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Structure of early old-growth Douglas-fir forests in the Pacific Northwest

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ABSTRACT

Few empirical studies exist on structural transitions from mature forests dominated by Douglas-fir to structurally complex older forests. Stand structure (live tree diameter, height distributions, snag and log metrics) and composition of nine early old-growth (200–350 years old) forests were quantified and compared with those of fully developed old-growth (400–600 years old) forests. We investigated Douglas-fir and western hemlock-dominated forests of the Pacific Northwest where Douglas-fir established following a single stand-replacing disturbance. Stand-level attributes were summarized using descriptive statistics, nonlinear regression, and old-growth indices. Variability in individual structural features was large between sites but broadly consistent with models of natural Douglas-fir forest development. Compared to older (>450 years old) forests, diameter distributions exhibited similar reverse J-shapes. Tree height distributions showed that shade tolerant species occupy lower canopy positions. Coarse woody debris was abundant in early old-growth forests for both snags (42–140 $m^3\ ha^{-1}$) and logs (172–584 $m^3\ ha^{-1}$). Early old-growth stands scored high enough on old-growth indices to qualify as old growth but their scores were significantly lower than older forests (400–600 years-old). Early old-growth structure fits well with the natural conceptual model of development providing a basis for ecologically focused management. Furthermore, structural conditions and variability of early old-growth forests provides a closer temporal target for managers seeking to accelerate the development of structure in younger stands or retain natural elements such as spatial patterning of trees.

1. Introduction

Naturally developing forests characteristically subject to stand-replacement disturbances undergo repeated cycles of stand initiation and development. Structural development in these forests involves many processes, such as those associated with recruitment, growth and maturation of individual trees, competitive interactions (Lutz et al., 2014), and small-scale disturbances (Barnes et al., 1998; Kimmins, 2004). Development of structurally complex forests can require many centuries, particularly in forest ecosystems that include long-lived tree species, such as those found in northwestern North America (Waring and Franklin, 1979; Franklin and Dyrness, 1988). Structural attributes commonly used to assess forest structural complexity include diameter distributions, spatial variation of density, basal area, and biomass (Lutz et al., 2012, 2013), tree crown structure (Van Pelt and Sillett, 2008; Kane et al., 2010, 2011), and development and persistence of coarse woody debris (Franklin et al., 2002).

Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco.) forests in the Pacific Northwest represent an example of forests in which centuries of structural development culminate in structurally complex old-growth forests (Franklin et al., 2002; Franklin and Van Pelt, 2004; Van Pelt and Nadkarni, 2004). Although Douglas-fir forests are broadly distributed, the structural attributes and driving ecosystem process of older populations are poorly understood (Franklin, 2009). Consequently, conceptual models of the age classes documenting how forests transition structurally over time are primarily based on a limited set of developmental stages (e.g., Franklin et al., 2002 and Spies and Duncan, 2009; Table 1). Some developmental stages – such as young (<100 years) and well developed old-growth (>400 year) forests – have received extensive study (e.g. Franklin and Spies, 1984; Spies and Franklin, 1991; Tappeiner et al., 1997; Van Pelt and Nadkarni, 2004, Lutz and Halpern, 2006, Larson et al., 2008; Halpern and Lutz, 2013). The intermediate stages (100–400 years), importantly the early old-growth stage (200–350 years old), remains poorly understood,

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Table 1
Terminology for forest age classes described in this study.

Forest age class	
Young	<100 years
Mature	100–190 years
Early old-growth	190–350 years
Old growth	>400 years

even while understanding of the intermediate age classes is becoming more important to forest management in a changing climate.

The conceptual model advanced by Franklin et al. (2002) on Douglas-fir forest structural development is largely based on empirical data and analyses of young, early-mature, and well-developed old-growth forests. Structural characterizations of old-growth in the Franklin et al. (2002) model are largely based on stands that originated ca. 1500 AD (Spies and Duncan, 2009) and may represent idiosyncratic stand developmental trajectories from stands originating in following centuries. For example, many of the old-growth stands used to construct the current conceptual model may have experienced one or more additional disturbances severe enough to regenerate new cohorts of Douglas-fir (Van Pelt, 2007; Tepley et al., 2013). Stages of structural development following single high severity disturbances have been investigated using space (e.g. stands of a particular age) for time substitutions. These chronosequence approaches have limitations (e.g. Pickett, 1989) but can be very useful when sequential data on the full developmental sequence are not available (Spies and Franklin, 1991). Intermediate disturbances such as fire or wind can also influence development of structure in different types of ways by reducing densities of tree species, consuming coarse woody debris, and changing crown morphology and canopy structure. Hence, it is important to examine the conceptual framework by analyzing preceding forest stages that developed in the absence of moderate severity disturbances. Structure, composition, and process of early old-growth forest stages remain largely undocumented (but see Spies and Franklin, 1991; Huff, 1995; Zenner, 2005). However, no study has yet specifically focused on characterizing early old-growth structure despite the apparent importance of this stage for old-growth development. General descriptions of this developmental stage have been provided by Franklin et al. (2002) and includes discussion of, (1) transitions in canopy architecture from single-layered canopies in young-mature forests to vertically continuous canopies in early old-growth, and (2) the period of development when chronic small-scale disturbances create canopy gaps that diversify forest structure in the horizontal plane (Franklin et al., 2002; Tepley et al., 2013). In this study, the structural and compositional conditions in natural, early old-growth Douglas-fir-dominated forests are reported. Above-ground attributes of nine forest stands that originated ca. 1650 to 1800 AD in western Washington and Oregon are analyzed and their characteristics are compared with both younger and older Douglas-fir forests. Three general questions are addressed: (1) What are the structural dimensions of early old-growth forests, including the variability between stands; (2) How do early old-growth stands score on existing structural indices in comparison with young-mature forests and well-developed old-growth forests; and (3) Will modeled Douglas-fir stem densities in the early old-growth be similar to the densities of existing well developed old-growth Douglas-fir stands?

2. Methods

2.1. Study area

A total of nine early old-growth stands were sampled during this study. Eight of nine sampled stands are distributed along the western slope of the Cascade Range between elevations of 318–799 m. These stands occupy moist to relatively dry sites representative of the Western Hemlock Zone (Franklin and Dyrness, 1988) (Table 2). One stand (Huckleberry) is located in the eastern Olympic Mountains, Washington in the cooler, moister Pacific Silver Fir Zone (Franklin and Dyrness, 1988) (Table 2). All sites have a maritime climate characterized by cool wet winters and warm dry summers (Table 2). Annual precipitation ranges from 1974 mm to 3622 mm with the majority occurring during the months of October through April; conditions in the Pacific Silver Fir zone are somewhat cooler and moister and include a significant winter snowpack accumulation. Maximum July temperatures range from 20 to 25 °C and minimum January temperatures range from −1 to −4 °C.

Douglas-fir is an important shade-intolerant, pioneer tree species in the Western Hemlock and Pacific Silver Fir zones growing to very large dimensions, developing complex crowns (Van Pelt and Sillett, 2008), and living up to 700 to 1000+ years. Common tree associates in this region include western hemlock, western redcedar (*Thuja plicata* Donn ex D. Don), western white pine (*Pinus monticola* (Dougl.), Pacific silver-fir (*Abies amabilis* (Dougl. ex. Loud) Dougl. ex Forbes), Pacific yew (*Taxus brevifolia* Nutt.), noble fir (*Abies procera*), big-leaf maple (*Acer macrophyllum* Pursh), and Pacific dogwood (*Cornus nuttallii* Aud.). Soils range from sandy loams to clay loams and great soil groups include Haplorthods, Xerumbrepts, and Vitrandepts.

Stand-replacement wildfire is the principal agent of disturbance in this forest zone with events occurring relatively infrequently every 200–400 years (Hemstrom and Franklin, 1982; Agee, 1993), although partial stand-replacement events are also characteristic in more southerly latitudes (Tepley et al., 2013). Smaller-scale disturbances include wind, pathogens, and insects, and are important in creating structural complexity in older stages of forest development (Franklin et al., 2002).

2.2. Site selection

Sites were selected in Douglas-fir-dominated stands ~200 to 350 years of age that established after a single wildfire event. Sites were selected after extensive reconnaissance (see Freund et al., 2014), which included aging Douglas-fir trees at each candidate location and eliminating sites with evidence of post-establishment fire. Concentrations of this age class are found in only a few locations, such as the Clackamas and Breitenbush River drainages in the northern Oregon Cascade Range, in the Lewis River and Ohanapecosh River drainages of the Washington Cascade Range, and in eastern portions of Washington's Olympic Peninsula. Candidate stands were located following review of regional fire-history studies (Morrison and Swanson, 1990; Agee, 1991; Impara, 1997; Weisberg and Swanson, 2003), stand age-class maps (US Forest Service), conversations with forest ecologists familiar with the region (personal communications with Ken Bible, Rolf Gersonde, Scott Gremel, Jan Henderson, Robin Lesher, and Robert Van Pelt), and extensive reconnaissance. Due to its restricted distribution on the landscape, the nine sites we selected are broadly representative of the remaining examples of this age class.

The youngest age class of forest sampled was ~200 years in age, and stands of this age were uncommon, which made it unfeasible to replicate sampling in this age class over a broad geographic range. Four suitable stands of this age class were located in the Lewis River drainage of southwestern Washington and probably originated from a single extensive wildfire event although we did not reconstruct fire histories (Cedar Flats, Drift Creek, Osprey, and Skynard). Hence, these four stands could be viewed as "pseudo-replicates" (Hurlbert, 1984). However, site conditions and behavior of large wildfires can produce high levels of

Table 2
Site characteristics for nine early old-growth stands.

Site	Lat.	Long.	Elevation (m)	Aspect	Stand age	Precipitation (mm)				Temperature (°C)	
						Annual	July mean	January mean	Growing season (June–September)	July max	Jan min
Olympic National Park, WA											
Sol Duc	47.95	−123.81	687	S	317	3622	61	483	80	20	−1
Cedar River Watershed, WA											
Huckleberry	47.31	−121.52	799	NE	328	2584	62	397	75	21	−3
Mt. Rainier National Park, WA											
Ohanapecosh	46.74	−121.55	670	SW	296	1974	35	306	47	24	−4
Gifford Pinchot National Forest, WA											
Cedar Flats	46.11	−122.01	400	NE	191	2972	45	455	65	25	−2
Drift Creek	46.03	−122.09	324	SE	193	2990	46	455	66	24	−1
Osprey	46.03	−122.08	318	W	190	2995	46	456	66	25	−1
Skynard	46.02	−122.08	379	W	193	3339	51	526	71	24	−1
Willamette National Forest, OR											
Bagby	44.94	−122.17	650	E	297	2123	31	301	52	24	−2
Breitenbush	44.79	−121.90	760	W	326	1997	33	304	46	25	−4

Note: Precipitation and temperature data obtained from PRISM database (Daly et al., 2002). Stand age based on oldest Douglas-fir tree in each site.

structural variation producing valuable information on structural development (Turner et al., 1997; Larson and Franklin, 2005).

2.3. Field methods

Six 0.2-ha fixed-radii plots were established along transects and spaced 100 m apart. Transects were established >50 m from edge influences (e.g. roads, rivers, clearcuts). Slope was measured at plot center using an Impulse Laser 200 (Laser Technology Inc.). Diameters of all trees ⩾5 cm at 1.37 m above ground were measured to the nearest tenth of a centimeter. In each 0.2 ha plot 10–15 trees were selected and measured for total height, height to live crown (lowest primary branch), and height to lowest epicormic branch. Seedlings <5 cm dbh were measured using belt transects and were measured for height. Diameter and height for snags ⩾10 cm in diameter and ⩾1.37 m in height were measured. Snags were assigned one of five decay classes depending on their level of fragmentation and decomposition (Cline et al., 1980). Logs were identified by species, assigned to a one of five decay classes and the intercept diameter of each piece ⩾10 cm was measured (Harmon and Sexton, 1996).

2.4. Analyses

Summary statistics for stand-level attributes of each early old-growth stand were calculated for live trees and coarse woody debris. Live tree and stand level attributes computed include: (1) mean, minimum, and maximum dbh, (2) standard deviation of dbh, (3) basal area, and (4) density. Mean height, mean crown length, and mean epicormic height were calculated for Douglas-fir, western hemlock, and western redcedar. Snag data were summarized by calculating stand-level statistics for total snag density, large snag (>50 cm dbh and >15 m in height) density, basal area, mean height, and standard deviation of height. Snag data were also summarized by calculating density, volume, mean height, and standard deviation of mean height by decay class. Similarly, log data were summarized by calculating stand level values for mean piece diameter, volume, volume per decay class, density, and large log (>50 cm at point of intercept) density. Seedling data were summarized by calculating density and height statistics (mean, range, and standard deviation).

Principal component analyses (PCA) were used to explore structural variability among early old-growth sites. PCAs were computed for a 9×17 covariance matrix of study sites ($n = 9$) and stand-level variables ($n = 17$) utilizing the R statistical software (R Development Core Team, 2008). Before analysis, variables were standardized by their maxima and then by site totals. Variables were: total live basal area, Douglas-fir basal area, western hemlock basal area, Douglas-fir tree density, shade-tolerant tree density (western hemlock, western redcedar, Pacific silver-fir, grand-fir, and Pacific yew), standard deviation of dbh, density of snags >50 cm dbh, mean live tree diameter, log volume, snag volume, density of trees >100 cm dbh, Douglas-fir age range, standard deviation of Douglas-fir age range, mean Douglas-fir crown depth, standard deviation of Douglas-fir crown depth, and standard deviation of western hemlock heights.

Histograms displaying size class distributions separated into 15 cm bins were created for each tree species. Cumulative diameter distributions were also created and used as a basis for comparing size distributions with known distributions of older stands. Two parameter exponential decay curves were fit to the cumulative diameter distributions to assess variability among live-tree populations except for one site (Huckleberry) which was fit with a 3 parameter sigmoid curve. Goodness of fit was assessed using r^2 values obtained from each fit curve using SigmaPlot version 11.0, from Systat Software Inc, San Jose, California USA. Histograms displaying tree height distributions separated into 5 m bins were created and line plots of the crown length distribution were overlaid onto total height histograms. Histograms displaying the coarse woody debris size distributions separated into 15 cm bins were created.

Two indices of old-growth characteristics were computed to address the question of whether structure of early old-growth forests is comparable to well developed old-growth forests. The first old-growth index (Iog) used in this analysis was developed by Acker et al. (1998) and utilizes four variables: (1) standard deviation of diameter at breast height, (2) density of large diameter trees >100 cm (dbh), (3) mean tree dbh, and (4) total tree density. Thorough descriptions of the index are provided elsewhere (Acker et al., 1998; Larson et al., 2008). The second index used is referred to as the Old Growth Habitat Index (OGHI). This OGHI incorporates both live and dead components of forests (Franklin et al., 2005) utilizing a set of five variables that receive scores between 0 and 100. The five variables of the OGHI are large trees per hectare (>100 cm), large snags per hectare (>50 cm dbh and 15 m tall), volume of downed woody debris, diameter diversity within each stand, and stand age. Total scores can be calculated in three forms of the OGHI. The “standard” OGHI is calculated from the average of the five element scores, the “modified” OGHI excludes stand age, and the “weighted” OGHI is scored using relative Spearman rank correlation coefficients of each structural element and stand age.

Structural comparisons between age classes were completed by calculating OGHI scores for early old-growth and for well developed old-growth. One-way ANOVA and post hoc Holm–Sidak multiple comparisons were used to test for significant differences ($\alpha = 0.05$) among age classes. Structural data from the older stands came from an independent data set reported in an earlier study (Spies and Franklin, 1991) that examined multiple Douglas-fir forest age classes ranging from 42 to 900 years. The stands included in the Spies and Franklin (1991) study are the same forest type of this study and similarly are located throughout the western Cascades of Oregon and Washington. Boxplots were generated that display the range of element scores for young and mature (combined), a subset of old-growth stands (400–900 yr) from Spies and Franklin (1991) and the early old-growth stands of this study. The Spies and Franklin (1991) plots selected include 27 younger stands (42–140 years-old) and a subset of 15 old-growth stands between 400–600 years-old; this subset was selected because it represents the most common age class of old-growth forest in the region. Means, ranges, and 95% confidence intervals of some early old-growth structural variables were compared with values for old-growth stands as a way to assess any structural overlap among age classes.

Comparisons of OGHI element scores between high and low productivity early old-growth sites was made using Mann–Whitney tests to compare the highest productivity sites with the lower productivity sites. Site index was determined using height growth curves (McArdle et al., 1961).

Projected Douglas-fir densities were calculated for the early old-growth stands to investigate what future densities might be at ages exceeding 400 years – i.e., to compare projected densities with those in existing well developed old-growth stands (question 4). Projections were made using current Douglas-fir densities and calculating a mortality equation in the form:

$$\text{Projected density} = N_1 * (1 - m_1)^t$$

where N_1 is the current Douglas-fir density, m_1 is annual mortality rate, and t is the number of years. Populations were projected for 300 years in 25 year increments. Three rates of annual mortality (0.28%, 0.5%, and 0.9%) were used in these projections based on researched rates of mortality of Douglas-fir in old-growth forests (Spies et al., 1990; Franklin and Debell, 1988; Bible, 2001). Projections were also made using a 1.1% annual mortality rate to represent a scenario in which mortality rates increased as a consequence of climate change (van Mantgem et al., 2009). Projected densities of early old-growth stands were compared with current densities of Douglas-fir in old-growth forests (Spies and Franklin, 1991; Lutz et al., 2013) using Mann–Whitney rank sum tests.

3. Results

3.1. Tree size structure

Cumulative diameter distributions generally followed a reverse J-shape (Appendix A) with a strong fit to a 2-parameter exponential–decay curve ($r^2 = 0.96$–0.99). Only the oldest stand (Huckleberry) showed a better fit to a 3-parameter sigmoid curve

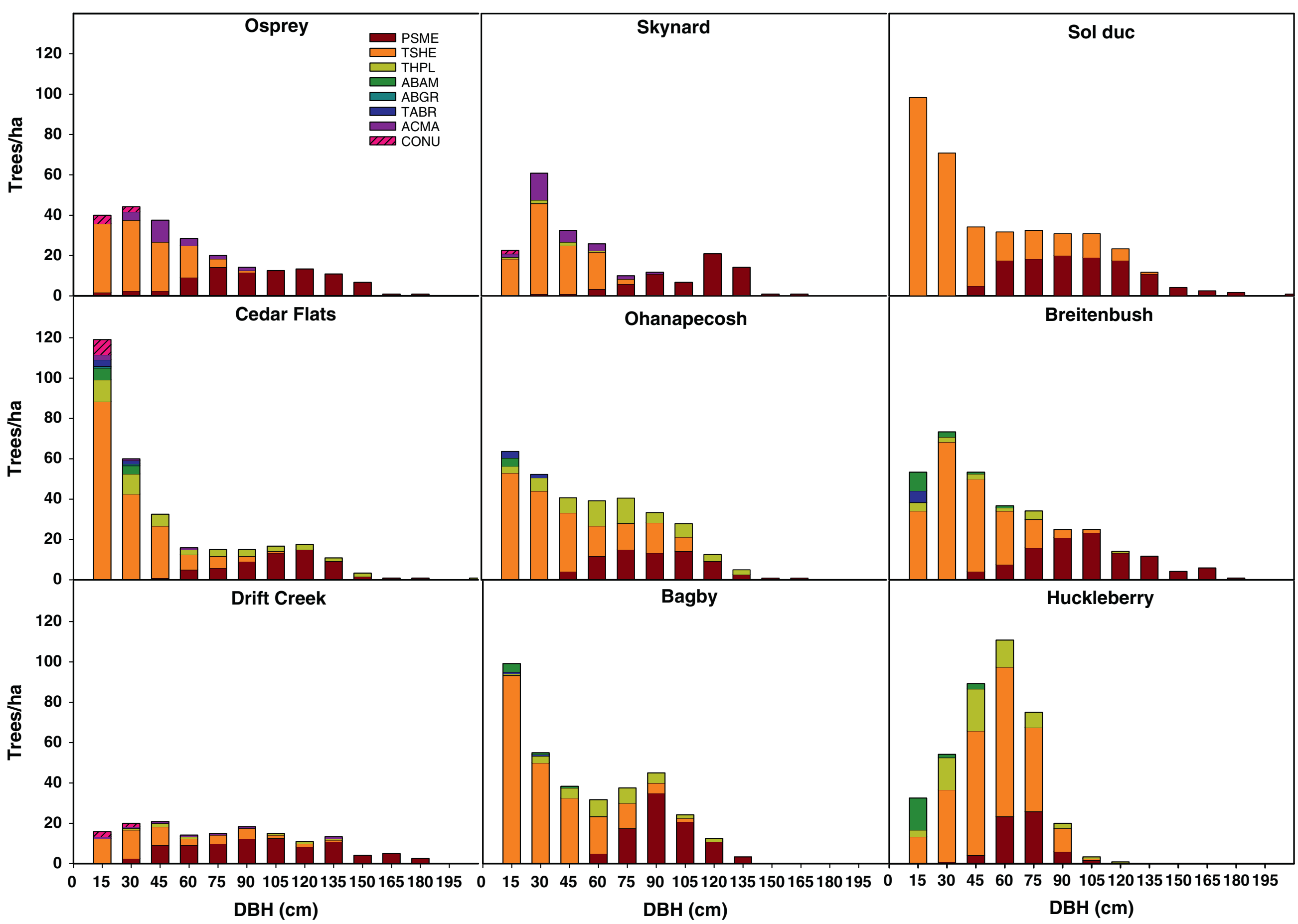

Fig. 1. Diameter distributions for live trees ⩾5 cm at diameter breast height (DBH). Colored bars represent species present in each site with trees per hectare (TPH) listed in the legend. Four letter species codes are as follows: PSME = Douglas-fir, TSHE = western hemlock, THPL = western redcedar, ABAM = Pacific silver-fir, ABGR = grand fir, TABR = Pacific yew, ACMA = bigleaf maple, CONU = Pacific dogwood.

Table 3
Tree and stand level structural variables calculated for all live trees ⩾5 cm dbh.

Site	Species	Maximum age of Douglas-fir (yr)	Basal area (m^2 ha^{-1})	Density trees/ha	Tree DBH (cm)			
					Mean	Min	Max	SD (DBH)
Osprey	Douglas-fir	190	65	85	93.6	23.3	168.6	33.4
	Western hemlock		10	114	28.0	5.2	83.1	17.2
	Western redcedar		0	0	n/a	n/a	n/a	n/a
	Other species		4	30	35.6	7.0	85.7	20.3
	Totals		79	231				
Cedar Flats	Douglas-fir	191	50	62	98.3	33.8	166.1	25.2
	Western hemlock		11	173	21.5	5.0	90.1	17.7
	Western redcedar		17	44	51.9	6.7	207.2	45.0
	Other species		1	29	16.8	5.1	116.5	19.7
	Totals		79	310				
Drift Creek	Douglas-fir	193	67	87	91.9	16.4	176.9	38.2
	Western hemlock		10	53	40.2	5.3	120.4	30.5
	Western redcedar		3	5	71.0	26.9	127.4	39.4
	Other species		3	17	34.7	5.9	120.2	33.3
	Totals		83	162				
Skynard	Douglas-fir	193	56	65	101.4	19.7	163.8	26.7
	Western hemlock		9	108	29.1	5.2	66.3	15.2
	Western redcedar		Trace	5	30.3	14	47.5	14.0
	Other species		3	29	30.8	6.8	80.1	17.4
	Totals		69	207				
Ohanapecosh	Douglas-fir	296	41	72	81.44	35.1	155.6	24.7
	Western hemlock		22	143	34.98	5.1	104.9	26.7
	Western redcedar		22	60	61.27	7.2	133.3	30.4
	Other species		1	9	20.53	5.0	115.3	31.7
	Total		86	284				
Bagby	Douglas-fir	297	58	93	87.56	54.2	129.1	16.0
	Western hemlock		19	213	25.83	5.0	97.9	21.1
	Western redcedar		11	34	59.22	6.5	117.7	25.1
	Other species		1	8	19.78	5.7	66.8	20.0
	Total		89	348				
Sol Duc	Douglas-fir	317	86	118	90.97	31.8	198	31.8
	Western hemlock		35	256	30.92	5.0	121.9	28.4
	Western redcedar		0	0	n/a	n/a	n/a	n/a
	Other species		0	0	n/a	n/a	n/a	n/a
	Total		121	374				
Breitenbush	Douglas-fir	326	85	108	95.68	35.2	166.4	29.3
	Western hemlock		22	195	32.74	5.0	102.2	19.4
	Western redcedar		3	16	40.66	9.7	117.0	27.8
	Other species		1	20	15.01	5.0	58.1	12.6
	Total		111	339				
Huckleberry	Douglas-fir	328	23	74	61.94	30.0	98.9	12.8
	Western hemlock		55	287	45.93	6.4	96.2	17.9
	Western redcedar		14	78	42.71	9.0	112.5	19.9
	Other species		1	25	14.02	5.0	63.7	14.4
	Total		93	464				
Mean (95% CI)			90 (±12.6)	302 (±71.4)				

Note: Other species includes Pacific silver-fir, grand fir, Pacific yew, bigleaf maple, and Pacific dogwood. Diameter at breast height (DBH = 1.37 m above ground).

(r^2 = 0.99). Highest tree densities were generally in the ⩽45 cm diameter classes and were dominated by shade-tolerant species (mostly western hemlock; Fig. 1). Douglas-fir size distributions were primarily unimodal and dominated the largest diameter classes, except at Huckleberry. Western hemlock was abundant and at least present throughout the diameter distribution in most sites (Fig. 1). Western redcedar was primarily limited to smaller diameter classes (<60 cm), but at three sites (Cedar Flats, Ohanapecosh, Huckleberry) occurred throughout the diameter distribution (Fig. 1).

Total tree density (stems >5 cm dbh) varied greatly among sites, ranging from 162 to 464 trees/ha (mean of 302 trees/ha). Density of Douglas-fir ranged from 62 to 118 trees/ha (mean of 85 trees/ha). Density of western redcedar was also highly variable (Range = 0–78 trees/ha mean 18, 95% CI = 17.05) and was either absent or scarce in four stands. Douglas-fir dominated the basal area of all sites except Huckleberry; western hemlock and western redcedar were of secondary importance (Table 3). Total basal area varied greatly among sites, ranging from 69 to 121 m^2 ha^{-1} (mean of 89.6 m^2 ha^{-1}) (Table 3).

Douglas-fir was the tallest tree species at all sites (Fig. 2). All stands indicate overlap in heights of Douglas-fir and western hemlock although most stands exhibit a separation (trough) between the tallest Douglas-firs and tallest shade tolerant species (western hemlock and western redcedar) (Fig. 2). Mean height of Douglas-fir ranged from 37.4 to 66.1 m among sites, with western hemlock occupying a shorter position in the forest canopy (range of mean heights = 17.5–34.2 m) (Appendix E). Epicormic branches were present on Douglas-fir trees at all sites, usually near the base of the primary crown with mean height to epicormic branching ranging from 18 to 25.7 m. Crown lengths varied among species with Douglas-fir exhibiting the longest crowns in the majority of stands

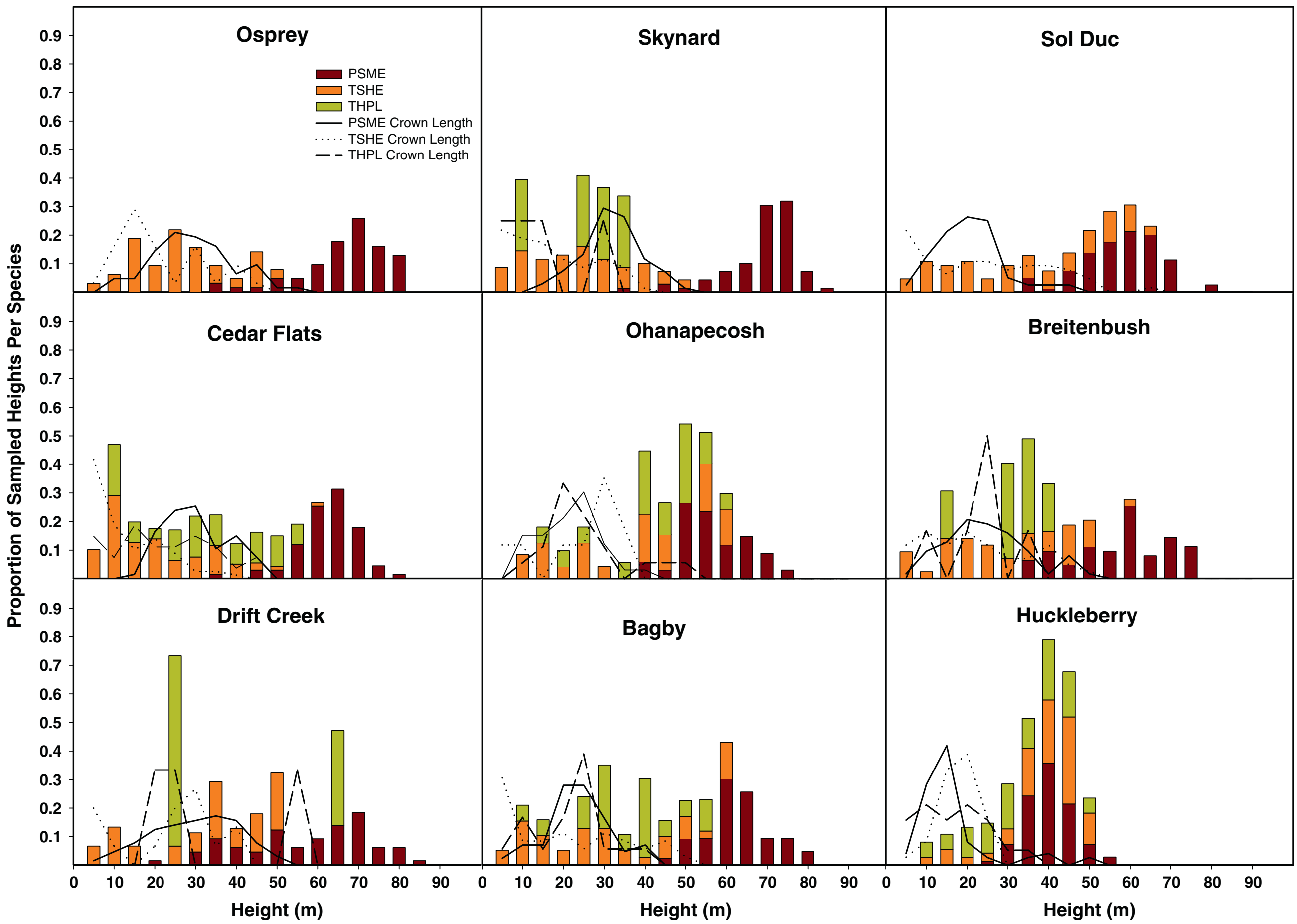

Fig. 2. Height distributions of Douglas-fir, western hemlock, and western redcedar. Red bars represent the distribution of Douglas-fir heights. Orange bars represent distribution of western hemlock heights. Green bars represent distribution of western redcedar heights. Lines indicate distributions of crown lengths for each of the three species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Characteristics of snags ⩾10 cm dbh and ⩾1.37 m in height and logs ⩾10 cm at intercept diameter.

Site	Snags/ha	Snag BA (m^2 ha^{-1})	Snag volume (m^3 ha^{-1})	Logs/ha	Log volume (m^3 ha^{-1})
Osprey	74	20.7	140.2	20	356.7
Cedar Flats	60	17.6	66.5	99	584.3
Drift Creek	34	13.6	42.6	61	236.0
Skynard	92	14.8	46.3	117	280.9
Ohanapecosh	89	21.5	129.7	78	240.5
Bagby	112	20.1	86.4	108	294.1
Sol Duc	85	16.9	95.7	98	186.1
Breitenbush	39	8.2	46.9	57	172.3
Huckleberry	100	10.5	49.4	100	182.3

Note: SD represents the standard deviation.

(mean crown lengths 12.4 22.9 m) Crown lengths of the shade tolerant western hemlock and western redcedar ranged from 0.3–49.5 m and 1.35–51.6 m respectively.

3.2. Snags and logs

Snags were abundant at all sites, but volume varied greatly (Table 4) (Fig. 3). Mean snag densities ranged from 34 to 112 snags/ha (mean = 76, standard deviation 26) and volume from 42.6 to 140.2 m^3 ha^{-1} (Table 4). Most snags were 15–60 cm in diameter (Fig. 3), but all sites (except Huckleberry) had at least a small number of large snags (>100 cm dbh). Log density and volume varied among sites with the majority of pieces in small to medium size classes with volumes ranging from 182.3 to 584.3 m^3 ha^{-1}. Five sites had close to or greater than 100 logs and all sites had at least some large logs (>50 cm at intercept diameter).

3.3. Principal components of early old-growth structure

Principal components analysis of sites and stand level variables identified four primary contributors to variation in structure along Axis 1: basal area of western hemlock, density of shade-tolerant trees, volume of logs, and density of large trees (>100 cm dbh) (Table 5). Structural elements correlated with axis two explained

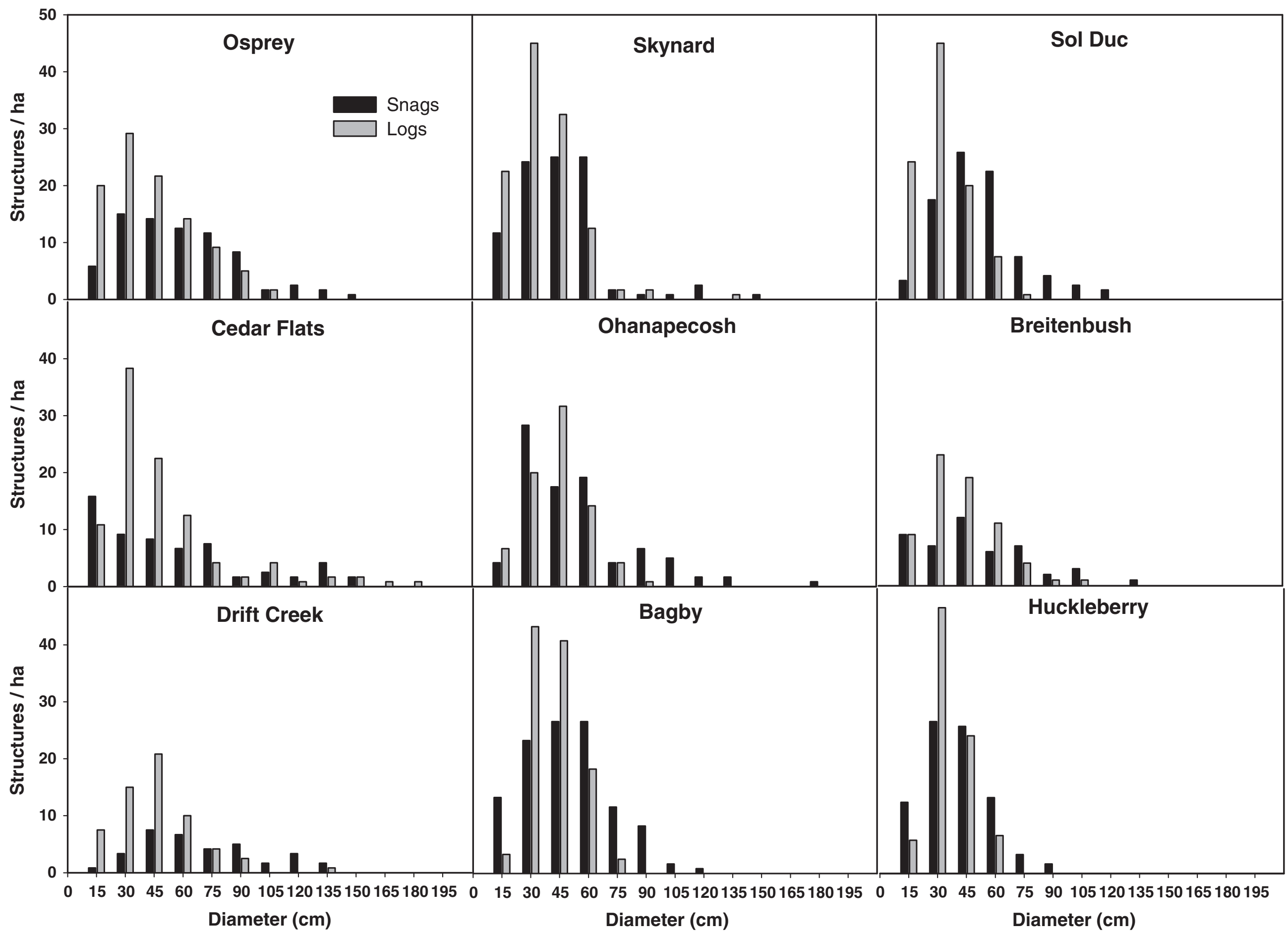

Fig. 3. Snag and log size distributions. Black bars indicate the diameter distribution of the snags measured at 1.37 m above ground. Gray bars indicate the diameter distribution of the logs measured at intercept diameter.

Table 5
Principal components analysis of early old-growth sites and 17 stand level variables.

Variable	PC1	PC2
Total basal area	0.173	−0.051
Basal area of Douglas-fir	−0.155	−0.303
Basal area of western hemlock	0.548	0.104
Basal area of western redcedar	0.022	−0.133
Density of Douglas-fir	0.104	−0.154
Density of shade-tolerant tree species	0.406	0.387
Standard deviation of dbh (all species)	−0.205	−0.072
Density of snags > 50 cm dbh	−0.072	0.282
Mean dbh of live trees	0.010	−0.139
Volume of logs	−0.353	0.413
Volume of snags	−0.210	0.438
Density of trees > 100 cm dbh	−0.360	−0.283
Age range of Douglas-fir	0.201	−0.374
SD of Douglas-fir ages	0.054	−0.013
Mean Douglas-fir crown depth	−0.269	0.027
SD of Douglas-fir crown depth	0.050	−0.109
SD of western hemlock height	0.056	−0.017

Note: Tree density for all stems ⩾5 cm dbh. Values represent loadings. Cumulative proportion of variance explained by the first two principal components = 62%.

18% of the additional variation and included volume of snags and logs, and to a lesser extent basal area of Douglas-fir.

3.4. Old-growth Indices

Based on the log old-growth index of Acker et al. (1998) all sites scored values of 100% except for Huckleberry (Table 6). Based on the OGHI index of Franklin et al. (2005), all sites except Huckleberry had values comparable to old-growth (albeit at the lower end of the old-growth range; Franklin et al., 2005; Gray et al., 2009) (Table 7). All three variants of the OGHI indicate similar scores for early old-growth forests, with the highest index scores under the Standard OGHI (Fig. 4, Appendix B).

3.5. Comparison of early old-growth with younger and older stands

Comparison of individual structural attributes indicates overlap between means and 95% confidence intervals for early old-growth and older stands (Table 8). However, two important differences were the mean values for tree density and stand basal area (Table 8). Element scores of early old-growth differed significantly ($\alpha = 0.05$) from scores of younger and older stands of Spies and Franklin (1991) (Table 9). Post-hoc Holms–Sidak multiple comparison tests indicated significant differences for young-mature, early old-growth, and old-growth age classes (Table 10). Comparisons of early old-growth sites with forests of similar age (Spies and Franklin, 1991; Franklin et al., 2005) did not result in statistically different scores (Table 10). Element scores from the four most productive sites (Site Index I) were generally higher than element scores from lower productivity sites, yet no significant difference ($\alpha = 0.05$, $p = 0.299$) existed.

3.6. Projections of future Douglas-fir densities

Future density of Douglas-fir is variable and is dependent on percent of annual mortality (Fig. 5). Under the 0.28% annual

Table 6
Element scores and ranking of the nine sites using the Iog index of old-growth (Acker **et al.,** 1998).

SITE	Max age (yr)	Iog_SD_DBH	Iog_TPH_>100 cm	Iog_Mean_DBH	Iog_TPH_>5 cm	Iog
Osprey	190	25	25	25	25	**100**
Cedar Flats	191	25	25	25	25	**100**
Drift Creek	193	25	25	25	25	**100**
Skynard	193	25	25	25	25	**100**
Ohanapecosh	296	25	25	25	25	**100**
Bagby	297	25	25	25	25	**100**
Sol Duc	317	25	25	25	25	**100**
Breitenbush	326	25	25	25	25	**100**
Huckleberry	328	9.	6	25	24	**65**

Bold values indicate total index score.

Table 7
Element scores and ranking of the nine sites using the old growth habitat index (Franklin **et al.,** 2005).

Site	Oldest canopy dominant	Big tree score	Large snag score	Log volume score	DDI	Age score	Standard OGHI	Modified OGHI	Weighted OGHI
Osprey	190	83.9	82.9	76.6	51.7	76.0	74.2	73.8	71.5
Cedar Flats	191	85.3	60.4	86.6	50.3	76.4	71.8	70.6	70.5
Drift Creek	192	86.1	41.7	65.7	42.0	76.8	62.4	58.8	60.8
Skynard	193	83.9	41.7	70.7	45.2	77.2	63.7	60.3	62.3
Ohanapecosh	296	75.3	60.4	71.5	37.2	87.6	66.4	61.1	59.8
Bagby	297	61.8	82.9	72.2	38.4	87.7	68.6	63.8	59.3
Sol Duc	317	96.1	79.1	56.7	37.8	89.3	71.8	67.4	65.8
Breitenbush	326	89.7	50.0	58.6	64.4	90.0	70.5	65.6	68.9
Huckleberry	328	3.1	60.4	56.3	23.9	90.2	46.8	35.9	29.7
Mean		73.9	62.1	68.3	43.5	83.5	66.2	61.9	61.0

mortality rate (Spies et al., 1990), early old-growth densities of Douglas-fir are not significantly different from old-growth densities 200 and 300 years in the future (Appendix C). Using the 0.5% annual mortality rate (Bible, 2001) no significant difference exists for the first 200 years, however a statistically significant difference exists at 300 years. Early old-growth Douglas-fir densities under both 0.9% and 1.1% rates of mortality indicate significantly lower densities than current old-growth stands (Appendix C).

4. Discussion

Early old-growth forests represent an intermediate level of structural development between younger and older forests. This intermediate structural space is evidenced by the tree size distributions, diversification of height distributions, and accumulated volumes of snags and logs. Early old-growth structural variation was primarily related to the density and basal area of Douglas-fir, density of shade-tolerant trees, and volumes of coarse woody debris. Composite measures of forest structure computed from one old-growth index (OGHI) provides strong evidence for structural differences between younger and older forests and bolsters support for conceptual descriptions of this developmental stage. The Iog developed by Acker et al. (1998) scored all stands (with the exception of Huckleberry) as fully old-growth however the Iog only accounts for elements of live tree structure. Additionally, Douglas-fir densities in early old-growth stands are projected to be similar or slightly lower than Douglas-fir densities in current well developed old-growth forests. However, increases in annual mortality rates, such as might be associated with climate change, could result in significantly lower Douglas-fir densities in the early old-growth stands of the future.

Many elements of early old-growth structure presented in this study are consistent with the conceptual model developed by Franklin et al. (2002)—with some exceptions. As described in the model, old-growth characteristics begin developing during the early old-growth period. Data on diameter distributions in the early old-growth stands, which show a shift to greater density of shade-tolerant species, are consistent with the conceptual model. Reverse-J or negative exponential tree size distributions have been used to characterize old-growth forests (Franklin and Spies, 1984; Zenner, 2005). Early old-growth tree size distributions were fit well with exponential decay curves, providing support for descriptions related to ongoing development of old-growth structure. The height distributions provide evidence for the development of a continuous canopy from the ground to the tops of the tallest trees with Douglas-fir occupying the highest canopy positions and western hemlock and western redcedar filling in the intermediate canopy positions. Furthermore, observed levels of CWD in early old-growth forests are consistent with conceptual model characterizations of snag and log accumulation during this period.

Structural variability among early old-growth stands is primarily explained by four variables: basal area of western hemlock, density of shade-tolerant trees, density of large-diameter trees, and volume of logs. Surprisingly, the standard deviation of dbh was not related to stand age and was not identified as a strong contributor to the explained variation which contrasts with other analyses of old-growth forest structure (Spies and Franklin, 1991; Acker et al., 1998; Van Pelt and Nadkarni, 2004). Rather, structural variation among early old-growth stands may reflect differences in site productivity or stand history. For example, the standard deviation of dbh was higher in our early old-growth stands (mean = 36.4, 95% CI = 5.3) compared with the old-growth (>400 year) data set, which is probably due to differences in shade-tolerant tree densities among these age classes.

Many structural attributes of early old-growth stands differ from those reported by Spies and Franklin (1991) for older (>400 year) old-growth stands. For example, mean tree densities are considerably lower in the early old-growth even though mean Douglas-fir densities are greater (Table 8). Moreover, density of large trees (>100 cm dbh) and total stand basal area are also higher in the early old-growth forests sampled in this study.

4.1. Old-growth indices

All but one of the early old-growth stands sampled in this study qualify as “old growth” using the index developed by Acker et al.

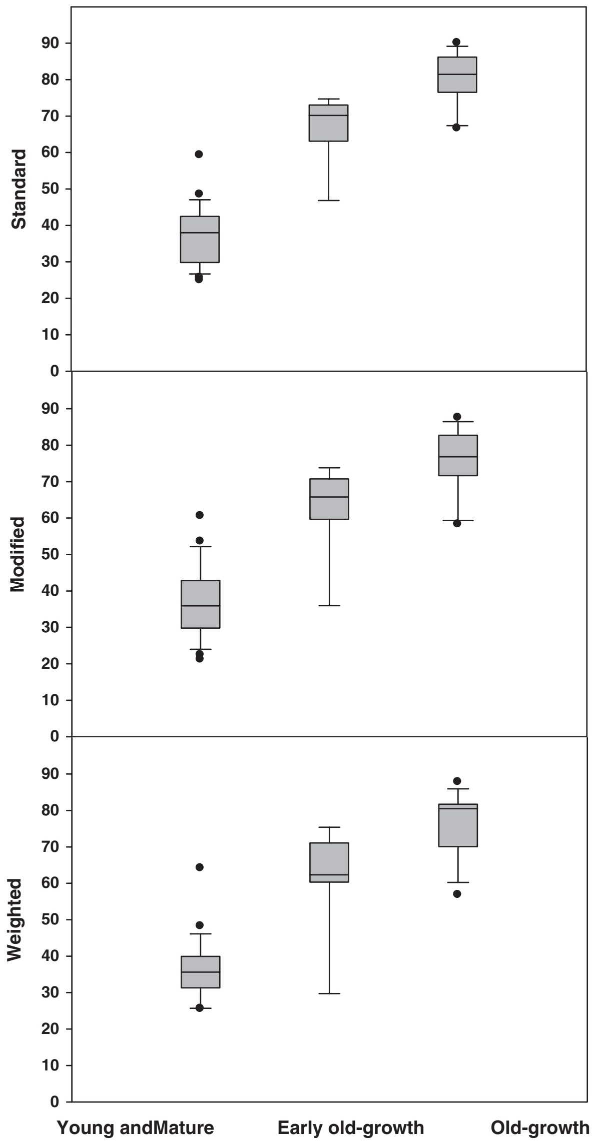

Fig. 4. Box plots of standard, modified, and weighted OGHI scores for early old-growth stands (this study) and index scores from Pabst (2005). Data on young-mature stands and old-growth stands originally come from Spies and Franklin (1991).

(1998). Every stand qualified as old-growth based on the Old Growth Habitat Index used in Franklin et al. (2005) with the exception of Huckleberry (Table 7), and this was true regardless of which index variant of the OGHI was used. Scores from all three variants of the OGHI place the early old-growth forests between both mature and older stands (Fig. 4). Furthermore, the OGHI scores for early old-growth forests are statistically different from OGHI scores for the older (400–600 years-old) and younger (42–140 years-old) stands that were used for the comparison; early old-growth stands have lower median values and little overlap with 50% of the scores for older stands (Fig. 4).

Table 9
ANOVA results for structural element scores of multiple age classes of forest using the OGHI method.

Group name	*N*	Mean	Standard deviation	SEM
Early old-growth (this study)	9	66.9	9.3	3.2
400–600 (Spies and Franklin, 1991)	16	80.3	7.2	1.8
40–150 (Spies and Franklin, 1991)	27	37.3	8.0	1.5
200–300 (Spies and Franklin, 1991)	9	64.0	11.8	4.1

Source of variation	DF	SS	MS	*F*	*P*
Age class	3	19403.19	6467.73	86.795	<0.001
Residual error	53	3949.395	74.517		
Total	56	23352.59			

Coarse-filter indices have great utility for classifying forest structure in a management context, yet vary in their ability to discriminate among stands in relation to old-growth structure. The OGHI index appeared to perform best in structurally distinguishing the different categories of stands (i.e., mature, early old-growth, and well developed old-growth). All of the early old-growth sites had values similar to, but slightly lower than, those of older stands (except Huckleberry), despite their simpler disturbance histories (single vs. multiple disturbance events). Ultimately, this supports hypotheses about structural complexity arising through multiple developmental pathways from a variety of disturbance and establishment histories (Franklin et al., 2002, 2005).

4.2. Projected future densities of Douglas-fir

Projections of future Douglas-fir population densities are similar among the early old-growth stands and generally result in similar or lower Douglas-fir densities than in present-day well-developed old-growth forests, depending upon the mortality rate used in the calculations. Using the lowest rates of mortality (0.28% or 0.5%/year) projected Douglas-fir densities in early old-growth stands 200 years in the future are similar to densities of current well-developed old-growth stands. Hence, these stands would have what is considered to be a characteristic and critical old-growth structure in the form of large and old Douglas-fir trees. These results are also inconsistent with the proposition that dense younger forests cannot develop old-growth characteristics without thinning (Tappeiner, 2009). Stands originating from a single disturbance from ca.1650 to 1800 did establish in less than 100 years (Freund et al., 2014) and generate Douglas-fir densities which are projected to be comparable to those in existing old-growth forests.

Using higher rates of mortality (0.9% and 1.1% annually), future densities of Douglas-fir are projected to be significantly lower than

Table 8
Means and 95% confidence intervals for 8 structural variables from early old-growth and older old-growth stands. Old-growth data come from Spies and Franklin, 1991.

Variable	Early old-growth (this study) mean (CI)		Old growth (Spies and Franklin, 1991) mean (CI)		Overlap
Tree density (trees/ha)	302	(231–373)	448	(394–511)	No
Mean Douglas-fir density (trees/ha)	84	(70–90)	63	(49–79)	Yes
Shade tolerant density (trees/ha)	171	(113–229)	270	(199–353)	Yes
Density of large trees (>100 cm) dbh	34	(22–45)	19	(16–23)	Yes
Mean basal area (m^2 ha^{-1})	90	(77–102)	69	(64–74)	No
Standard deviation of dbh (cm)	36.4	(31–42)	32	(30–34)	Yes
Snag volume (m^3 ha^{-1})	78	(183–464)	159	(128–199)	Yes
Log volume (m^3 ha^{-1})	281	(136–377)	266	(219–324)	Yes

Note: Shade tolerant density for this study represents western hemlock and shade tolerant density for Spies and Franklin (1991) represents pacific silver-fir, white fir, grand-fir, Port-Orford-cedar, Alaska-cedar, western redcedar, western hemlock, and mountain hemlock.

Table 10
Holms–Sidak multiple comparison procedure for ANOVAs of age class structural element scores.

Comparison	Diff of means	*t*	Unadjusted *P*	Critical level
Early old-growth (this study) vs. 40–150 years	29.647	8.495	**<0.001**	0.01
Early old-growth (this study) vs. 400–600 years	13.341	3.53	**<0.001**	0.025
Early old-growth (this study) vs. 190–320 years	2.889	0.669	0.506	0.05

Note: Comparisons are made with data from Spies and Franklin (1991). Significant results are in bold. Comparisons made using values calculated for the standard variant of the OGHI.

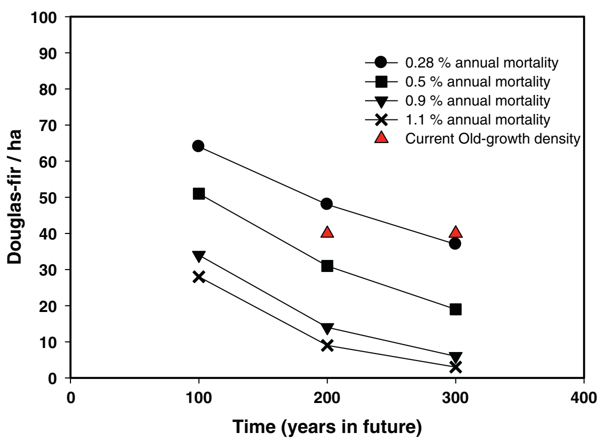

Fig. 5. Projected Douglas-fir densities for 9 early old-growth sites. Lines represent early old-growth Douglas-fir densities at 100, 200, 300 years in the future based on 4 rates of annual mortality. The 0.28% annual mortality is used from Spies et al. (1990). The 0.5% and 0.9% annual mortality rates from Bible (2001). The 1.1% annual mortality rate was subjectively selected to represent a potential future increase in mortality rates.

densities in existing well-developed stands (Fig 5, Appendices C and D). Van Mantgem et al. (2009) identified a general increase in mortality rates in older forests in their (van Mantgem et al., 2009). If the annual tree mortality rate were to increase from 0.9% to 1.1% per annum, Douglas-fir densities could decline by 80% when these forests reach 500 years of age. Future declines in Douglas-fir densities as a result of climate change may have impacts on wildlife habitat (Wilsey et al., 2013).

4.3. Influence of site productivity on forest development

It has been proposed that rates of stand development increase with site productivity on both theoretical (Franklin et al., 2002) and empirical bases (Larson et al., 2008; Gray et al., 2009). This study provides further evidence regarding this hypothesis. In early old-growth, higher-productivity sites (those rated as Douglas-fir Site Class I based on McArdle et al., 1961) generally had higher element scores using the OGHI index, despite the fact that these higher productivity sites are all from the younger (~200 year) cohort of stands.

4.4. Improving indices of stand development

Indices that combine multiple structural parameters can be useful as surrogates for ecological function (e.g., as wildlife habitat; Gray et al., 2009). However, most indices that are currently available use a few easily measured variables. Current indices could be enhanced with the inclusion of additional variables known to be associated with stand age, such as additional measures of crown complexity and decadence (Spies and Franklin, 1991; Van Pelt and Sillett, 2008; Carey, 2007). For example, the complexity of tree crowns has been documented as increasing with forest age (Van Pelt and Nadkarni, 2004; Van Pelt and Sillett, 2008). One or more measures of crown complexity associated with epicormic branch systems and decadent features (broken tops, reiterations, and size of limb systems) could be a useful metric as well as having a direct relationship with niche diversification (Carey et al., 1999; Carey, 2009). Another possibility would be to rate dominant Douglas-firs as to whether the crowns still retain a model-conforming appearance (as defined by Van Pelt and Sillett, 2008) or exhibit individualist crown forms (e.g., dead, broken, and reiterated tops) characteristic of many older trees.

Some other easily measured aspects of decadence might also be considered for inclusion in old-growth indices. Examples include abundance of western-hemlock dwarf mistletoe (*Arceuthobium tsugense* subsp. *tsugense*) in western hemlock and abundance of Douglas-fir trees that have collapsed as a result of velvet top fungus (*Phaeolus schweinitzii*). Mistletoe-generated brooms are important structural features for a variety of animals and are largely a feature of old-growth forests. Velvet top fungus is a slow-developing rot that decays the heartwood at the butt (root crown and lower bole), eventually resulting in mechanical failure (breakage) and death. Velvet top fungus is the most important single cause of death of old-growth Douglas-fir trees (Bible, 2001) and affects many other species. Onset of mortality due to velvet top fungus first becomes apparent during the transition from mature to old forests (Franklin et al., 2002), thus making it a potential useful indicator of old-growth development. Although there was no systematic collection of data on occurrence of velvet-top-related mortality in this study, we would include it in any future study of stand development.

4.5. Management implications

Conservation and restoration of structurally complex forest stands is emphasized in United States federal land management objectives within the Douglas-fir region (Franklin and Spies, 1991; USDA and USDI, 1994; Carey, 2003; Larson et al., 2008; Larson and Churchill, 2012). The structural data on early old-growth forests from this study provides forest managers with additional natural reference points for management. Common approaches to accelerating old-growth structures in young stands include: (1) increasing growth of live trees and the abundance of large trees; (2) increasing canopy complexity, including the number and size of epicormic branch structures; and (3) accelerating development of vertically-continuous canopies. The goal of such treatments generally is to improve habitat conditions for late-successional wildlife (Carey, 2003, 2007).

Structural data from these early old-growth forests provide closer temporal targets for managers, especially when management objectives are aimed at creating characteristic densities and sizes for Douglas-fir trees as forests enter the "old-growth" stage. Managers seeking to manipulate dense, younger stands may find the range of variation among shade-tolerant trees and dead wood as useful guides for thinning, planting shade-tolerant species (western hemlock, western redcedar, Pacific yew), and managing for snags. We also acknowledge that one possible inference that could be made from this study is that many single-cohort early old-growth forests are probably on trajectories that will produce suitable structural complexity and do not require any active management. As the conservation of forest biodiversity remains of paramount importance to society and land management agencies it is imperative that management incorporate the known variability found throughout the forest sere. Baseline data on natural forest stands, such as we present here, provide the scientific basis of managing for ecological values.

4.6. Conclusions

Structural analyses of forests early in development of old-growth attributes fill a significant gap in our knowledge of stand development. Furthermore, this investigation highlights the continuity of structural development well past 300 years, suggesting that strictly age based management approaches may be inadequate to fulfill management objectives (Price et al., 2009). Structural attributes of these early old-growth are intermediate between mature and well-developed old-growth forests, but early old-growth stands already have many structural attributes characteristic of older forests (e.g. tree size distributions, vertically continuous canopies, and large volumes of CWD). This study enhances understanding of forest structure that develops following a single initiating disturbance since many older stands have developed following multiple disturbances. Yet, despite differences in the developmental sequences associated with intermediate fire, the structural future of these early old-growth forests is projected to be similar to current old-growth forests in terms of Douglas-fir densities unless conditions are created in which mortality rates increase.

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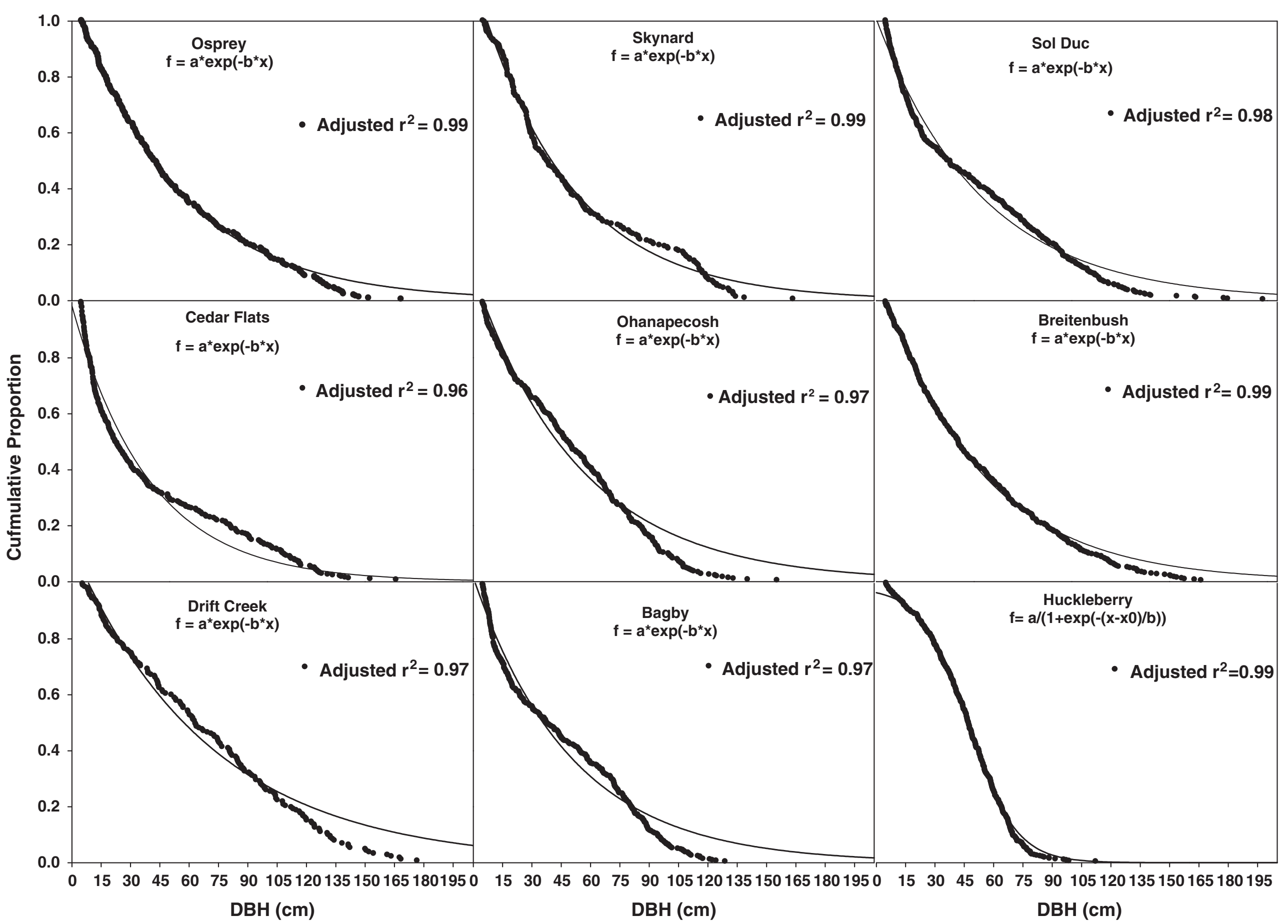
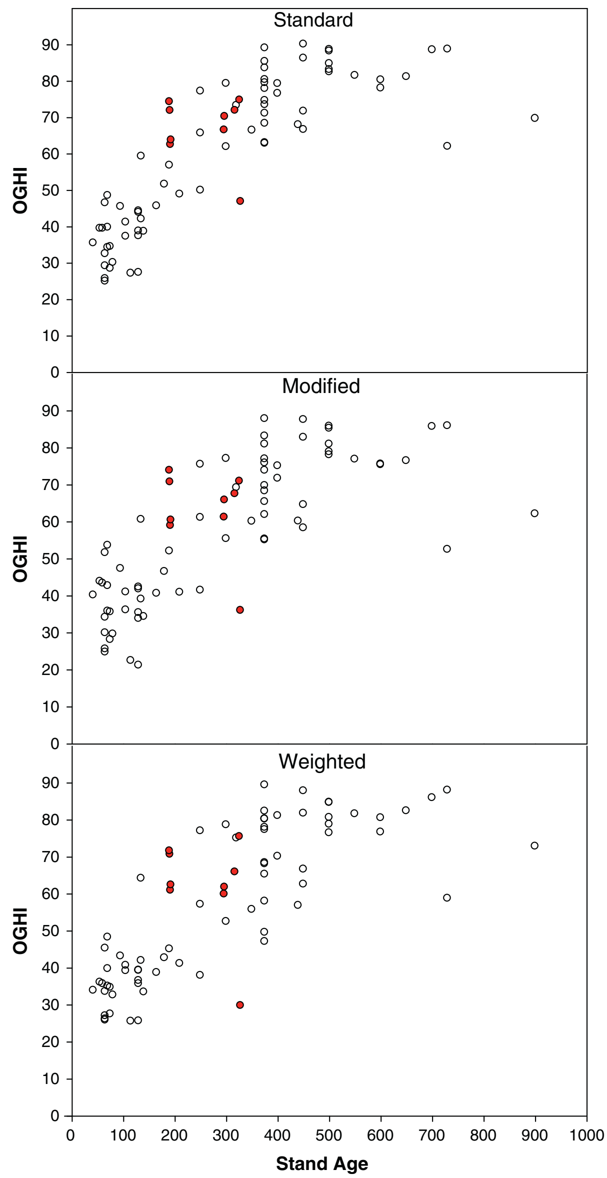
Appendix A

Non-linear regression curves fit to the cumulative diameter distributions at each early old-growth site. Distributions were best fit with 2 parameter exponential decay curves with the exception of Huckleberry.



Appendix B

Stand age versus index score using the standard, modified, and weighted Old Growth Habitat Index (OGHI). Open circles represent data from Spies and Franklin (1991) and filled red circles represent early old-growth sites from this study.



Appendix C

Projections of early old-growth Douglas-fir density at 100, 200, and 300 years in the future.

	Current Douglas-fir density					Projected Douglas-fir density							
		100 years				200 years				300 years			
Annual mortality Rate		0.28%	0.50%	0.90%	1.10%	0.28%	0.50%	0.90%	1.10%	0.28%	0.50%	0.90%	1.10%
Osprey	85	64	51	34	28	49	31	14	9	37	19	6	3
Cedar Flats	62	47	38	25	21	35	23	10	7	27	14	4	2
Drift Creek	87	66	53	35	29	50	32	14	10	38	19	6	3
Skynard	65	49	39	26	22	37	24	11	7	28	14	4	2
Ohanapecosh	72	54	44	29	24	41	26	12	8	31	16	5	3

Appendix C (*continued*)

	Current Douglas-fir density					Projected Douglas-fir density							
		100 years				200 years				300 years			
Bagby	93	70	56	38	31	53	34	15	10	40	21	6	3
Sol Duc	118	89	71	48	39	67	43	19	13	51	26	8	4
Breitenbush	108	82	65	44	36	62	40	18	12	47	24	7	4
Huckleberry	74	56	45	30	24	42	27	12	8	32	16	5	3
Mean (CI)		64 ± 11	51 ± 8	34 ± 5	28 ± 4	48 ± 8	31 ± 5	13 ± 2	9 ± 1	37 ± 6	18 ± 3	5 ± 1	3 ± 0.5
Sig. Different from Old-growth density		$P = 0.008$	$P = 0.142$	$P = 0.593$	$P = 0.205$	$P = 0.282$	$P = 0.385$	$P = 0.005$	$P = <0.001$	$P = 0.481$	$P = 0.019$	$P = <0.001$	$P = <0.001$

Note: Mortality rates from Spies et al. (1990), Debell and Franklin (1987), and Bible (2001). Highest mortality rate represents potential increase in annual mortality (van Mantgem et al., 2009). Bold *p* values indicate significant difference.

Appendix D

Douglas-fir density from 13 old-growth forests. Douglas-fir density data come from Spies and Franklin (1991) and the Wind River Forest Dynamics Plot (Lutz et al., 2013).

Area	Stand	Age	PSME/density
2_25	25	450	44.02
2_27	27	450	44.90
2_30	30	450	84.93
2_98	98	450	32.37
3_16	16	500	60.31
3_17	17	500	43.28
3_2	2	500	30.00
3_32	32	600	62.49
4_1	1	500	20.01
4_3	3	500	10.01
Wind river	WFDP	500	21.90
4_18	18	550	50.79
3_3	3	600	11.09
Mean density (95% CI)			39.7 (±13.19)

Appendix E

Height characteristics for live trees ⩾5 cm at 1.37 m above ground.

Site	Species	Mean height (m)	(SD)	Mean crown length (m)	(SD)	Mean epicormic height (m)	(SD)
Osprey							
	Douglas-fir	62.5	13.0	16.2	15.4	22.5	7.4
	Western hemlock	23.7	11.9	4.2	9.2	n/a	n/a
	Western redcedar	n/a	n/a	n/a	n/a	n/a	n/a
Cedar Flats							
	Douglas-fir	60.1	7.5	27.6	7.9	21.5	6.8
	Western hemlock	17.5	12.4	10.3	8.9	n/a	n/a
	Western redcedar	28.6	15.2	19.9	12.4	n/a	n/a
Drift Creek							
	Douglas-fir	54.5	15.3	17.6	16.6	18	6.5
	Western hemlock	29.1	15.4	5.2	11.0	n/a	n/a
	Western redcedar	34.8	22.1	23.3	21.4	n/a	n/a
Skynard							
	Douglas-fir	66.1	11.1	25.6	12.8	25.7	5.6
	Western hemlock	21.5	12.4	7.9	10.4	n/a	n/a
	Western redcedar	22.7	11.0	8.4	10.8	n/a	n/a

(*continued on next page*)

Appendix E (*continued*)

Site	Species	Mean height (m)	(SD)	Mean crown length (m)	(SD)	Mean epicormic height (m)	(SD)
Ohanapecosh							
	Douglas-fir	52.7	12.3	18.6	7.4	19.9	12.0
	Western hemlock	34.2	17.4	21.8	11.3	n/a	n/a
	Western redcedar	40.3	11.9	23.2	10.6	n/a	n/a
Bagby							
	Douglas-fir	60.5	7.7	12.4	14.0	25.3	7.0
	Western hemlock	28.2	7.7	18.4	13.9	n/a	n/a
	Western redcedar	32.1	11.9	18.4	8.9	n/a	n/a
Breitenbush							
	Douglas-fir	55.4	11.5	22.4	10.0	19.0	8.3
	Western hemlock	26.9	14.6	19.7	12.7	n/a	n/a
	Western redcedar	28.0	8.4	21.1	8.8	n/a	n/a
Sol Duc							
	Douglas-fir	55.3	9.4	17.9	8.1	24.9	6.0
	Western hemlock	31.5	18.4	21.3	15.3	n/a	n/a
	Western redcedar	n/a	n/a	n/a	n/a	n/a	n/a
Huckleberry							
	Douglas-fir	37.4	5.9	12.9	9.3	21.8	4.3
	Western hemlock	33.6	11.0	15.7	5.5	n/a	n/a
	Western redcedar	30.0	10.1	14.0	8.4	n/a	n/a

Appendix F

Characteristics of logs ⩾10 cm in intercept diameter.

Site	Mean diameter (cm)	Volume (m^3 ha^{-1}) of logs by decay class				
		1	2	3	4	5
Osprey	35.9	66.0	104.0	70.6	94.0	22.1
Cedar Flats	42.4	5.7	379.0	96.6	88.4	14.4
Drift Creek	38.6	15.0	144.0	51.5	17.9	6.9
Skynard	30.1	1.3	4.1	99.4	75.6	165.4
Ohanapecosh	36.1	39.2	28.8	69.6	19.3	22.9
Bagby	34.6	33.9	28.2	129.4	40.3	4.9
Sol Duc	25.0	12.4	44.0	78.1	13.6	6.9
Breitenbush	34.3	64.3	29.4	37.1	5.5	2.3
Huckleberry	28.1	20.4	35.3	68.7	11.0	7.1
Total		258.2	796.8	701.0	365.6	252.9

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