Sampling utilized a nested plot design featuring four randomly sited fixed area plot structures per stand.

Live stems with diameter at breast height (dbh = 1.37 m) ≥ 25 cm were inventoried in 0.1-ha overstory plots, while those with dbh ≥ 5 cm and < 25 cm were inventoried in a nested plot 0.025 ha in size. In all cases, species, total tree height, and dbh were recorded, the latter to the nearest 0.1 mm. Total tree height was measured to the nearest 0.5 m using a Vertex VL5 Laser (Haglöf Sweden AB, Långsala, Sweden) or a telescopic height pole, and each stem was assigned to one of seven canopy classes for calculation of the Berger-Parker Index of canopy classes: understorey shrub, understorey tree, suppressed, intermediate, codominant, dominant, emergent (modified from North et al. 1999). For a minority of stems ($< 10\%$ of total stems), it was not possible to obtain height measurements, and in these circumstances, height was estimated based on measured dbh using height equations for western Oregon (Garman et al. 1995). Saplings (stems ≥ 1.37 m height and < 5 cm dbh of species capable of attaining ≥ 15 m height when mature) and regeneration (woody stems < 1.37 m height of conifer and hardwood tree species) were tallied by species in four nested understorey plots of 0.00125 ha and 0.0003 ha size, respectively, located 9 m from overstory plot center along 45°, 135°, 225°, and 315° azimuths. Stems of shrub species were tallied by species in four nested 0.0003-ha plots, with the exception of salal and dwarf Oregon grape, whose cover was visually estimated to the nearest 10%. We supplemented these measurements of woody understorey

vegetation by calculating the biomass of herbaceous vegetation and the cover of forest floor bryophytes. Herbaceous biomass and bryophyte cover were sampled using four 0.25-m² clip-plots per overstory plot, located 9 m from overstory plot center in the cardinal directions (Williams and Powers 2019).

Snags (stems ≥ 1.37 m height) were sampled in identically sized plots to those used for live stems, with the addition of four 0.25-ha plots per stand for snags measuring ≥ 50 cm dbh. In all cases, decay class (I–V, Harmon et al. 2011) and species were recorded. For snags with intact tops, dbh and height were measured, while for those with broken tops, basal diameter, top diameter, and height were recorded. Bole volume was computed as the frustum of a cone or a paraboloid (Harmon and Sexton 1996), after initially converting dbh to basal diameter for stems with an intact top (Chojnacki et al. 2014). Down woody debris was sampled using a line intercept method (Brown 1974). Two 20-m transects were established per overstory plot, oriented at 180° and 270° azimuths. Intersection diameter, species, and decay class were recorded along the entire transect for all pieces with intersection diameter ≥ 7.6 cm (defined as coarse woody debris, CWD; Sollins 1982). Plot-wise CWD volume, V (m³/m²) per species and decay class, was calculated using the formula (Harmon and Sexton 1996):

$$V = \pi^2 * \sum_{i=1}^n \left(\frac{d}{8L} \right)$$

where d is piece diameter (m), L is the total transect length per plot (m), and n is the number of pieces of dead wood per plot. Stumps (standing dead stems < 1.37 m in height) were inventoried in a single 0.025-ha plot per overstory tree plot. In all cases, basal diameter, top diameter, and stump height were measured to the nearest cm, and species and decay class recorded. The volume of each stump was then calculated as the frustum of a neiloid using the formula (Ares et al. 2007):

$$V = 0.00007854 \left(\frac{d + D}{2} \right)^2 \left(\frac{H}{100} \right)$$

where V is stump volume (m³), d is top diameter outside bark, D is basal diameter outside bark measured above lateral root protrusions, and H is stump height (m).

In addition to sampling individual live and dead stand structural elements, we computed a variety of indirect and direct measures of vertical stand structure. Indirect measures of vertical structure included the Berger-Parker Index of live tree canopy classes and live tree height classes (BPI_{CC} and BPI_{HC} , respectively). BPI_{CC} and BPI_{HC} , each of which has been employed in previous studies of stand structure in the Pacific Northwest, describe evenness among canopy classes and height classes (see Appendix S1 for formulae). Direct observations of foliage structure were used to calculate an index of foliage height diversity (FHD). Foliage height diversity was developed and derived based on the approaches of MacArthur and MacArthur (1961), and Berger and Puettmann (2000). Although reliant on visual assessment, and thus inherently subjective, FHD measurements were gathered using a step-wise methodology by a single observer, also the individual responsible for protocol development and data analysis.

Foliage height diversity was sampled in four nested plots (FHD plots) per 0.1-ha overstory plot, each located 9 m from overstory plot center in the cardinal directions. Each FHD plot is cylindrical in shape, extending from forest floor to the top of the canopy, the base with a radius of 3 m, and is divided horizontally along the four quadrants of the compass, and vertically into three height layers, 0 to <0.61 m, ≥ 0.61 to <7.62 m, and ≥ 7.62 m. These approximate the three major life habits of forest vegetation: herbaceous plants, shrubs, and trees. For each compass quadrant per FHD plot, a visual estimate was made (observer standing at FHD plot center, facing outward) of the contribution of each layer to the total foliage volume present in the cylinder quadrant. Estimates were made in percent terms (to the nearest five percent), with a maximum of 100%. These raw estimates were then adjusted to reflect the extent to which foliage within each height layer was vertically concentrated or vertically continuous. Adjustments to the raw estimates were made via a reallocation of up to 20 percentage points from layers in which foliage was particularly concentrated, to layers in which foliage was particularly continuous. Adjustments were only made in instances in which the distribution of foliage in one height layer was substantially more concentrated/continuous than in

other layers in the same quadrant. Foliage height diversity scores were calculated separately for each quadrant per FHD plot (formulas provided in Appendix S1), averaged across quadrants within each plot, and a mean FHD score was then computed across the four FHD plots within each overstory plot.

Statistical analysis

We used a combination of multivariate analytical techniques and linear mixed models to address the research objectives outlined above. We compiled an array of 35 non-spatial structural indices and common forest inventory statistics for live and dead vegetation for use in describing the structure of mature stands (henceforth simplified to structural attributes). Criteria used in the selection of structural attributes were (1) previously demonstrated utility in describing forest structure in coniferous forests of western Oregon, or late-successional temperate forests elsewhere, (2) suitability as a surrogate for ecological processes or functions of importance in late-successional temperate forests, and (3) representation of as many aspects of forest structure as was logistically feasible.

A full list of the structural attributes used in data analysis, and formulas for their calculation, is presented in Appendix S1. These attributes include characteristics associated with overall stand biomass (e.g., total basal area, stand density index, carbon storage), live overstory trees (e.g., density of stems ≥ 100 cm dbh, mean dbh, standard deviation of height and diameter), live understory vegetation (e.g., sapling and regeneration density, shrub density, herbaceous biomass), and dead wood (e.g., CWD volume, density of large snags, number of decay classes present). Compositional diversity is represented by the Shannon Index of tree species diversity and shrub species richness. Other non-spatial structural indices in our final dataset included both the Gini coefficient of stem diameter, and Shannon Index of diameter size class diversity, as well as FHD, BPI_{CC} , and BPI_{HC} . All variables were converted to stand-scale averages for use in data analysis, after initially expanding plot-level values to per ha estimates where necessary. Mean scores for each management condition, with respect to the 35 structural variables included in the structural analysis are provided in

Appendix S2. Scores for each stand, with respect to the 35 structural variables are provided in Appendix S3. Raw data used in computing these scores is presented in Data S1.

Research component 1: Mature stand structure and the impact of active management

We used principal components analysis (PCA) to describe the structure of mature stands, as a group, and the association of structure with management and site characteristics. Principal components analysis attempts to reduce a large number of variables contained in a primary matrix into a smaller number of synthetic variables (components, or axes) that best represent covariation among variables in the original matrix (McCune et al. 2002). This analytical technique was selected for use in our analysis after preliminary visual analysis of our structural variables revealed predominantly linear bivariate relationships.

Principal components analysis was conducted on a primary matrix composed of our 35 structural attributes using PC-ORD version 7 (McCune and Mefford 2016). A generalized log transformation was applied to four stem-density-related variables prior to analysis. The Dust Bunny Index (DBI, McCune and Root 2015) for the transformed matrix had a value of 0.513 on a scale from 0 to 1, with DBI = 0.5 indicative of a multivariate normal distribution and DBI = 1 indicative of a strong dust bunny distribution. Principal components analysis axes were constructed from a cross-product matrix of correlation coefficients and therefore incorporate an in-built relativization of columns by standard deviate. Relationships between individual structural variables, ordination axes and stands in ordination space, were assessed visually using simple scatterplots and hilltop plots, and numerically using Pearson coefficients.

Relationships between stands in ordination space and management condition were assessed visually and numerically by overlaying the ordination space with a secondary matrix containing management condition as a categorical variable. Also included in this secondary matrix were eight site- and climate-related variables. These variables, which included both annual averages and monthly extremes for temperature and precipitation, were incorporated into the analysis as

a means of assessing the role of factors other than management in current forest structure. Our PCA analysis revealed little evidence of this; of the eight numeric variables in our secondary matrix, only stand age exhibited a Pearson correlation $>|0.4|$ with any PCA axis. As such, further analysis focuses solely on the relationship between management condition and stand structure, and does not consider these environment/site variables.

Multivariate differences in stand structure between management condition classes were assessed using perMANOVA (Anderson 2001). PerMANOVA, or non-parametric MANOVA, is a novel permutation-based approach to the analysis of multivariate differences between groups that does not require assumptions of strict bivariate linearity between pairs of variables. PerMANOVA was conducted on our 35-variable structure matrix using PC-ORD version 7 (McCune and Mefford 2016) after initially relativizing columns by standard deviate. Differences between management conditions were calculated based on Gower distances, with overall differences in structure between management conditions revealed using a pseudo F-ratio constructed from 5000 randomizations. Significant differences were investigated via pairwise comparisons. *P*-values generated for individual treatment comparisons in PC-ORD were adjusted, post-hoc, by applying the Benjamini-Hochberg procedure for controlling the false discovery rate in multiple comparison testing (Benjamini and Hochberg 1995, Kwong et al. 2002). Adjustments were implemented in R (R Core Team 2018) using the *p.adjust* function. In all cases, *P*-values <0.05 were considered significant.

To assess the drivers of differences in stand structure between management conditions, revealed by perMANOVA, we employed a Random Forests analysis (Breiman 2001). Random Forests is a machine learning tool for classification and regression in multivariate settings. For a given set of predictor variables and sample units, Random Forests creates multiple decision trees using randomly selected subsets of variables and sample units, with majority vote used to determine those variables most important, on aggregate, in the classification of sample units. Random Forests analysis was performed in R using the *randomForest* package (Liaw and

Wiener 2018, R Core Team 2018). The tuneRF function was used to determine the optimal number of variables sampled at each split in decision trees in order to minimize the out-of-box error rate (OOB), and the full set of sample units was used in training the model. Although OOB was relatively high (30%), testing of model accuracy against a larger dataset, consisting of plot-scale measurements, revealed predictive accuracy approaching 85%. Variable importance, the primary objective from our Random Forests analysis was assessed using scores for predicted mean decrease in model accuracy and visualized using the VarImpPlot function.

Development of old-growth structure in mature stands

Progress in the development of structural characteristics associated with old-growth forests in the Western Hemlock Zone, and the impact of active management on old-growth structural development, was examined using two indices of structural complexity. The Index of Old-Growth (I_{OG} ; Acker et al. 1998) and the Old-Growth Habitat Index (OGHI; Franklin et al. 2005) distill forest structure into a small number of attributes thought to be strongly associated with moist temperate forests in the Pacific Northwest. The I_{OG} combines four attributes of live tree structure: standard deviation of tree diameters, density of large (≥ 100 cm dbh) Douglas-fir, mean tree diameter, and density of all trees. The OGHI similarly emphasizes live tree structure, but also incorporates attributes of dead wood structure. We used the modified OGHI (Franklin et al. 2005; henceforth simply OGHI), which comprises density of large (≥ 100 cm dbh) live trees, density of large (≥ 50 cm dbh and 15 m height) snags, CWD volume, and tree size diversity. As the I_{OG} and OGHI include only a limited set of structural attributes, we augmented these structural indices with eight additional variables derived from structural elements that are commonly associated with temperate old-growth forest structure. A full list of these additional variables is provided in Table 6.

Differences in late-successional structural development between management conditions were assessed using linear mixed models and multiple comparisons in R (R Core Team 2018). Mixed-effects models were constructed using the package nlme (Pinheiro et al. 2017), with treatment

modeled as a fixed effect and block as a random effect. Model residuals were evaluated for evidence of non-normality and heteroscedasticity using graphical outputs, and logarithmic transformation or heterogeneous variance structures utilized when necessary to satisfy these assumptions of the linear model setting. Least squares means and measures of model fit were obtained using the lsmeans and MuMIn packages, respectively (Lenth 2016, Barton 2018). Significant differences were further investigated using Tukey-Kramer multiple comparison 95% confidence intervals (Multcomp package; Hothorn et al. 2008).

RESULTS

Mature stand structure and the impact of active management

Variability in forest structure between the active and passive management condition classes that we examined was evident in the location of stands in structure space from our principal components ordination, and in outputs from our perMANOVA analysis.

The structure of mature stands: PCA

Randomization tests recommended interpretation of PCA axes 1–3 ($P < 0.05$ in all cases), although only axes 1 and 2 were highly significant ($P < 0.01$). Variance in stand structure explained by PCA axes 1, 2, and 3 was 33%, 15%, and 10%, respectively, for a cumulative total of 58% across these axes. Overlay of structural attributes on stands in ordination space indicated few strong correlations between elements of forest structure and PCA axis 3. The following interpretation therefore focuses on axes 1 and 2 (displayed in Fig. 2).

Principal components analysis axis 1 described a gradient from stands with high total basal area, carbon storage, and SDI (the majority of which are attributable to live overstory trees), and in which standing dead wood was relatively abundant (Pearson $r < -0.7$ for total basal area, carbon storage, SDI and snag volume, among others), to stands with high stem density in the shrub, sapling and regeneration, and mid-canopy layers, and in which stumps were relatively important structural components (Table 3). Interestingly, the Shannon Index of live tree diameter class diversity (H_{DBH}) was strongly

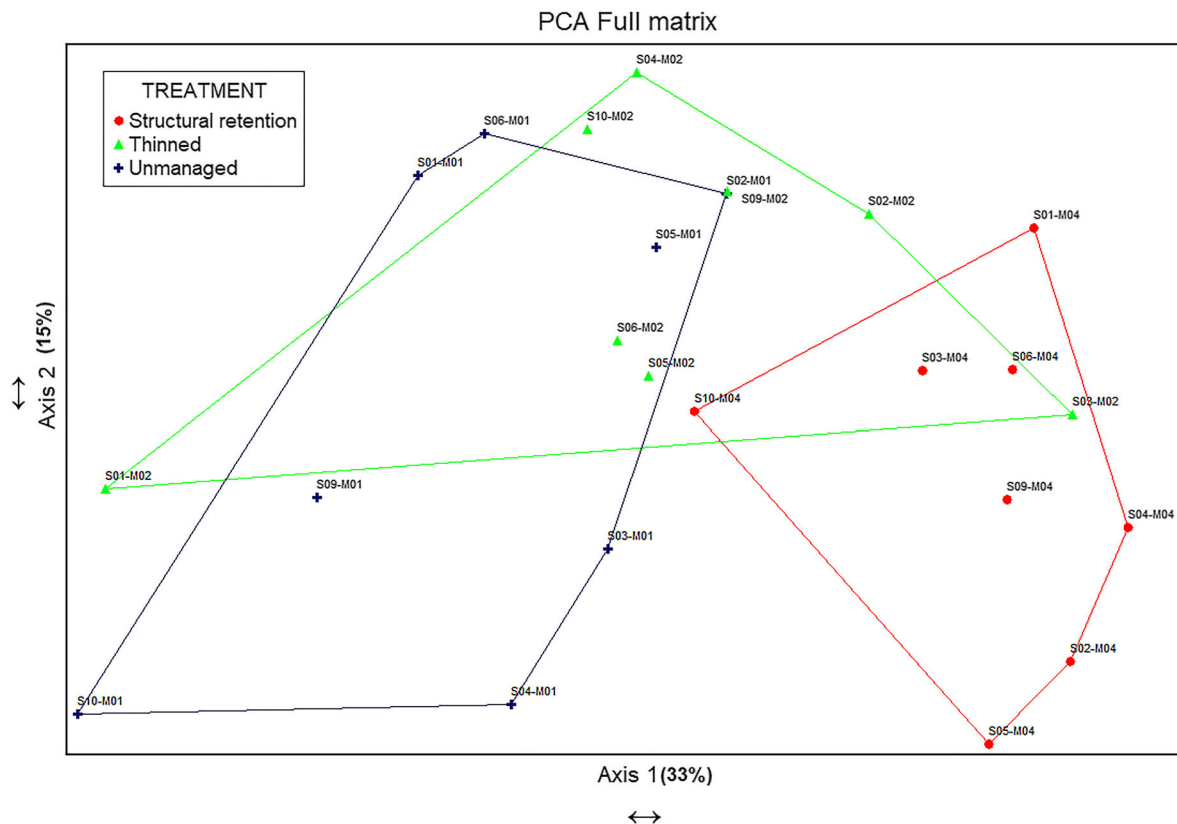


Fig. 2. Principal components analysis of the structure of 24 stands in western Oregon, subject to passive management (Unmanaged), management over extended rotations with thinning (Thinned), and retention harvesting (Structural retention). Points represent stands, and polygons enclose the perimeter of stands in each management condition examined here, when ordinated in stand structure space. Distances between points approximate the degree of similarity in aggregate structure among them.

negatively correlated with PCA axis 1 (Pearson $r = -0.87$), while the Gini coefficient for diameter equality ($Gini_{DBH}$) was moderately positively associated with this axis (Pearson $r = 0.52$). With the exception of stump volume and density, all structural elements related to dead wood were negatively correlated with axis 1. Negative correlations with respect to PCA axis 1 were also evident for the most direct indicators of vertical heterogeneity in our set of structural attributes, FHD, BPI_{CC} , and BPI_{HC} , as well as for standard deviation of tree height (SD_{Hgt}).

Negative correlations with PCA axis 2 were strongest among variables related to dead wood (Table 3), as well as total stem density (Pearson $r < -0.65$ for decay class richness, logs encountered per transect, and total stem density). Consistent with this last observation, mean tree

diameter was among the variables with the strongest positive correlation with axis 2 (Pearson $r = 0.55$). Other variables with the strongest positive correlations with PCA axis 2 include standard deviation of tree diameter and FHD (Pearson $r > 0.5$ in both cases, Table 3). The most direct indicators of vertical heterogeneity in our set of structural attributes, FHD, BPI_{CC} , and BPI_{HC} , exhibited positive correlations with PCA axis 2, as did SD_{Hgt} (Pearson r of 0.2–0.52). In general, the strength of correlation between structure variables and axis 2 was lower than that for axis 1 (Table 3), and this was particularly true for positive correlations with axis 2, the strongest of which should still only be viewed as evidence of a moderate association. Despite these modest scores, graphical overlay methods suggested that few of the observed coefficient values

Table 3. Correlations of the eight strongest associations (positive and negative) between structure variables and PCA axes 1 and 2.

Variable	Pearson correlation for PCA axis 1	Variable	Pearson correlation for PCA axis 2
Density _{STP}	0.62	SD _{DBH}	0.56
Density _{SHB}	0.59	Mean _{DBH}	0.55
Stump _{VOL}	0.54	FHD	0.52
Density _{S&R}	0.52	SD _{Hgt}	0.45
Gini _{DBH}	0.52	Density ₁₀₀	0.34
Density _{MID}	0.52	BPI _{HC}	0.29
N _{SHB}	0.43	Density ₈₀	0.24
Density _{TOTAL}	0.33	Log _{S60}	0.22
Snag _{VOL}	-0.74	LSD	-0.509
Mean _{DBH}	-0.74	HDC	-0.531
LSD ₅	-0.76	Snag _{VOL}	-0.532
LSD	-0.78	Density _{MID}	-0.537
H _{DBH}	-0.87	LSD ₅	-0.542
SDI _{TOTAL}	-0.88	Log _{S#}	-0.673
TNS _{carbon}	-0.93	Density _{TOTAL}	-0.697
BA _{TOTAL}	-0.95	N _{DC}	-0.706

Notes: FHD, foliage height diversity; PCA, principal components analysis; BPI_{HC}, Berger-Parker Index of live tree height classes; SD_{Hgt}, standard deviation of tree height; LSD, large snag density (where large refers to snags with diameter at breast height ≥ 50 cm); TNS, total non-soil (i.e. all live and dead vegetation pools).

were artifacts of complex non-linear relationships or the influence of strong outlying observations, each of which reduce the practical relevance of correlation scores.

Visual assessment of PCA outputs suggested a strong association between management condition and stands in ordination space (Fig. 2). Unmanaged stands occupied the left side of axis 1, while stands managed using structural retention harvest were clustered on the opposite end of this axis. Thinned stands spanned a wide range of scores on axis 1 but were almost entirely located on the upper half of axis 2, while unmanaged stands and, to a lesser extent, retention harvest stands occupied a broader section of axis 2. Convex hull overlays of management condition on the ordination space defined by axes 1 and 2 showed a clear separation of unmanaged and retention harvest stands based on structure (Fig. 2). Thinned stands exhibited a degree of overlap with both alternative management conditions in ordination space, but this overlap was greater for unmanaged stands than for retention harvest stands.

Active management impacts on stand structure: perMANOVA and Random Forests

PerMANOVA results were consistent with visual examination of stands in structure space (Fig. 2). Overall randomization test statistics indicated a difference in structure between stands managed using active and passive approaches (pseudo F -value = 5.127, $P < 0.001$). Pairwise comparisons suggested that the aggregate structure of unmanaged stands was significantly different from that of stands managed using a retention harvest approach, based on the 35 structural attributes included in our analysis (adjusted $P = 0.024$). Differences in aggregate structure were also apparent between thinned and retention harvest management conditions (adjusted $P = 0.0303$), but the adjusted P -value for the difference between thinned and unmanaged conditions was 0.097.

Variables with the greatest discriminatory power when classifying stands into management conditions based on structure were stump volume, the Gini coefficient of live tree diameter equality, the Berger-Parker Index of canopy classes, and the Shannon Index of live tree diameter class diversity (Fig. 3). Permutation-based omission of these variables from our Random Forests model resulted in the greatest decrease in model accuracy of the 35 structural attributes in the analysis. Each of these variables also exhibited moderately high or high absolute correlations with PCA axis 1, although none were among the most strongly associated with this axis. Other important variables in the Random Forests classification were stump density, density of saplings and regeneration, density of mid-canopy trees, and mean live tree diameter. Once again, these variables were among the most strongly associated with PCA axis 1 (stump density had the highest positive correlation with axis 1 of any variable in the dataset), and mean diameter was also moderately correlated with PCA axis 2. Total basal area, carbon storage, and SDI, variables with the strongest absolute correlation with either PCA axis, were only of moderate importance in the Random Forests model.

Development of old-growth structure in mature stands

Mature stands displayed a wide range of values for both I_{OG} and $OGHI$, from scores

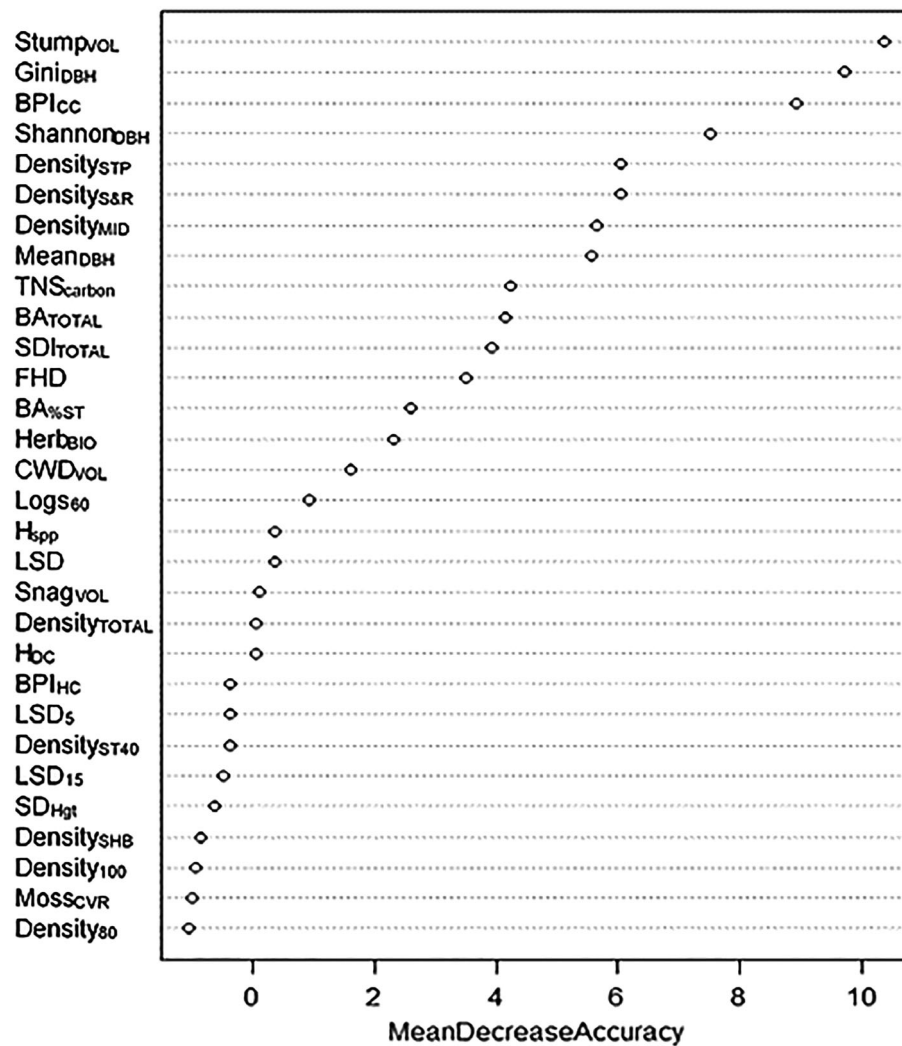


Fig. 3. Mean decrease in model accuracy for a Random Forests classification of management condition based on 35 structural variables for 24 mature stands in western Oregon.

indicative of old-growth (100 and >60, for these indices, respectively), to scores more comparable with younger stands. Four stands scored 100 on the I_{OG} and another eight scored ≥ 80 for this index (Table 4). Mean values of I_{OG} for unmanaged, thinned, and retention harvest management conditions were 82 (range: 55–100), 76 (range: 46–100), and 47 (range: 11–98), respectively, with the difference between unmanaged and retention harvest stands being statistically significant (difference in means of 22.63, 95% confidence interval of 5.53–39.72; Fig. 4). Mean OGHl was also significantly higher for unmanaged stands than stands managed using a

retention harvest approach (difference in means of 34.5, Tukey-Kramer 95% confidence interval of 6.07–62.93). Scores on the OGHl for unmanaged mature stands varied from 29 (a value more indicative of conditions in young stands) to 78 (a score associated with old-growth stands in the sample used to develop the OGHl), while those for retention harvest stands ranged from 18 to 48 (Table 5). Thinned stands, as a group, were not different from either alternative management condition with respect to the OGHl (Fig. 4), although the comparison between thinned and retention harvest conditions approached significance (difference in means of 28.88, Tukey-Kramer 95%

Table 4. Scores for 24 mature stands in western Oregon for the Index of Old-Growth (Acker et al. 1998), with accompanying statistics from mature stands sampled in this publication.

Stand	I _{OG} scores				
	SD of tree dbh	Density PSME ≥100 cm dbh	Mean tree dbh (cm)	Density of all trees (no. ha ⁻¹)	I _{OG} score
Unmanaged					
S01-M01	36.73	20.0	71.9	185	100
S02-M01	25.12	10.0	56.34	273	79
S03-M01	16.81	0.0	48.06	495	53
S04-M01	18.95	2.5	45.73	548	55
S05-M01	24.68	20.0	54.6	345	90
S06-M01	36.24	22.5	58.37	328	100
S09-M01	31.48	10.0	48.4	398	87
S10-M01	27.26	20.0	55.61	523	90
Mean	27.16	13.13	54.88	387	82
Thinned					
S01-M02	30.24	22.5	52.33	753	82
S02-M02	15.98	0.0	54.3	205	54
S03-M02	22.86	0.0	30.33	748	46
S04-M02	33.67	22.5	57.68	318	100
S05-M02	24.62	0.0	45.66	580	59
S06-M02	28.59	12.5	48.72	460	86
S09-M02	28.37	10.0	48.71	463	82
S10-M02	35.73	20.0	57.51	390	100
Mean	27.51	10.94	49.41	489	76
Retention harvest					
S01-M04	33.61	5.0	26.86	548	39
S02-M04	23.38	7.5	18.44	838	28
S03-M04	30.64	7.5	47.03	333	83
S04-M04	19.79	0.0	15.96	640	24
S05-M04	17.11	5.0	15.96	2318	11
S06-M04	28.98	5.0	29.85	645	64
S09-M04	28.58	7.5	21.56	933	31
S10-M04	33.52	17.5	44.25	385	98
Mean	26.95	6.88	27.49	830	47
Mature stand mean (Acker et al. 1998)	17	0.6	42	373	54

Notes: The I_{OG} developed in unmanaged Douglas-fir forests regenerating following natural disturbance, can take values between 0 and 100. Scores of 0 indicate structural conditions typical of young stands (40–80 yr of age), while scores of 100 indicate conditions typical of old-growth (>200 yr of age).

confidence interval of -0.37 to 58.13). OGH scores for thinned stand were even more variable than unmanaged or retention harvest stands, with a range from 22 to 79 (Table 5).

Management condition was also associated with four of the eight ancillary variables selected as representative of old-growth structure in temperate forests, including both FHD and BPI_{CC} (Table 6, Fig. 4). Mean FHD was significantly greater in our thinned condition than either unmanaged or retention harvest conditions (F -test $P = 0.0182$) but did not differ between these last management conditions (Fig. 4). Mean

BPI_{CC} was higher in unmanaged and thinned stands than in retention harvest stands (F -test $P = 0.0002$), but values for this index did not differ between unmanaged and thinned management conditions (Fig. 4). By contrast, density of saplings and regeneration was positively associated with active management (F -test $P = 0.0009$); median sapling and regeneration stem densities were 16 times higher in retention harvest stands than in unmanaged stands (95% confidence interval of 4–62 times higher) and were 5 times higher in thinned than unmanaged stands (95% confidence interval of 1–21 times higher; Fig. 5).

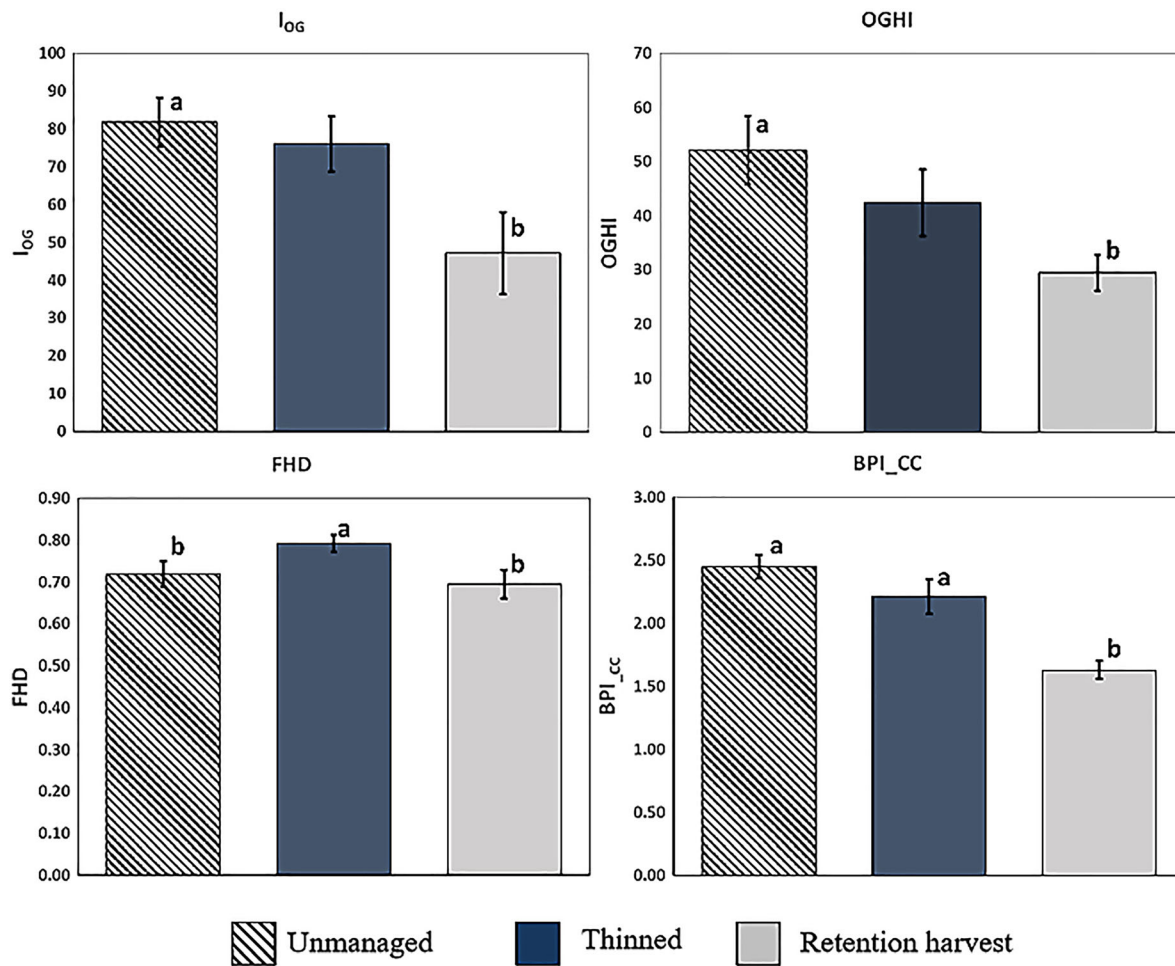


Fig. 4. Differences in mean scores for two old-growth indices, and two measures of vertical complexity, for alternate management conditions in mature Douglas-fir forests in western Oregon. Error bars represent one standard error of the mean, and letters indicate significant differences between management conditions against an $\alpha = 0.05$.

Neither shrub density nor shrub species richness differed significantly among management conditions (Fig. 5), although absolute scores for mean shrub density in retention harvest stands were almost double that of thinned stands, which, in turn, exhibited much higher mean shrub density than unmanaged stands.

DISCUSSION

Our results support the role of active management as a driver of long-term differences in stand structure (Siitonen et al. 2000, Janowiak et al. 2008, Young et al. 2017). The multivariate analyses we employed illustrate major differences in

foliage distribution between canopy layers that may result from alternative management regimes. Alongside stumps—structural elements that are often overlooked in analyses of forest structure—indices of heterogeneity in stem diameter and canopy classes, which reflect these differences in foliage distribution, emerged as the most significant drivers of variability in overall stand structure between management conditions. Divergent stand structure between management conditions did not materialize as significant differences in progress toward old-growth structure between unmanaged and thinned stands, as expressed via the I_{OG} and OGHI. We did, however, note significant differences in understory

Table 5. Scores of 24 mature stands in western Oregon for the Old-Growth Habitat Index (Franklin et al. 2005), with accompanying statistics from mature stands sampled in this publication.

Stand	OGHI scores				
	Density of trees ≥100 cm dbh (no. ha ⁻¹)	Density of snags ≥50 cm dbh and ≥15 m height (no. ha ⁻¹)	Log volume (m ³ /ha)	Diameter density index	OGHI score
Unmanaged					
S01-M01	75	0	68.47	76.34	55
S02-M01	31	0	35.50	67.00	33
S03-M01	0	10	53.27	54.58	29
S04-M01	8	60	64.41	60.69	48
S05-M01	58	10	36.94	81.96	47
S06-M01	64	0	60.37	75.81	50
S09-M01	69	90	54.60	96.85	78
S10-M01	58	100	62.62	86.37	77
Mean	45	34	54.52	74.95	52
Thinned					
S01-M02	64	95	65.91	92.14	79
S02-M02	0	0	57.32	51.70	27
S03-M02	0	0	51.20	38.75	22
S04-M02	64	20	23.63	82.16	47
S05-M02	0	40	43.47	60.00	36
S06-M02	39	30	50.93	76.33	49
S09-M02	39	0	28.33	77.35	36
S10-M02	58	0	31.20	83.99	43
Mean	33	23	44.00	70.30	43
Retention harvest					
S01-M04	16	20	7.77	30.58	18
S02-M04	23	30	54.26	30.09	34
S03-M04	23	20	39.30	42.45	31
S04-M04	0	0	50.72	27.87	20
S05-M04	16	10	51.63	36.97	29
S06-M04	16	20	30.90	32.30	25
S09-M04	31	0	56.23	38.03	31
S10-M04	53	20	51.27	67.44	48
Mean	22	15	42.76	38.22	30
Mature stand mean (Franklin et al. 2005)	11	35	50.93	58.62	39

Notes: OGHI can take values of 0–100. Lower scores indicate greater dissimilarity compared to the structure of old-growth forests (with most old-growth stands used in development of the OGHI scoring >60 on the index).

development, foliage height diversity, and dead wood characteristics between these management conditions. Moreover, our results suggest that in mature stands managed using a high-intensity harvest regime, a large stump population may help mitigate some of the ecological consequences of conventional active management on dead wood supplies.

The structure of mature stands and the impact of active management

Two to four decades following overstory density reduction, the aggregate structure of stands

managed using a retention harvest approach differed markedly from that of unmanaged stands, resulting in clear separation of these management conditions along axis 1 in our PCA. This axis loosely represented a gradient in harvest intensity, unmanaged stands on one side exhibiting high total basal area, carbon storage and SDI, and retention harvest stands, exhibiting high density of understory vegetation and stumps, but low overstory density, on the other. Consistent with this interpretation, thinned stands—as a group—were positioned between unmanaged and retention harvest stands along PCA axis 1,

Table 6. Linear model outputs for a test of differences in 10 structural variables between unmanaged, thinned, and retention harvest management conditions.

Variable	Unmanaged (mean \pm SE)	Thinned (mean \pm SE)	Retention harvest (mean \pm SE)	F-statistic	P-value	Marginal R^2	Conditional R^2	RMSE
I _{OG}	81.8 \pm 6.5	76.1 \pm 7.3	47.2 \pm 10.9	4.046	0.041	0.410	0.528	21.336
OGHI	52.1 \pm 6.3	42.4 \pm 6.2	29.5 \pm 3.3	4.843	0.025	0.274	0.350	13.748
Density _{ST40}	22.6 \pm 9.3	10.4 \pm 3.0	8.0 \pm 4.2	1.641	0.230	0.125	0.125	16.209
FHD	0.72 \pm 0.03	0.79 \pm 0.02	0.70 \pm 0.03	5.403	0.018	0.211	0.550	0.065
BPI _{CC}	2.45 \pm 0.09	2.21 \pm 0.14	1.63 \pm 0.07	16.762	<0.001	0.593	0.593	0.274
N _{SHB}	2.39 \pm 0.46	2.59 \pm 0.32	2.66 \pm 0.42	0.234	0.795	0.011	0.473	0.893
Density _{S&R}	476 \pm 286	1593 \pm 567	4500 \pm 1991	12.139	<0.001	0.424	0.580	1.132
Density _{SHB}	3866 \pm 888	5438 \pm 1014	9649 \pm 3400	2.252	0.142	0.149	0.241	5315
N _{DC}	4.19 \pm 0.16	3.91 \pm 0.15	4.06 \pm 0.23	0.601	0.562	0.050	0.050	0.481
H _{DC}	1.23 \pm 0.04	1.08 \pm 0.05	1.19 \pm 0.05	2.913	0.088	0.201	0.206	0.125

Notes: BPI_{CC}, Berger-Parker Index of canopy classes; FHD, foliage height diversity; SE, standard error; OGHI, Old-Growth Habitat Index; RMSE, root mean square error.

although were associated with regions of lower structural diversity among dead wood attributes than either alternative management condition. Similar relationships between stand structure and harvest intensity have been found in managed older forests elsewhere, with higher-intensity disturbances resulting in structures bearing progressively less resemblance to unmanaged stands (Gronewold et al. 2010). However, while unmanaged old-growth forests are widely regarded as structurally complex (Franklin and Van Pelt 2004, Keeton et al. 2007, Bauhus et al. 2009), departure (among actively managed stands) from the structural conditions found in our unmanaged mature stands was not an indicator of lower levels of complexity, but of different forms of it.

The different forms of structural complexity exhibited by stands in the three management conditions that we examined are exemplified by variability in foliage distribution among the understory, mid-canopy, and overstory. Overstory trees are an important driver of complexity in old-growth forests (Chen et al. 2004, North et al. 2004) and were particularly central to the structure of unmanaged stands in our dataset. Unmanaged stands were associated with the highest scores for Shannon's Index of diameter class diversity (H_{DBH}) and also the Berger-Parker Index of canopy classes (BPI_{CC}), potentially because the absence of management preserved existing natural variability in overstory tree characteristics. However, while unmanaged stands

were also associated with higher density of live trees in the largest diameter classes than retention harvest stands, large live trees were a poor discriminator of management condition. This is likely because much of the live retention in retention harvest stands was among the largest diameter classes. In contrast to unmanaged stands, retention harvest stands were associated with high densities of mid-canopy and understory trees, saplings and regeneration, and shrubs. Greater understory development in our retention harvest stands is consistent with increased growth of planted seedlings (Palik et al. 2014), and shrubs (Aubry et al. 2009), in stands managed using variable retention harvest, compared to untreated stands. As a result of the pronounced size difference between the matrix of understory vegetation in our retention harvest stands, and the large residual overstory trees, retention harvest stands were associated with maximum size inequality, as measured by the Gini coefficient of stem diameter ($Gini_{DBH}$). $Gini_{DBH}$, and the aforementioned indices associated with unmanaged stands, H_{DBH} , and BPI_{CC}, were among the most important variables in our Random Forests classification of stands by management condition. Thus, although previous analyses have often compared the relative merits of several of these indicators of complexity (Peck et al. 2014, Del Río et al. 2016), each yielded valuable perspectives on the complexity of live vegetation in our managed and unmanaged mature stands.

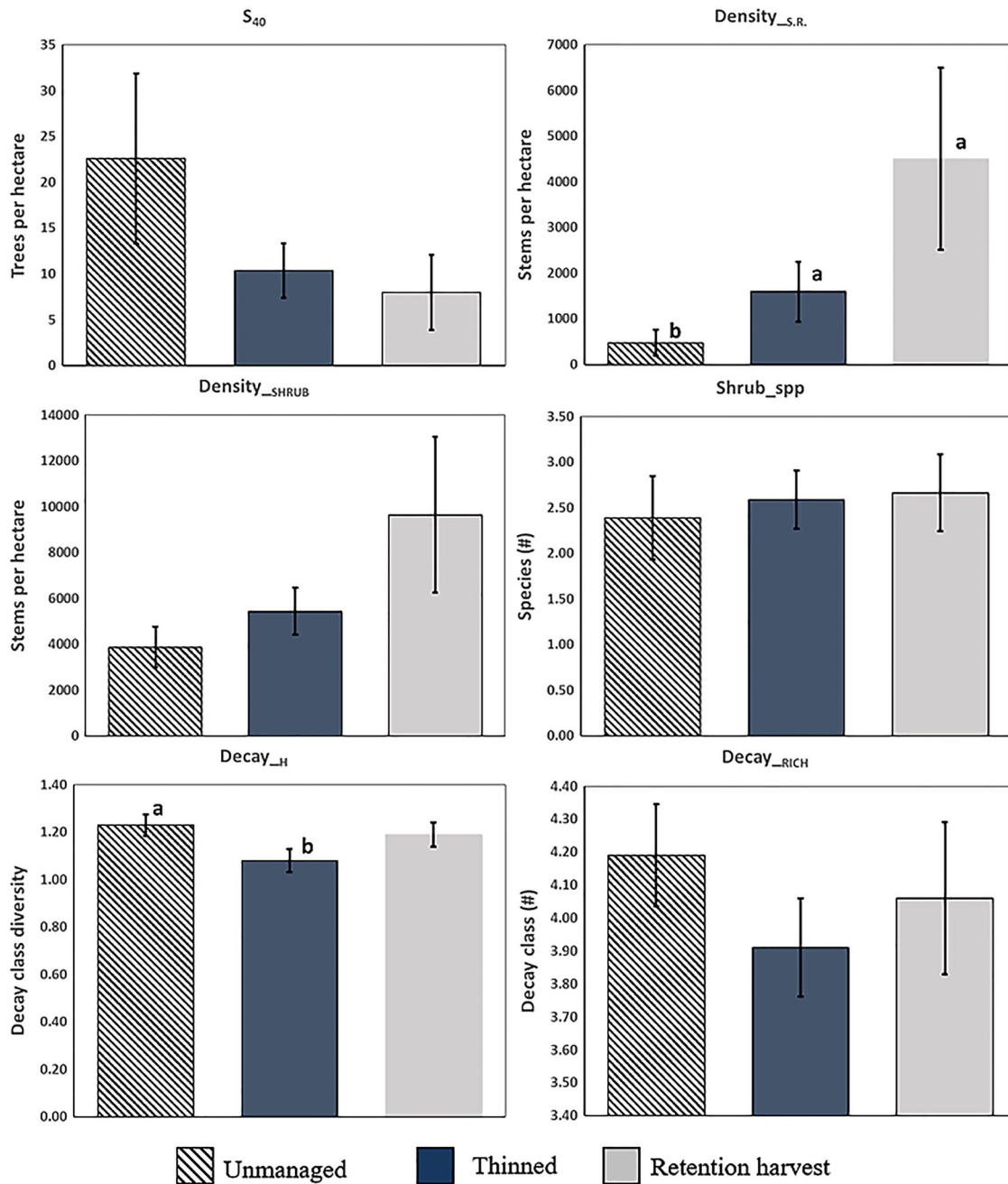


Fig. 5. Differences in mean scores for six attributes of stand structure, between alternate management conditions in mature Douglas-fir forests in western Oregon. Error bars represent one standard error of the mean, and letters indicate significant differences between management conditions against an $\alpha = 0.05$.

Dead wood characteristics are frequently cited among the primary differentiators of actively managed and unmanaged stands (Hansen et al. 1991, Franklin et al. 2007, Silver et al. 2013), but

while many analyses focus on snag and log availability, differences in the stump pool were more important discriminators of management condition in our mature stands. Previous work in

temperate forests of Southern and Eastern Europe has revealed elevated stump volume and density in older stands managed using a selection system, compared to unmanaged stands (Burrascano et al. 2008, Keren and Diaci 2018). The correlation we observed between high stump volume and density, and the location of retention harvest stands in ordination space, is consistent with these findings and indicates that large Douglas-fir stumps remain significant structural elements in mature stands managed using retention harvest two to four decades following treatment. Indeed, the persistence of large stumps in retention harvest stands, and their relative absence from unmanaged stands, was such that stump characteristics contributed more to the discriminatory power of our Random Forests model than did any other structural element.

The development of old-growth structure in mature stands

Overall rates of structural development in our mature stands were largely consistent with classic models of succession following stand-replacing disturbance and were not significantly affected by active management using thinning. Mean scores on the Index of Old-Growth (I_{OG} ; Acker et al. 1998) for unmanaged and thinned management conditions were approximately 75% of that expected for old-growth and are comparable with scores from the sample of 140-yr-old mature Douglas-fir stands studied by Acker et al. (1998). Quantifying progress toward old-growth structure using the Old-Growth Habitat Index (OGHI; Franklin et al. 2005) yielded similar conclusions despite the different constitution of this index; mean scores on the OGHI for unmanaged and thinned management conditions were 87% and 71%, respectively, of the minimum scores from old-growth stands in the moist temperate forests of Washington, in which this index was developed (Franklin et al. 2005). Given mean stand ages of 150 and 144 yr for our unmanaged and thinned conditions, respectively, it is not unreasonable to expect that overall scores on the OGHI and I_{OG} will exceed the thresholds for classification as old-growth on these indices within the next 100 yr. This time-frame accords with the emergence of old-growth characteristics, and transition to the vertical

diversification stage of stand development, in models of succession following stand-replacing fire in low- to moderate-elevation Douglas-fir forests (Spies and Franklin 1988, Franklin et al. 2002).

By contrast, I_{OG} and OGHI scores for our retention harvest stands imply structural conditions more akin to those present following moderate- to high-severity fire in Douglas-fir forests. Although most retention harvest stand scores were significantly lower than expected for old-growth forest, application of the I_{OG} and OGHI revealed a more prominent role for residual live trees than was the case in the young unmanaged stands, originating following high-severity fire, studied by Acker et al. (1998) and Franklin et al. (2005). Levels of overstory retention not dissimilar to that in our retention harvest management condition are thought to promote structural complexity in the regenerating stand (Zenner 2000, 2005), and this is likely to be particularly true when residual trees include shade-tolerant associates (Keeton and Franklin 2005), such as those in stand S10-M04 (our highest-scoring retention harvest stand on both old-growth indices). The modest amount of residual overstory present in our retention harvest stands may, therefore, result in greater structural heterogeneity by the time the present understory cohort reaches 80–100 yr of age than would be true in the absence of live structural retention (Tappeiner et al. 1997). Recovery following moderate-severity fire is now understood to be a relatively common stand development pathway in the moist low- to moderate-elevation forests of western Oregon (Poage et al. 2009, Tepley et al. 2013), and the mosaic of live overstory retention and patchy pre-forest vegetation of our retention harvest stands may be analogous to the early phase of this development trajectory.

In addition to these differences in progress toward old-growth structure between management conditions, which revealed using the I_{OG} and OGHI, analysis of individual old-growth elements revealed three important trends to complement our multivariate analysis of stand structure: (1) depletion of dead wood in thinned stands, and the potential ability of retained stumps to mitigate some of the ecological consequences of this depletion; (2) greater understory development in actively managed stands,

relative to unmanaged stands; and (3) higher vertical foliage diversity in thinned stands than either alternative management condition.

High standing and down wood volumes are characteristic of old-growth forests (Spies et al. 1988, Burrascano et al. 2013, Freund et al. 2015), and, consistent with a growing body of literature, our results suggest that conventional harvest operations may reduce dead wood availability in older managed stands. Dead wood is a critical resource for forest wildlife (Nelson 1989, Goodburn and Lorimer 1998), plays an important role in nutrient cycling (Harmon et al. 1986), and is a preferred regeneration site for many species of tree and shrub (Harmon and Franklin 1989, D'Amato et al. 2015). Prior research in older forests has highlighted the potential for long-term disruption to dead wood recruitment and accumulation as a result of active management (Duvall and Grigal 1999, Debeljak 2006, Silver et al. 2013). Thinned stands were associated with low snag and down wood availability, relative to unmanaged stands, in our PCA analysis, and this result was reflected in significantly lower dead wood decay class diversity in thinned than unmanaged stands, and lower absolute decay class richness in thinned stands than either alternative management condition. Together, these results indicate an impoverished dead wood pool in thinned stands and imply that even a single thinning entry in mature stands may have longer-term consequences for the continuity of dead wood supply.

Stands managed using a retention harvest approach exhibited similarly low snag and down wood volume to thinned stands, but unlike the latter, also possessed a large population of stumps two to four decades following harvest. The majority of our retention harvest stands were originally planned as conventional shelterwood treatments, and the shelterwood cut in most stands was implemented before dead wood retention during regeneration harvest became common (as a result of best practice guidance and regulation; e.g., FSC-US 2010; ODF 2018). Our estimates of medium-term dead wood availability in retention harvest stands, therefore, likely represent the lower range of potential dead wood availability at a similar point in time following application of current best practice for retention harvesting in mature stands in the

Douglas-fir region (Franklin et al. 2002, Franklin and Johnson 2012, Gustafsson et al. 2012). Despite this, our findings indicate that the presence of a large stump population in actively managed older stands may help mitigate some of the ecological effects of unavoidable harvest-related reductions in dead wood supplies. Decay characteristics provide an insight into the potential ecological functioning of a dead wood structure at a given instant in time (Harmon et al. 1986, Keren and Diaci 2018). Our retention harvest stands exhibited lower snag and log biomass than unmanaged stands (Williams and Powers 2019), but comparable dead wood decay class diversity and richness due to the compensatory effect of a large stump population. Our results, therefore, imply the potential for a degree of functional substitution by stumps in retention harvest stands with respect to other dead wood structures in unmanaged stands (although we recognize that differences in decay rates between stumps and snags, in particular, will influence temporal trends in decay class diversity in stands with different allocations of dead wood between pools). Size, dimensions, and habit are integral to the functional capacity of dead wood (Bunnell and Houde 2010, Hjältén et al. 2010, Vítková et al. 2018). Although certain species associated with snags will also utilize stumps (as defined in this study to be <1.37 m in height) to derive key resources (Mannan et al. 1980, Vonhof and Barclay 1997), others including cavity-nesting vertebrates, saproxylic invertebrates, and lichens will not or will use them for different purposes than snags (Bull and Holthausen 1993, Onodera et al. 2017, Santaniello et al. 2017). Any functional substitution of stumps for other dead wood structures is likely to be most pertinent to large down logs, although it is necessary to recognize that the original vertical orientation of logs may have legacy effects on the invertebrate, fungal, and bryophyte communities for which the dead wood acts as host. Thus, while there is overlap between stump and log habitat functions, these structures also appear to support unique flora and fauna (Gustafsson et al. 2010, Brin et al. 2013, Tullus et al. 2018). Moreover, the extent to which stumps may function in a similar capacity to logs is likely to be magnified in the forests of the Pacific Northwest region of North America, where overstory trees in mature stands

frequently exceed 1 m dbh (Williams and Powers 2019); in stands sampled for this research, the upper and/or basal diameters of stumps regularly measured between one and two meters. Such large stumps have been associated with use by a variety of wildlife species in the forests of the Pacific Northwest, although the smaller stumps in interior temperate conifer and boreal forests of western North America appear to receive less use (Bunnell and Houde 2010). In the western hemlock zone, in which our stands are located, the ability of large stumps to function similarly to large logs may also be consequential to the development of old-growth structure; large logs are a preferred regeneration site for shade-tolerant western hemlock and numerous shrub species (Harmon and Franklin 1989, Huffman et al. 1994), and anecdotal observations from our stands confirm similar utilization of stumps by these species. Thus, our results imply that a large stump population, in actively managed stands, may provide a degree of functional substitution, with respect to the role of down wood, but it is equally apparent that the extent to which this substitution occurs will vary by forest type. Our findings therefore point to the need for further research on the function of stumps in forest stands, and the sensitivity of this functionality to differences in down wood availability.

Previous research in Douglas-fir forests has established the potential of active management as a tool for promoting understory development, and our results are broadly supportive of the use of overstory density reduction in this capacity. The presence of a sapling and regeneration layer in old-growth Douglas-fir forests contributes to live tree diameter distributions that may approach a reverse J-shape (Zenner 2005), despite the high leaf area carried by overstory and mid-canopy trees in many older western coniferous forests (Van Pelt and Franklin 2000, North et al. 2004). Greater sapling and regeneration density in our thinned management condition than in unmanaged stands is consistent with the idea that overstory density reduction stimulates this component of old-growth structure, and also agrees with previous work on the effects of thinning on regeneration, saplings, and understory tree development in young to mature Douglas-fir forests (Bailey and Tappeiner 1998, Shatford et al. 2009). Moreover, the differences in sapling

and regeneration density between management conditions, that we observed, were matched by trends in absolute density of mid-canopy trees in our dataset and in other temperate forests in the Pacific Northwest (Comfort et al. 2010). Although reduced resource pre-emption as a result of overstory density reduction may contribute to understory development in thinned stands (Reich et al. 2012), increased seed production has also been observed among large Douglas-fir trees following thinning (Reukema 1982). Similar effects on flower and seed production in the shrub layer of thinned Douglas-fir stands have been noted in the Pacific Northwest (Wender et al. 2004), and the development of several common shrub species with clonal growth habits also appears to benefit from overstory density reduction, potentially as a result of the associated soil disturbance (Tappeiner and Zasada 1993, O'Dea et al. 1995). Higher absolute shrub density in our thinned management condition, than in unmanaged stands, is consistent with these potential drivers of shrub development, and also with the trend toward greater shrub cover and diversity in thinned than unmanaged Douglas-fir forests reported previously from western Oregon (Bailey and Tappeiner 1998, Chan et al. 2006). Thus, in an overall sense, our results support the role of low- to moderate-intensity overstory density reduction in hastening the re-establishment of understory complexity in mature stands.

Understory and mid-canopy vegetation contributes to the vertical complexity typical of many old-growth forests in western North America (Franklin et al. 2002, Van Pelt and Nadkarni 2004), and greater development of these canopy layers in thinned than unmanaged stands in our mature stands may underlie the elevated FHD that we observed for this management condition. Few previous studies have examined the impact of management on canopy layering using direct, field-based observations of foliage structure. Higher mean FHD in our thinned management condition than in unmanaged stands indicates that, on average, these stands exhibited a more continuous distribution of foliage from forest floor to upper canopy. In young Douglas-fir forests, thinning may increase vertical foliage continuity by delaying crown recession (Chan et al. 2006), while epicormic branching may similarly deepen the crowns of older Douglas-fir trees

surrounding canopy gaps (Ishii and McDowell 2002, Ishii et al. 2004). An alternative explanation for the elevated FHD in thinned stands in our dataset, and one that is better supported by our structural data, is the presence of a denser understory and mid-canopy. Unmanaged and thinned stands exhibited similar values for BPI_{CC} , a ratio of total stem density to stem density in the most common canopy class, despite the tendency for thinning from below to preferentially remove trees in the suppressed and intermediate canopy classes. Higher stem density among understory/mid-canopy trees (classed here as those with $dbh \geq 5 \text{ cm} < 25 \text{ cm}$) in thinned stands could mitigate the effect of this removal of suppressed overstory trees on BPI_{CC} , while higher stem density among saplings, regeneration, and shrubs (vegetation that is not incorporated into BPI_{CC} but is included in visual FHD measurements) would boost FHD scores for thinned stands. Although the elevated FHD scores for thinned stands than other management conditions are illustrative of a vertical canopy profile in which foliage is less concentrated in a single height band, we recognize that FHD does not provide a complete measure of vertical foliage heterogeneity. Continuity in foliage from forest floor to upper canopy is assumed to facilitate niche differentiation and thereby contribute toward a more diverse forest biota (Ishii et al. 2004). However, the foraging strategy of certain mature forest species requires openings within the canopy (Herter et al. 2002; <https://birdsna.org/Species-Account/bna/home>), suggesting that a balance between continuity of foliage, and the presence of gaps, may be desirable. None of the indices of foliage structure examined here provide a measure of the relative gapiness, vs. continuity, in foliage distribution. However, more detailed methods of assessing foliage distribution do exist (Van Pelt et al. 2016) and may be appropriate in situations in which a more complete picture of canopy structure is required.

Although the variables used to characterize progress toward old-growth structure in this analysis were chosen based on the findings of previous research in temperate forests (Spies and Franklin 1991, McElhinny et al. 2005, Burrascano et al. 2008), the analysis presented here could be complemented by more explicit consideration of the horizontal variability that is characteristic of

old-growth forests (Bormann and Likens 1979, Franklin et al. 2002). Fine-scale horizontal variability is incorporated into our analysis through a number of proxy variables, such as the standard deviation of stem diameter, but we did not include any estimates of larger-scale variability. Future work on structural development in mature stands could attempt to assess such variability by (1) evaluating attributes directly associated with horizontal heterogeneity (e.g., canopy gap sizes, Spies et al. 1990) or (2) employing considerably larger sample plots, or achieving much greater sample coverage within stands (Gray 2003, Sensenig et al. 2013). Further research on the structure of late-successional temperate forests, particularly those in the western hemlock zone, may also benefit from assessing the correlations between structural variables that we report (Appendix S4). Our analysis included variables associated with a wide range of structural components. While this variety adds to the value of exploratory studies, we noted a number of instances in which variables representing similar structural attributes exhibited high correlation and similar locations in stand structure space for our PCA. The most notable examples are total carbon storage, total SDI, and total basal area. However, we caution against variable selection purely based on the results of our multivariate analysis and correlation scores, without also considering differences in ecological functioning and circumstances in which the associations between variables reported in this analysis would not apply.

The retrospective analysis of management impacts on mature stand structure, presented here, provides information for immediate use, but does not lessen the value of further research on mature stand structure in controlled, experimental settings. Structurally complex old-growth forests are an object of interest in social (Kohm and Franklin 1997, O'Hara 2014), management (Bauhus et al. 2009, Fahey et al. 2018), and policy contexts (USDA and USDI 1994), but widespread disruption to natural disturbance regimes and other global change phenomena (Dale et al. 2001, Millar and Stephenson 2015, Trumbore et al. 2015) may influence the extent to which contemporary mature forests will, in future, resemble today's old-growth (Keeton et al. 2012, Sensenig et al. 2013). Experimental research on

the structure of mature stands developing today can help address this uncertainty and overcome a number of limitations inherent in retrospective analyses. In the case of the analysis presented here, these limitations include the likelihood that stands were not selected for treatment in an entirely random fashion. In the topographically complex terrain of the Cascade and Coast Ranges, of Oregon, accessibility and logistical concerns are likely to have influenced treatment layout. However, without pre-treatment structural baselines, it is not possible to rule out pre-existing differences in stand structure. It is notable that any deterministic assignment of management treatments to stands, based on structure, would almost certainly have favored stands with a high stem density for thinning. As such stands are less likely exhibit a well-developed understory (Bailey and Tappeiner 1998, Hagar 2003, Cole and Newton 2009), this influence would tend to reinforce our observations concerning the role of thinning in stimulating understory development. Conversely, any deterministic assignment of shelterwood treatments to stands (in our retention harvest condition) is likely to have favored exposed sites subject to harsher conditions where regeneration establishment would benefit from the ameliorated environment generated by the residual shelterwood trees (Ashton and Kelty 2018). On such exposed sites, the large live trees retained during harvest are likely to have been selected for the same size and canopy features that also rendered them important contributors to overall stand complexity in our retention harvest management condition. Essential site characteristics for each of the stands included in our analysis are presented in Tables 1 and 2, and provide useful context for the interpretation of our findings.

This information on site characteristics also highlights a degree of variability in site conditions between stands within treatment blocks, an inevitable consequence of the randomization built into our site selection process, and the spatial distribution of treated stands meeting our site selection criteria. Although such differences are random with respect to treatment, and unlikely to influence the overall trends in structure identified here, there are instances in which such differences in site conditions may influence certain within-block structural trends. An example

of this is in Block 1, in which our retention harvest stand was located on a drier site than the unmanaged and thinned stands, and exhibited some differences in herb and shrub composition as a result.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Two to five decades following treatment, the imprint of overstory density reduction on the aggregate structure of our mature stands remains evident. Overstory trees are the characteristic feature of the mature phase of stand development and contributed to different forms of complexity in the management conditions that we examined. Variability in overstory tree diameters and crown classes contributed to structural heterogeneity in unmanaged stands. Retention harvest stands, meanwhile, were characterized by the sharp contrast in diameter between large residual overstory trees, and complex understory mosaics comprising smaller trees, saplings, and shrubs. Understory and mid-canopy vegetation was also more prominent in thinned stands than those with no previous history of active management, and, when combined with a higher density of overstory trees than in retention harvest stands, contributed to greater vertical foliage continuity than in either unmanaged or retention harvest alternative management conditions. However, our findings suggest that the development of other structural features associated with old-growth forests, such as dead wood, may be negatively impacted by active management. Thus managers using silvicultural treatments to accelerate the development of vertical complexity should also consider strategies for dead wood creation and recruitment such as topping, girdling, or intentional wounding of live trees to produce snags and high stumps (Lewis 1998, Maguire and Chambers 2005, Vítková et al. 2018), or pulling over live trees to produce coarse woody debris and tip-up structures (Keeton 2006).

The differences in stand structure and progress toward old-growth conditions that we observed have implications for the management of contemporary, even-aged mature stands. On average, our unmanaged mature stands displayed limited canopy layering and a sparse understory.

In such stands, our results are consistent with the idea that low- to moderate-intensity overstory density reduction may stimulate understory and mid-canopy development, and increase vertical foliage continuity (Bailey and Tappeiner 1998, Latta and Montgomery 2004, Shatford et al. 2009, Comfort et al. 2010, Cole et al. 2017). However, in common with many previous studies, our findings also imply a need to implement specific provisions for the retention or creation of dead wood during harvesting operations, in order to avoid depletion of this critical ecological resource (Sippola et al. 1998, Gibb et al. 2005, Fassnacht and Steele 2016). The decay characteristics and size of stumps present in our retention harvest stands, two to four decades following harvest, suggest that management over extended rotations may provide opportunities for a degree of functional substitution by stumps, with respect to down woody debris, as a result of the greater basal dimensions of mature trees. This compensatory effect of stumps may complement intentional snag and down wood creation as a means of sustaining dead wood functions in actively managed stands over the decades following harvest (Keren and Diaci 2018).

Our findings concerning the impact of active management on the structure of mature stands are also relevant to the management of the large areas of younger forest currently regenerating following extensive clearcutting in many temperate and boreal regions during the latter half of the 20th century. The differences in understory development and vertical complexity between mature unmanaged and thinned stands that we observed imply that young Douglas-fir/western hemlock stands in the Pacific Northwest may require extended periods to develop vertical complexity in the absence of gap-generating disturbances during the mature phase or earlier. Our results support findings from other studies that suggest thinning younger stands prior to, and potentially during the mature phase, promotes recruitment of understory and midstory trees into midstory and overstory positions, thereby helping accelerate structural development beyond that of the simplified mature stands common in our dataset (Andrews et al. 2005, Kuehne et al. 2015, Willis et al. 2018).

Considerable structural diversity was also evident when comparing stands within each of the

management conditions that we examined, and this diversity cautions against blanket application of any single management strategy, even to stands in the same age class and forest type, and when enhancing structural complexity is a primary management objective. While some unmanaged stands in our dataset exhibited limited structural diversity, others displayed a complex structure and would be inappropriate targets for overstory density reduction. Thus, the extent to which active management is appropriate will vary from stand to stand, based on existing stand structure. Utilizing a broad range of structural variables during stand inventory, as demonstrated here, is a first step in evaluating the appropriateness of active management for old-growth structure.

ACKNOWLEDGMENTS

The authors would like to thank a great many employees of the Willamette National Forest and the Oregon Bureau of Land Management for their assistance during the stand selection process, in particular Cheryl Friesen (USDA FS), and Kenneth Ruzicka Jr and Dan Couch (Oregon BLM). We also thank Drs Joan Hagar and John Tappeiner, and two anonymous reviewers, for their constructive feedback on earlier drafts of this manuscript. This work was supported by fellowship funding provided by the Oregon State University (OSU) Graduate School; the OSU College of Forestry; and the OSU Department of Forest Engineering, Resources and Management.

LITERATURE CITED

- Acker, S. A., T. E. Sabin, L. M. Ganio, and W. A. McKee. 1998. Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands. *Forest Ecology and Management* 104:265–280.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.
- Andrews, L. S., J. P. Perkins, J. A. Thraillkill, N. J. Poage, and J. C. Tappeiner II. 2005. Silvicultural approaches to develop northern spotted owl nesting sites, central Coast Ranges, Oregon. *Western Journal of Applied Forestry* 20:13–27.
- Ares, A., et al. 2007. The Fall River Long-Term Site Productivity study in coastal Washington: site characteristics, methods, and biomass and carbon and nitrogen stores before and after harvest. PNW-

- GTR-691. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Ashton, M. S., and M. J. Kely. 2018. The practice of silviculture: applied forest ecology. Wiley & Sons, New York, New York, USA.
- Aubry, K. B., C. B. Halpern, and C. E. Peterson. 2009. Variable-retention harvests in the Pacific Northwest: a review of short-term findings from the DEMO study. *Forest Ecology and Management* 258:398–408.
- Bailey, J. D., and J. C. Tappeiner. 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. *Forest Ecology and Management* 108:99–113.
- Barton, K. 2018. MuMIn: Multi-Model Inference. R package version 1.40.4. <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. *Forest Ecology and Management* 258:525–537.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of Royal Statistical Society B* 57:289–300.
- Berger, A. L., and K. J. Puettmann. 2000. Overstory composition and stand structure influence herbaceous plant diversity in the mixed aspen forest of northern Minnesota. *American Midland Naturalist* 143:111–126.
- Berner, L. T., B. E. Law, and T. W. Hudiburg. 2017. Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. *Biogeosciences* 14: 365–378.
- Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. *American Scientist* 67:660–669.
- Breiman, L. 2001. Random Forests. *Machine Learning* 45:5–32.
- Brin, A., C. Bouget, L. Valladares, and H. Brustel. 2013. Are stumps important for the conservation of saproxylic beetles in managed forests? Insights from a comparison of assemblages on logs and stumps in oak-dominated forests and pine plantations. *Insect Conservation and Diversity* 6:255–264.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. General Technical Report INT-16. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. *Journal of Wildlife Management* 57:335–345.
- Bunnell, F. L., and I. Houde. 2010. Down wood and biodiversity—implications to forest practices. *Environmental Review* 18:397–421.
- Burrascano, S., W. S. Keeton, F. M. Sabatini, and C. Blasi. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. *Forest Ecology Management* 291:458–479.
- Burrascano, S., F. Lombardi, and M. Marchetti. 2008. Old-growth forest structure and deadwood: Are they indicators of plant species composition? A case study from central Italy. *Plant Biosystems* 142:313–323.
- Carey, A. B., and R. O. Curtis. 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. *Wildlife Society Bulletin* 24:610–620.
- Carey, A. B., J. Kershner, B. Biswell, and L. D. de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monographs* 142:1–71.
- Chan, S. S., D. J. Larson, K. G. Maas-Hebner, W. H. Emmingham, S. R. Johnston, and D. A. Mikowski. 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. *Canadian Journal of Forest Research* 36:2696–2711.
- Chen, J., B. Song, M. Rudnicki, M. Moeur, K. Bible, M. North, D. C. Shaw, J. F. Franklin, and D. M. Braun. 2004. Spatial relationship of biomass and species distribution in an old-growth *Pseudotsuga-Tsuga* forest. *Forest Science* 50:364–375.
- Chojnacky, D. C., L. S. Heath, and J. C. Jenkins. 2014. Updated generalized biomass equations for North American tree species. *Forestry* 87:129–151.
- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-Fir Forests, Western Oregon. *Journal of Wildlife Management* 44:773–786.
- Cole, E., and M. Newton. 2009. Tenth-year survival and size of underplanted seedlings in the Oregon Coast Range. *Canadian Journal of Forest Research* 39:580–595.
- Cole, E., M. Newton, and J. D. Bailey. 2017. Understory vegetation dynamics 15 years post-thinning in 50-year-old Douglas-fir and Douglas-fir/western hemlock stands in western Oregon, USA. *Forest Ecology and Management* 384:358–370.
- Comfort, E. J., S. D. Roberts, and C. A. Harrington. 2010. Midcanopy growth following thinning in

- young-growth conifer forests on the Olympic Peninsula western Washington. *Forest Ecology and Management* 259:1606–1614.
- Crotteau, J. S., C. R. Keyes, S. M. Hood, A. J. Larson, E. K. Sutherland, D. K. Wright, and J. M. Egan. 2018. Stand dynamics 11 years after retention harvest in a lodgepole pine forest. *Forest Ecology and Management* 427:169–181.
- Curtis, R. O. 1995. Extended rotations and culmination age of coast Douglas-fir: old studies speak to current issues. PNW-RP-485. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Curzon, M. T., A. W. D'Amato, S. Fraver, B. J. Palik, A. Bottero, J. R. Foster, and K. E. Gleason. 2017. Harvesting influences functional identity and diversity over time in forests of the northeastern USA. *Forest Ecology and Management* 400:93–99.
- Dale, V. H., et al. 2001. Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience* 51:723–734.
- D'Amato, A. W., P. F. Catanzaro, and L. S. Fletcher. 2015. Early regeneration and structural responses to patch selection and structural retention in second-growth northern hardwoods. *Forest Science* 61:183–189.
- Davis, R. J., J. L. Ohmann, R. E. Kennedy, W. B. Cohen, M. J. Gregory, Z. Yang, H. M. Roberts, A. N. Gray, and T. A. Spies. 2015. Northwest Forest Plan—the first 20 years (1994–2013): status and trends of late-successional and old-growth forests. PNW-GTR-911. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Debeljak, M. 2006. Coarse woody debris in virgin and managed forest. *Ecological Indicators* 6:733–742.
- Del Río, M., et al. 2016. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *European Journal of Forest Research* 135:23–49.
- Duvall, M. D., and D. F. Grigal. 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes states, USA. *Canadian Journal of Forest Research* 29:1926–1934.
- Ecoshare, USDA (U.S. Department of Agriculture) Forest Service and USDI BLM (Bureau of Land Management). 2016. Landtype Associations. <https://ecoshare.info/projects/landtype-associations/>
- Fahey, R. T., et al. 2018. Shifting conceptions of complexity in forest management and silviculture. *Forest Ecology and Management* 421:59–71.
- Fassnacht, K. S., and T. W. Steele. 2016. Snag dynamics in northern hardwood forests under different management scenarios. *Forest Ecology and Management* 363:267–276.
- Franklin, J. F., D. F. Berg, D. Thornburg, and J. C. Tapeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st Century: the science of ecosystem management*. Island Press, Washington D.C., USA.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Franklin, J. F., and K. N. Johnson. 2012. A restoration framework for federal forests in the Pacific Northwest. *Journal of Forestry* 110:429–439.
- Franklin, J. F., K. N. Johnson, and D. L. Johnson. 2018. *Ecological forest management*. Waveland Press, Long Grove, Illinois, USA.
- Franklin, J. F., R. J. Mitchell, and B. Palik. 2007. *Natural disturbance and stand development principles for ecological forestry*. NRS-GTR-19. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newton Square, Pennsylvania, USA.
- Franklin, J. F., T. Spies, D. Perry, M. Harmon, and A. McKee. 1986. Modifying Douglas-fir management regimes for nontimber objectives. Pages 373–379. Paper 45 in C. D. Oliver, D. P. Hanley, and J. A. Johnson, editors. *Douglas-fir: Stand management for the future: (Proceedings of a Symposium)*. Contribution No. 55. University of Washington, College of Forest Resources, Seattle, Washington, USA.
- Franklin, J. F., T. Spies, and R. Van Pelt. 2005. *Definition and Inventory of old growth forests on DNR-managed state lands*. Washington State Department of Natural Resources, Olympia, Washington, USA.
- Franklin, J. F., and R. Van Pelt. 2004. Spatial aspects of structural complexity in old-growth forests. *Journal of Forestry* 102:22–28.
- Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399–423.
- Freund, J. A., J. F. Franklin, and J. A. Lutz. 2015. Structure of early old-growth Douglas-fir forests in the Pacific Northwest. *Forest Ecology Management* 335:11–25.
- FSC-US (Forest Stewardship Council, United States). 2010. *FSC-US Forest Management Standard (v1.0)*. Forest Stewardship Council, Bonn, Germany.

- Garman, S. L., S. A. Acker, J. L. Ohmann, and T. A. Spies. 1995. Asymptotic height-diameter equations for twenty-four tree species in western Oregon. Research Contribution 10. Research Contribution 10. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Gibb, H., J. P. Ball, T. Johansson, O. Atlegrim, J. Hjältén, and K. Danell. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scandinavian Journal of Forest Research* 20:213–222.
- Goodburn, J. M., and C. G. Lorimer. 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Canadian Journal of Forest Research* 28:427–438.
- Gray, A. 2003. Monitoring stand structure in mature coastal Douglas-fir forests: effect of plot size. *Forest Ecology and Management* 175:1–16.
- Gronewold, C. A., A. W. D'Amato, and B. J. Palik. 2010. The influence of cutting cycle and stocking level on the structure and composition of managed old-growth northern hardwoods. *Forest Ecology and Management* 259:1151–1160.
- Gustafsson, L., J. Kouki, and A. Sverdrup-Thygeson. 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. *Scandinavian Journal of Forest Research* 25:295–308.
- Gustafsson, L., et al. 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience* 62:633–645.
- Hagar, J. C. 2003. Functional relationships among songbirds, arthropods, and understory vegetation in Douglas-fir forests, western Oregon. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* 41:382–393.
- Harmon, M. E., and J. F. Franklin. 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. *Ecology* 70:48–59.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. <https://andrewsforest.oregonstate.edu/publications/2255>
- Harmon, M. E., C. W. Woodall, B. Fasth, J. Sexton, and M. Yatkov. 2011. Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. Research Paper NRS-15. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newton Square, Pennsylvania, USA.
- Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Herter, D. R., L. L. Hicks, H. C. Stabins, J. J. Mills, A. J. Stabins, and L. D. Melampy. 2002. Roost site characteristics of northern spotted owls in the nonbreeding season in central Washington. *Forest Science* 48:437–444.
- Hjältén, J., F. Stenbacka, and J. Andersson. 2010. Saproxylic beetle assemblages on low stumps, high stumps and logs: implications for environmental effects of stump harvesting. *Forest Ecology and Management* 260:1149–1155.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.
- Huffman, D. W., J. C. Tappeiner II, and J. C. Zasada. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. *Canadian Journal of Botany* 72:39–51.
- Ishii, H., and N. McDowell. 2002. Age-related development of crown structure in coastal Douglas-fir trees. *Forest Ecology and Management* 169:257–270.
- Ishii, H. T., S. I. Tanabe, and T. Hiura. 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science* 50:342–355.
- Janowiak, M. K., L. M. Nagel, and C. R. Webster. 2008. Spatial scale and stand structure in northern hardwood forests: implications for quantifying diameter distributions. *Forest Science* 54:497–506.
- Jules, M. J., J. O. Sawyer, and E. S. Jules. 2008. Assessing the relationships between stand development and understory vegetation using a 420-year chronosequence. *Forest Ecology and Management* 255:2384–2393.
- Keeton, W. S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecology and Management* 235:129–142.
- Keeton, W. S., M. Chernyavskyy, G. Gratzner, M. Main-Knorn, M. Shpylchak, and Y. Bihun. 2010. Structural characteristics and aboveground biomass of old-growth spruce-fir stands in the eastern Carpathian mountains, Ukraine. *Plant Biosystems* 144:148–159.
- Keeton, W. S., and J. F. Franklin. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Monographs* 75:103–118.
- Keeton, W. S., C. E. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. *Ecological Applications* 17:852–868.

- Keeton, W. S., A. A. Whitman, G. C. McGee, and C. L. Goodale. 2012. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *Forest Science* 57:489–505.
- Keren, S., and J. Diaci. 2018. Comparing the quantity and structure of deadwood in selection managed and old-growth forests in South-East Europe. *Forests* 9:76.
- Kohm, K. A., and J. F. Franklin, editors. 1997. *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washington, D.C., USA.
- Kuehne, C., A. R. Weiskittel, S. Fraver, and K. J. Puettmann. 2015. Effects of thinning-induced changes in structural heterogeneity on growth, ingrowth, and mortality in secondary coastal Douglas-fir forests. *Canadian Journal of Forest Research* 45:1448–1461.
- Kwong, K. S., B. Holland, and S. H. Cheung. 2002. A modified Benjamini-Hochberg multiple comparisons procedure for controlling the false discovery rate. *Journal of Statistical Planning and Inference* 104:351–362.
- Latham, P., and J. Tappeiner. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiology* 22:137–146.
- Latta, G., and C. A. Montgomery. 2004. Minimizing the cost of stand level management for older forest structure in western Oregon. *Western Journal of Applied Forestry* 19:221–231.
- Lenth, R. V. 2016. Least-squares means: the R package lsmeans. *Journal of Statistical Software* 69:1–33. <https://cran.r-project.org/web/packages/lsmeans/index.html>
- Lewis, J. C. 1998. Creating snags and wildlife trees in commercial forest landscapes. *Western Journal of Applied Forestry* 13:97–101.
- Liaw, A., and M. Wiener. 2018. Classification and regression by randomForest. *R News*. Volume 2: 18–22. <https://cran.r-project.org/web/packages/randomForest/index.html>
- Lindenmayer, D. B., and J. F. Franklin. 2002. *Conserving forest biodiversity: a comprehensive multiscaled approach*. Island Press, Washington, D.C., USA.
- Lindenmayer, D. B., et al. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters* 5:421–431.
- Long, J. N., and T. W. Daniel. 1990. Assessment of growing stock in uneven-aged stands. *Western Journal of Applied Forestry* 5:93–96.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- Maguire, C. C., and C. L. Chambers, editors. 2005. *Ecological and socioeconomic responses to alternative silvicultural treatments*. Oregon State University, College of Forestry, Forest Research Laboratory, Corvallis, Oregon, USA.
- Maguire, D. A., C. B. Halpern, and D. L. Phillips. 2007. Changes in forest structure following variable-retention harvests in Douglas-fir dominated forests. *Forest Ecology and Management* 242:708–726.
- Mannan, R. W., E. C. Meslow, and H. M. Wight. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:787–797.
- McCain, C., and N. Diaz. 2002. *Field Guide to the Forested Plant Associations of Westside Central Cascades of Northwest Oregon*. R6-NR-ECOL-TP-02-02. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, USA.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- McCune, B., and M. J. Mefford. 2016. *PC-ORD. Multivariate analysis of ecological data*. MjM Software Design, Gleneden Beach, Oregon, USA. <https://www.wildblueberrymedia.net/software>
- McCune, B., and H. T. Root. 2015. Origin of the dust bunny distribution in ecological community data. *Plant Ecology* 216:645–656.
- McElhinny, C., P. Gibbons, C. Brack, and J. Bauhus. 2005. Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management* 218:1–24.
- Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826.
- Nelson, S. K. 1989. *Habitat use and densities of cavity-nesting birds in the Oregon Coast Range*. Thesis. Oregon State University, Corvallis, Oregon, USA.
- North, M., J. Chen, B. Oakley, B. Song, M. Rudnicki, A. Gray, and J. Innes. 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. *Forest Science* 50: 299–311.
- North, M. P., J. F. Franklin, A. B. Carey, E. D. Forsman, and T. Hamer. 1999. Forest stand structure of the northern spotted owl's foraging habitat. *Forest Science* 45:520–527.
- O'Dea, M. E., J. C. Zasada, and J. C. Tappeiner. 1995. Vine maple clone growth and reproduction in managed and unmanaged coastal Oregon Douglas-fir forests. *Ecological Applications* 5:63–73.
- ODF (Oregon Department of Forestry). 2018. *Forest Practice Administrative Rules and Forest Practices Act*. Oregon Department of Forestry, Salem, Oregon, USA.

- O'Hara, K. L. 2014. Multiaged silviculture: managing for complex forest stand structures. Oxford University Press, New York, New York, USA.
- Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* 68:151–182.
- Oliver, C. D., and B. C. Larson. 1990. Forest stand dynamics. McGraw-Hill, New York, New York, USA.
- Onodera, K., S. Tokuda, Y. Hirano, and S. Yamamoto. 2017. Vertical distribution of saproxylic beetles within snag trunks retained in plantation forests. *Journal of Insect Conservation* 21:7–14.
- Oswalt, S. N., W. B. Smith, P. D. Miles, and S. A. Pugh. 2014. Forest Resources of the United States, 2012: a technical document supporting the Forest Service 2010 update of the RPA Assessment. WO-GTR-91. U.S. Department of Agriculture, Forest Service, Washington Office, Washington, D.C., USA.
- Palik, B. J., R. A. Montgomery, P. B. Reich, and S. B. Boyden. 2014. Biomass growth response to spatial pattern of variable-retention harvesting in a northern Minnesota pine ecosystem. *Ecological Applications* 24:2078–2088.
- Peck, J. E., E. K. Zenner, P. Brang, and A. Zingg. 2014. Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. *European Journal of Forestry Research* 133:335–346.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131 <https://CRAN.R-project.org/package=nlme>
- Poage, N. J., and J. C. Tappeiner II. 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. *Canadian Journal of Forest Research* 32:1232–1243.
- Poage, N. J., P. J. Weisberg, P. C. Impara, J. C. Tappeiner, and T. S. Sensenig. 2009. Influences of climate, fire, and topography on contemporary age structure patterns of Douglas-fir at 205 old forest sites in western Oregon. *Canadian Journal of Forest Research* 39:1518–1530.
- PRISM Climate Group. 2018. 30-year climate totals. Oregon State University, Corvallis, Oregon, USA. <http://prism.oregonstate.edu>
- Puettmann, K. J., K. D. Coates, and C. C. Messier. 2009. A critique of silviculture: managing for complexity. Island Press, Washington, D.C., USA.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P. B., L. E. Frelich, R. A. Voldseth, P. Bakken, and E. C. Adair. 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. *Journal of Ecology* 100:539–545.
- Reukema, D. L. 1982. Seedfall in a young-growth Douglas-fir stand: 1950–1978. *Canadian Journal of Forest Research* 12:249–254.
- Santaniello, F., L. B. Djupström, T. Ranius, J. Weslien, J. Rudolphi, and G. Thor. 2017. Large proportion of wood dependent lichens in boreal pine forest are confined to old hard wood. *Biodiversity Conservation* 26:1295–1310.
- Schmiedinger, A., J. Kreyling, M. J. Steinbauer, S. E. Macdonald, A. Jentsch, and C. Beierkuhnlein. 2012. A continental comparison indicates long-term effects of forest management on understory diversity in coniferous forests. *Canadian Journal of Forest Research* 42:1239–1252.
- Sensenig, T., J. D. Bailey, and J. C. Tappeiner. 2013. Stand development, fire and growth of old-growth and young forests in southwestern Oregon, USA. *Forest Ecology and Management* 291:96–109.
- Sharik, T. L., et al. 2010. Emerging themes in the ecology and management of North American forests. *International Journal of Forestry Research* 2010:1–11.
- Shatford, J. P., J. D. Bailey, and J. C. Tappeiner. 2009. Understory tree development with repeated stand density treatments in coastal Douglas-fir forests of Oregon. *Western Journal of Applied Forestry* 24:11–16.
- Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* 128:211–225.
- Silver, E. J., A. W. D'Amato, S. Fraver, B. J. Palik, and J. B. Bradford. 2013. Structure and development of old-growth, unmanaged second-growth, and extended rotation *Pinus resinosa* forests in Minnesota, USA. *Forest Ecology Management* 291:110–118.
- Sippola, A. L., J. Siitonen, and R. Kallio. 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scandinavian Journal of Forest Research* 13:204–214.
- Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research* 12:18–28.
- Spies, T. A., and J. F. Franklin. 1988. Old-growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Natural Areas Journal* 8:190–201.
- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature and old-growth Douglas-fir forests in Oregon and Washington. Pages 71–82 in

- L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation in unmanaged Douglas-fir forests. PNW-GTR-285. U.S. Department of Agriculture, Pacific Northwest Research Station, Portland, Oregon, USA.
- Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20:649–658.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse Woody Debris in Douglas-Fir Forests of Western Oregon and Washington. *Ecology* 69:1689–1702.
- Tappeiner, J. C., D. W. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. *Canadian Journal of Forest Research* 27:638–648.
- Tappeiner, J. C., and J. C. Zasada. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. *Canadian Journal of Forest Research* 23:1775–1780.
- Tepley, A. J., F. J. Swanson, and T. A. Spies. 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. *Ecology* 94:1729–1743.
- Thomas, J. W., J. F. Franklin, J. Gordon, and K. N. Johnson. 2006. The northwest forest plan: origins, components, implementation experience, and suggestions for change. *Conservation Biology* 20:277–287.
- Trumbore, S., P. Brando, and H. Hartmann. 2015. Forest health and global change. *Science* 349:814–818.
- Tullus, T., R. Rosenvald, M. Leis, and P. Lõhmus. 2018. Impacts of shelterwood logging on forest bryoflora: distinct assemblages with richness comparable to mature forests. *Forest Ecology and Management* 411:67–74.
- USDA (U.S. Department of Agriculture) Forest Service and USDI BLM (Bureau of Land Management). 1994. Record of Decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl and standards and guidelines for management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. USDA Forest Service, Portland, Oregon, USA and BLM, Moscow, Idaho, USA.
- Van Pelt, R., and J. F. Franklin. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Canadian Journal of Forest Research* 30:1231–1245.
- Van Pelt, R., and N. M. Nadkarni. 2004. Development of canopy structure in *Pseudotsuga menziesii* forests in the southern Washington Cascades. *Forest Science* 50:326–341.
- Van Pelt, R., S. C. Sillett, W. A. Kruse, J. A. Freund, and R. D. Kramer. 2016. Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. *Forest Ecology and Management* 375:279–308.
- Vítková, L., R. Bače, P. Kjučukov, and M. Svoboda. 2018. Deadwood management in Central European forests: key considerations for practical implementation. *Forest Ecology and Management* 429:394–405.
- Vonhof, M. J., and R. M. Barclay. 1997. Use of tree stumps as roosts by the western long-eared bat. *Journal of Wildlife Management* 61:674–684.
- Wender, B. W., C. A. Harrington, and J. C. Tappeiner. 2004. Flower and fruit production of understory shrubs in western Washington and Oregon. *Northwest Science* 78:124–140.
- Williams, N. G., and M. D. Powers. 2019. Carbon storage implications of active management in mature *Pseudotsuga menziesii* forests of western Oregon. *Forest Ecology and Management* 432:761–775.
- Willis, J. L., S. D. Roberts, and C. A. Harrington. 2018. Variable density thinning promotes variable structural responses 14 years after treatment in the Pacific Northwest. *Forest Ecology and Management* 410:114–125.
- Young, B. D., A. W. D'Amato, C. C. Kern, D. N. Kastendick, and B. J. Palik. 2017. Seven decades of change in forest structure and composition in *Pinus resinosa* forests in northern Minnesota, USA: comparing managed and unmanaged conditions. *Forest Ecology and Management* 395:92–103.
- Zenner, E. K. 2000. Do residual trees increase structural complexity in Pacific Northwest coniferous forests? *Ecological Applications* 10:800–810.
- Zenner, E. K. 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. *Ecological Applications* 15:701–714.
- Ziegler, S. S. 2000. A comparison of structural characteristics between old-growth and postfire second-growth hemlock-hardwood forests in Adirondack Park, New York, USA. *Global Ecology and Biogeography* 9:373–389.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2830/full>