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Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California

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Abstract. Despite its importance to biodiversity and ecosystem function, patterns and drivers of regional scale variation in forest structure and development are poorly understood. We characterize structural variation, create a hierarchical classification of forest structure, and develop an empirically based framework for conceptualizing structural development from 11,091 plots across 25 million ha of all ownerships in Oregon, Washington, and inland Northern California, USA. A single component related to live tree biomass accounted for almost half of the variation in a principal components analysis of structural attributes, but components related to live tree density and size, dead wood, and understory vegetation together accounted for as much additional variation. These results indicate that structural development is more complex than a monotonic accumulation of live biomass as other components may act independently or emerge at multiple points during development. The classification revealed the diversity of structural conditions expressed at all levels of live biomass depending on the timing and relative importance of a variety of ecological processes (e.g., mortality) in different vegetation zones. Low live biomass structural types (<25 Mg/ha) illustrated the diversity of early-seral conditions and differed primarily in density of live trees and abundance of snags and dead wood. Moderate live biomass structural types (25–99 Mg/ha) differed in tree size and density and generally lacked dead wood, but some structurally diverse types associated with partial stand-replacing disturbance had abundant live and dead legacies. High live biomass structural types (>100 Mg/ha) substantiated the diversity of later developmental stages and exhibited considerable variation in the abundance of dead wood and density of big trees. Most structural types corresponded with previously described stages of development, but others associated with protracted early development, woodland/savannah transitions, and partial stand-replacing disturbance lacked analogs and indicated alternative pathways of development. We propose a conceptual framework that distinguishes among families of pathways depending on the range of variation along different components of structure, the relative importance of different disturbances, and complexity of pathways. Our framework is a starting point for developing more comprehensive models of structural development that apply to a wider variety of vegetation zones differing in environment and disturbance regimes.

Key words: disturbance history; early-seral vegetation; forest structural development; live and dead biomass; logging; old-growth; Pacific Northwest; tree density and size; understory vegetation; wildfire.

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INTRODUCTION

Despite the importance of forest structure to ecosystem function (Waring and Running 2007) and biodiversity (MacArthur and MacArthur 1961), variation in structure at the regional scale is poorly understood. Past regional scale studies have focused primarily on how climate constrains biomass (Gholz 1982, Malhi et al. 2006, Urquiza-Haas et al. 2007, Hudiburg et al. 2009), but more detailed investigations of other structural attributes such as standing dead trees (snags) and dead or downed wood are rare (Spies and Franklin 1991, Ohmann and Waddell 2002, Ohmann et al. 2007, Ares et al. 2012). Although structural development has been conceptualized for a few well-studied forest types following stand-replacing disturbance (e.g., Bormann and Likens 1979, Oliver and Larson 1990, Franklin et al. 2002), we lack a conceptually or empirically based biogeographic understanding of how variation in the distribution of live and dead biomass results in different structural conditions and developmental pathways across regional (>100,000 ha) gradients in climate, disturbance regimes, and species composition.

Vegetation structure can be broadly defined as the vertical and horizontal distribution and arrangement of live and dead vegetation (Spies 1998). In most temperate forest ecosystems, structure can be broken down into three major components including live trees, dead wood, and non-arborescent understory plants (Franklin et al. 2002). The live tree component is the most commonly studied component of forest structure and is often described using simple metrics (e.g., biomass, basal area, tree density) as well as variation in size and spatial arrangement of trees (e.g., Pommerening 2002). The dead wood component can be broken down into the number and size of snags and dead and downed wood. Snag abundance is often quantified by density (per unit area), but because dead wood is continually breaking down through fragmentation and decomposition, biomass estimates offer more precise measures of the abundance of snags and dead and downed wood in ecosystem studies (Harmon et al. 1986). Understory vegetation can be further characterized into functional groups (e.g., forbs, shrubs, graminoids) and is generally quantified with estimates of cover or biomass. All three components are intimately linked as the cumulative result of the processes of growth, mortality, and decomposition (Spies 1998). As a result, forest structure is an inherently complex multivariate concept with broad ecological implications that vary by individual components and ecological context.

Much of our current conceptualization of structural variation at the stand scale (1–100 ha) has focused on structural development following stand-replacing disturbances such as wildfire and logging (e.g., Bormann and Likens 1979, Oliver and Larson 1990, Franklin et al. 2002). These conceptual models are founded on a linear age- and/or process-based framework of stand development. Chronological stages proceed along a single pathway and represent unique structural conditions resulting from the dominant endogenous processes occurring during each stage (e.g., stand initiation/ reorganization, stem exclusion/self-thinning, understory re-initiation/ maturation, old-growth). Forest structure may be simple or complex during early developmental stages depending on disturbance type and the presence of biological legacies such as large live trees, snags, and downed wood (Franklin et al. 2002, Swanson et al. 2010, Donato et al. 2012). Structure during mid developmental stages is generally considered less diverse since live trees are typically dominated by a single cohort and the dead wood and snags created by stand-replacement disturbances have largely decomposed (Spies et al. 1988). Structural diversity increases during later developmental stages when a variety of live and dead tree sizes, as well as dead wood on the forest floor, are all present (Spies 1998).

Although these models are useful for conceptualizing structural development in forests subject to stand-replacing disturbances, they are typically idealized, based on theory, and have yet to be evaluated against large empirical data sets of existing forest conditions across a regional extent including a variety of vegetation zones. Multiple, non-linear developmental pathways are possible in vegetation zones where disturbances operate at a range of severities (Frelich 2002). Frequent low-severity disturbances have the potential to maintain structure (Platt et al. 1988) while moderate-severity, partial stand-replacing disturbances may accelerate structural

development (Veblen et al. 1991). Additionally, some forests may develop from non-forested states including grasslands and shrublands (e.g., Archer 2010) and savannahs and woodlands may be intermediate stages between states. Although it is evident that a variety of structural conditions in early (Halpern 1988, Donato et al. 2012) and later developmental stages are possible within a single vegetation zone (McCune and Allen 1985), we lack a generalizable framework to describe the diversity of potential pathways of structural development across multiple vegetation zones.

Forest structure is a major component of biological diversity (Spies 1998, McComb 2008) and focus of regionally based planning efforts (USDA Forest Service, DOI, and BLM 1994). Maintaining, creating, and restoring particular elements of forest structure have been much of the focus of coarse and meso filter strategies (Hunter 2005) pertaining to the conservation of biological diversity in many parts of the world (Australian and New Zealand Environmental Conservation Council 2000, U.S. Fish and Wildlife Service 2003, 2011, Montreal Process Working Group 2009). Despite the importance of forest structure as a major component of habitat diversity (McComb et al. 1993, Franklin and Van Pelt 2004, Verschuyl et al. 2008) and application of forest structure types in forest state and transition models and wildlife management guides (Johnson and O'Neil 2001, Hemstrom et al. 2004), we are not aware of any empirically based regional scale characterizations of stand structure. Developing an understanding of regional scale variation is important for conservation planning and monitoring, as well as for developing advanced theoretical models and frameworks capable of quantifying regional forest dynamics in response to a warming climate and altered disturbance regimes.

We used a regional forest inventory representing over 11,000 plots to characterize forest structure on lands of all ownerships across 25 million ha of forested land in Oregon, Washington, and inland Northern California to address the following questions:

1. What are the major components of forest structure at a regional scale?
2. What unique structural conditions are created from different combinations of individual structural components?
3. How do these unique structural conditions differ in age in different vegetation zones?
4. How do empirically defined developmental stages relate to those in theoretical models of structural development?
5. How do potential pathways of structural development differ among vegetation zones?

Methods

Study region

Our study region is approximately 25 million ha and includes all forest lands in Oregon, Washington, and inland Northern California (Fig. 1). The region is highly diverse and includes a variety of vegetation zones that follow broad climatic and topographic gradients (Franklin and Dyrness 1973, Barbour and Major 1988, Ohmann and Spies 1998). The climate is generally mediterranean with most precipitation falling in the winter (though some portions of the eastern part of the region receive a large proportion in summer thunderstorms), but large gradients in precipitation, temperature, and elevation create a wide range of climatic conditions from warm and moist at low elevations near the coast to cold and dry at higher elevation further east.

We acquired a map of the major vegetation zones of the study region (Simpson 2013) from the Ecoshare Interagency Clearinghouse of Ecological Information (www.ecoshare.info/category/gis-data-vegzones; Fig. 1). Each vegetation zone represents a single potential climax vegetation type that would develop in the absence of major disturbance and represents a unique species pool within a defined biophysical setting with similar climatic and topographic conditions and historical disturbance regimes (Winthers et al. 2005). Vegetation zones enable the interpretation of structural types in a broader context since the same structural type may represent different developmental stages in different vegetation zones. Major vegetation zones correspond to those presented by Franklin and Dyrness (1973) and can generally be broken into wet and dry forests. Major wet forest vegetation zones are located in the western part of the region and include those dominated by redwood (*Sequoia sempervirens*) Sitka spruce (*Picea sitch-*
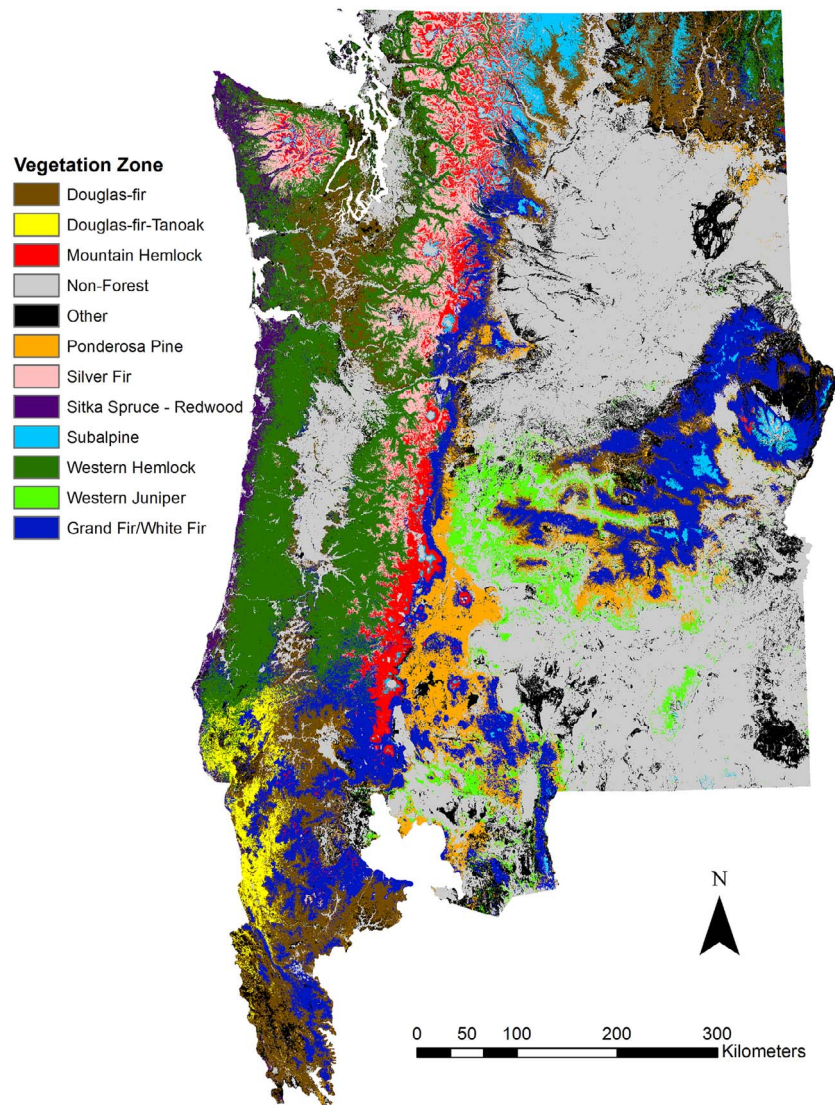
Fig. 1. Map of major forested potential vegetation types (from Simpson 2013) in Oregon, Washington, and inland Northern California, USA.

ensis) and redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*) and tanoak (*Lithocarpus densiflorus*), western hemlock (*Tsuga occidentalis*), Pacific silver fir (*Abies amabilis*), and mountain hemlock (*Tsuga mertensiana*). Major dry forest vegetation zones are located in the eastern part of the region and include those dominated by western juniper (*Juniperus occidentalis*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziziii*), grand fir (*Abies grandis*) and white fir (*Abies concolor*), and subalpine forests dominated by subalpine fir (*Abies lasiocarpa*),

Engelmann spruce (*Picea engelmanii*), and white-bark pine (*Pinus albicaulis*).

Natural and anthropogenic disturbances influenced the development of forest structure in all vegetation zones. Wildfire played a major role across the entire study region but varied over time (Agee 1993, Weisberg and Swanson 2003). Historic fire regimes range from high frequency, low-severity fire in warm, dry forests to low frequency, high-severity fire in cold and wet forests. Much of the vegetation in the region was historically subject to a mixed-severity fire

regime where the proportion of high-severity fire varied spatially and temporally (Agee 1993, Perry et al. 2011). Several decades of fire exclusion are believed to have altered forest composition and structure across much of the region, particularly in dry forests of the eastern and southern portions of the region (Perry et al. 2011), but wildfires have increased in frequency and extent since the mid-1980s (Littell et al. 2009). Wind-storms and landslides associated with storms off the Pacific Ocean play a far greater role in wet forests than in dry forests, particularly in coastal areas on steep, exposed landforms (Sinton et al. 2000).

In wet forests of the western portion of the study area, widespread clearcut logging in lower elevation private forests began in the late 1800s, but started on federal lands in the 1940s and reached its peak in the 1970s and 1980s (Johnson and Swanson 2009). The passage of the North-west Forest Plan (NWFP) in 1994 essentially stopped clearcutting of older forests on federal lands within the range of the Northern Spotted Owl (*Strix occidentalis caurina*), but clearcutting is still the dominant practices on private forests managed for timber production. Forests in the drier eastern and southern parts of the region were directly affected by grazing of domestic animals and high grade logging with the selective removal of large old-growth ponderosa pine in the early to middle part of the 20th century (Langston 1995, Hessburg and Agee 2003). Although removal of fine fuels by livestock grazing reduced the role of fire in dry forests during this time, high-severity wildfires affected some areas in the eastern part of the region prior to the adoption of fire suppression policies that began in the early 1900s (Brown 1968, Langston 1995). Logging has occurred in most vegetation zones but substantial tracts of unlogged forest still remain on federal lands (Moeur et al. 2011).

Field data

We acquired field data on forest structure from 11,091 one ha plots from the USDA Forest Service Pacific Northwest Research Station Annual Forest Inventory and Analysis program (FIA) PNW-FIA Integrated Database (IDB). Plots were located systematically at a density of approximately one every 2,400 ha in areas capable of supporting forest across all land

ownerships in Oregon, Washington, and inland northern California and give an unbiased of forest conditions across the region during the study period. Data collection began in 2001 and continued until 2010 with approximately one-tenth of the plots sampled each year. Plots included a series of four variable radius subplots. Live trees and snags <12.7 cm dbh and of cover of understory vegetation (shrubs, forbs, and graminoids) were measured in 2.1 m radius microplots. Live trees and snags >12.7 cm dbh were measured in 7.32 m radius subplots. Live trees and snags >76.2 cm dbh on the west side of the Cascade Crest and >61 cm dbh on the east side were measured in 18 m radius subplots. Dead and downed wood was sampled along two 7.32 m transects in each subplot.

We acquired plot scale (one ha) summaries of variables describing live tree structure from the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) Project (http://lemma. forestry.oregonstate.edu). These variables included the following: basal area (BA), density (TPH), live tree biomass (BPH), quadratic mean diameter of all dominant and codominant trees (QMD), basal area-weighted mean dbh of all live trees (DBH), a diameter diversity index (DDI) based on the tree densities in different size classes (Spies et al. 2007), standard deviation of dbh (SDDBH), average height of all dominant and codominant trees (STNDHT), and percent canopy cover of all live trees (CC) as calculated using methods in the Forest Vegetation Simulator (FVS) (Crookston and Stage 1999). This method corrects for overlapping canopies and canopy closure occurs at about 65%. Variables describing dead wood included the density (SDPH), and biomass (SBPH) of snags >12 cm dbh and >2 m tall, as well as the biomass of dead and downed wood >12 cm at the large end and >3 m long (BDW). The only non-tree variable included total cover of understory vegetation (USC) which was calculated as the summed total percent cover of shrubs, forbs, and graminoids.

We acquired spatial data on the perimeters of wildfires greater than 400 ha from 1984 to 2010 from the Monitoring Trends in Burn Severity Program (www.mtbs.gov) and overlaid plot locations to classify plots as burned or unburned.

Table 1. Proportion of variance explained for the first five dimensions of a principal components analysis on attributes of forest structure in Oregon, Washington, and inland Northern California, USA.

Attribute	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Proportion of variance explained (total = 0.90)	0.47	0.16	0.13	0.09	0.06
Basal area	−0.39	. . .	. . .	. . .	. . .
Live tree density	. . .	0.60	−0.33	. . .	. . .
Live tree biomass	−0.40	. . .	. . .	. . .	. . .
Quadratic mean diameter	−0.25	−0.53	. . .	. . .	. . .
Diameter diversity index	−0.38	. . .	. . .	. . .	. . .
Standard deviation of diameter at breast height	−0.34	−0.27	. . .	. . .	. . .
Stand height	−0.35	−0.24	. . .	. . .	. . .
Canopy cover	−0.33	0.29	−0.3	. . .	. . .
Snag density	. . .	0.24	0.56	. . .	0.42
Snag biomass	−0.23	. . .	0.58	. . .	. . .
Biomass of dead and downed wood	. . .	. . .	0.32	−0.34	−0.81
Understory cover	. . .	. . .	. . .	−0.92	0.35

Data analysis

We used principal components analysis (PCA) to reduce the dimensionality of the previously listed metrics of stand structure since many structural attributes are linearly related (e.g., live tree biomass and basal area). We used the princomp function in R with the cross-products matrix based on the correlation matrix among variables. All variables were centered to a mean of zero and standardized in order to equalize variance among variables measured in different units.

We performed hierarchical agglomerative clustering with Euclidean distance and Ward's method (Ward 1963) to assign each plot into structure-based clusters. Agglomerative clustering works by iteratively merging the most similar plots into groups until all groups are merged. We used the hclust.vector algorithm in the package fastcluster in R (R Development Core Team 2011). Plots were clustered on the axis scores of the first five dimensions of the PCA to reduce redundancy of correlated structural variables (e.g., basal area and biomass) as well as subjectivity or bias in selection of specific variables.

We used data on ages of dominant and co-dominant trees to assign an estimated stand age for each plot. Age of individual trees was estimated in the field from increment cores taken from one live dominant and co-dominant tree for each species. In cases where trees were too large for the increment borer to reach the pith of the tree, age was estimated based on growth in the inner five cm of the core. Stand age was then estimated as the basal area weighted average age of all dominant and co-dominant tree ages in a plot. We compared the plot level median basal area weighted ages of dominant and co-dominants first among structural classes and then among vegetation zones by individual structural classes using notched boxplots. Notched boxplots show the median, interquartile range, and notches that approximate a 95% confidence interval around median values where the lack of overlap between the notches of two boxes provides strong evidence that medians differ (Chambers et al. 1983).

RESULTS

Principal components analysis of structural variation

The first five PCA components accounted for 90% of the variance explained (Table 1). Component 1 was strongly and negatively correlated with live tree biomass and basal area. Component 2 had a strong positive correlation with the density of trees per ha and strong negative correlation with quadratic mean diameter. Component 3 had a strong positive correlation with the biomass and density of snags and biomass of dead and downed wood, but a strong negative correlation with density of live trees. Component 4 was negatively correlated with the cover of understory vegetation and biomass of dead and downed wood. Component 5 was negatively with the biomass of dead and downed wood, but was also strongly and positively correlated with the density of snags per ha and the cover of understory vegetation.
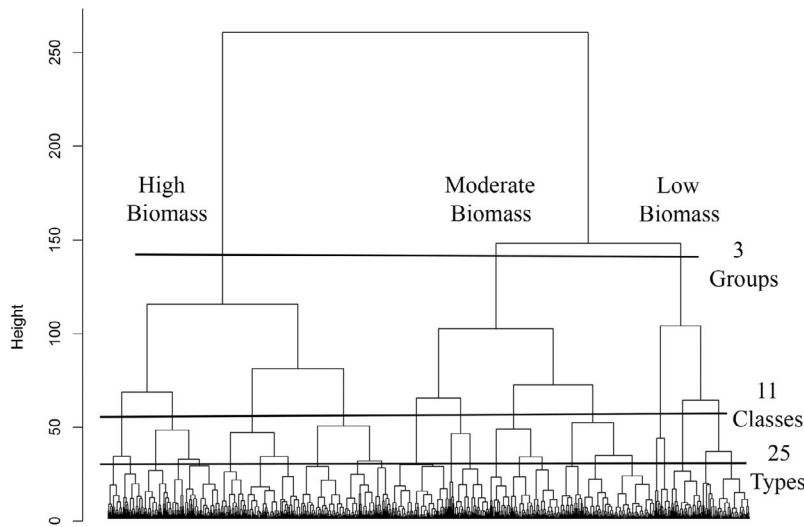
Fig. 2. Dendrogram with hierarchical classification of forest structural groups, classes, and types in Oregon, Washington, and inland Northern California.

Classification of structural types

We began interpreting clusters from the classification by iteratively "cutting" the dendrogram (Fig. 2) at increasing numbers of clusters representing broad but ecologically interpretable structural groupings with the goal of representing variation along all five PCA components while still maintaining a manageable number of clusters. The hierarchy of clusters begins with "groups" at the coarsest level which are then broken into "classes," and then finally into "types." The initial cut resulted in three clusters representing low (<25 Mg/ha), moderate (25–99 Mg/ha), and high live tree biomass (>100 Mg/ha) structural groups. The second cut resulted in eleven clusters that broke groups into "structural classes" that differed in live tree density and QMD (Fig. 3). We continued identifying clusters to include structural variation along the other components including snags, understory cover, and biomass of dead and downed wood (Table 2). Structural types also varied in relative abundance among vegetation zones (Table 3), geographic distributions (Appendix A), size class distributions of live trees, snags, dead and downed wood, and the proportion of understory cover composed of shrubs, forbs and graminoids (Appendix B).

Age differences among structural classes

Median age of structural classes varied among vegetation zones (Figs. 4 and 5). Age generally increased with live biomass in wet vegetation zones, but showed little relationship to biomass in dry vegetation zones, with the exception of Douglas-fir and grand fir/white fir where median age was greatest in the highest biomass classes. Median age of dominant and co-dominant trees frequently differed among vegetation zones for individual structural classes (Appendix C). The major exceptions to this were in dry vegetation zones and in Structural Class 1 (Very Low Live Biomass and Density) where the median age was zero and there was no evidence of differences among vegetation zones. Median age of structural classes was generally lowest in western hemlock and Sitka spruce-redwood vegetation zones and highest in mountain hemlock and western juniper zones.

DISCUSSION

This study is the first empirically based characterization of multiple components of forest structure for any region and reveals the complexity of forest structure across vegetation zones and environments. Although most variation in forest structure was related to live tree biomass, basal area, and the presence of big trees, other
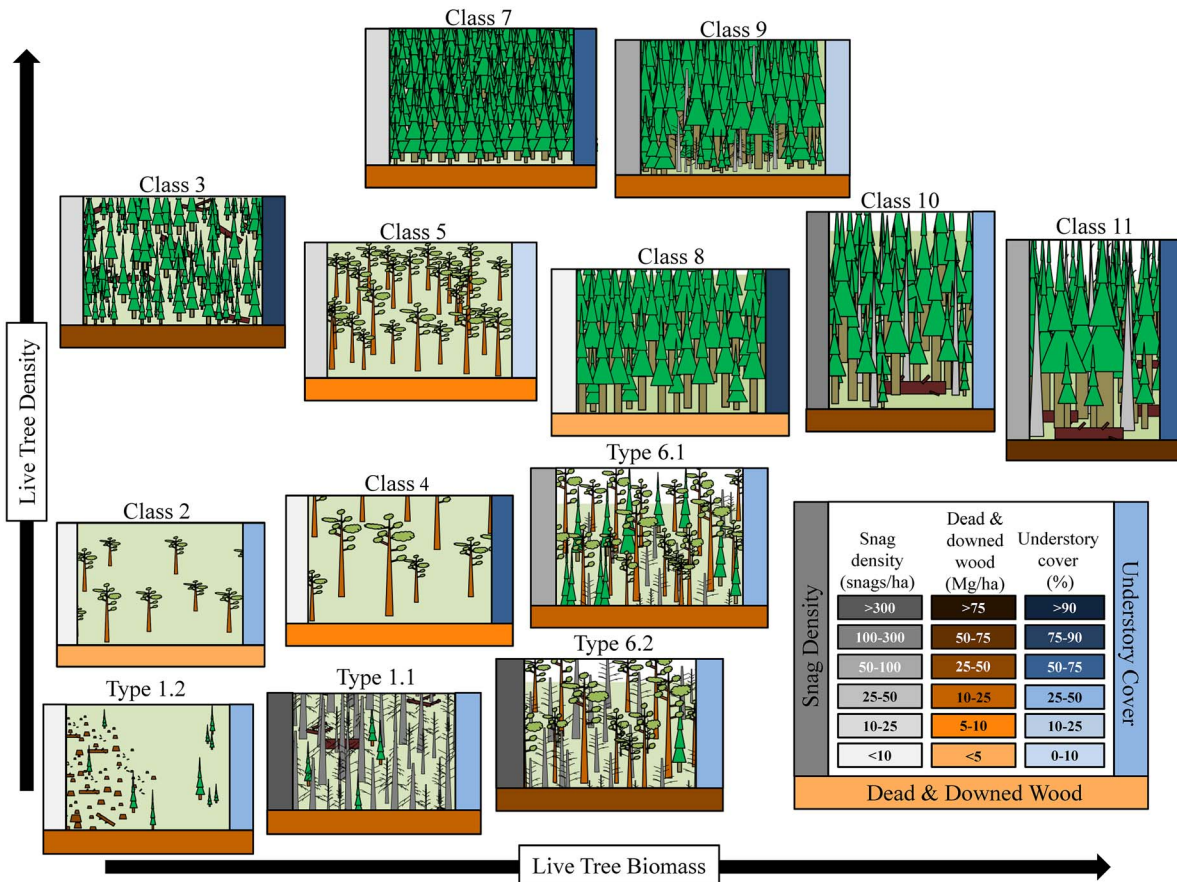
Fig. 3. Illustrations of structural classes and selected structural types in Oregon, Washington, and inland Northern California in relation to live tree biomass and density. Levels of snag density, biomass of dead and downed wood, and understory vegetation are indicated in boxes along the borders of each cell.

components related to size and density of trees, the abundance of snags and dead and downed wood, and understory vegetation accounted for almost as much additional variation. Understory vegetation acted independently while snags and dead and downed wood emerged at multiple points during biomass development suggesting that the timing and importance of various ecological processes (e.g., mortality, growth, recruitment) likely varies during different developmental stages in different vegetation zones. These results indicate that conceptual models of stand development based on a monotonic trajectory of biomass accumulation following stand-replacing disturbance are inadequate to account for the diversity of ways that interactions among vegetation, environment, and disturbance may be expressed through combinations of individual structural components.

Structural pattern and ecological processes

Our study of forest structure is novel in that it provides an unbiased sample of the variety of structural conditions across 25 million ha of forest as they "existed" during the study period without having to fit observations into preconceived classes. The traditional approach to the study of structural development is based on observations at a few subjectively selected sites to characterize conditions that fit preconceived stages identified by tree size or age (e.g., "old-growth or "early-seral"; e.g., Spies and Franklin 1991). This traditional approach has the ability to control for environment and disturbance history while making inferences about the roles of ecological processes during structural develop-

Table 2. Mean and standard deviation of nine stand level structural attributes† used in the hierarchical cluster analysis for eleven forest structural classes and twenty-five structural types in Oregon, Washington, and inland Northern California, USA.

Class/ type	BPH (Mg/ha)	BA (m²/ha)	CC (%)	QMD (cm)	TPH (/ha)	SDPH (/ha)	SBPH (Mg/ha)	BDW (Mg/ha)	USC (%)
1	0 ± 0.1	0 ± 0.1	0 ± 3	0.2 ± 0.9	19 ± 116	129 ± 205	24 ± 50	19 ± 21	45 ± 35
1.1	0 ± 0.2	0.1 ± 0.2	1 ± 5	0.4 ± 1.4	47 ± 186	343 ± 225	64 ± 70	20 ± 26	40 ± 33
1.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0.3	4 ± 44	16 ± 29	3 ± 7	19 ± 18	47 ± 36
2	8 ± 7	4 ± 3	13 ± 9	23 ± 13	166 ± 164	8 ± 30	1 ± 4	4 ± 10	48 ± 30
2.1	10 ± 6	6 ± 3	15 ± 9	26 ± 13	175 ± 154	3 ± 8	0.3 ± 1	2 ± 5	46 ± 28
2.2	2 ± 3	1 ± 1	8 ± 6	16 ± 9	146 ± 183	19 ± 49	2 ± 6	8 ± 16	54 ± 34
3	16 ± 14	9 ± 5	45 ± 17	11 ± 4	923 ± 538	13 ± 20	2 ± 6	28 ± 34	84 ± 36
4	42 ± 25	14 ± 7	30 ± 13	37 ± 16	195 ± 145	7 ± 13	1 ± 3	7 ± 13	55 ± 35
5	42 ± 38	17 ± 10	45 ± 20	19 ± 9	784 ± 596	21 ± 38	3 ± 8	8 ± 12	18 ± 20
5.1	27 ± 21	14 ± 8	47 ± 18	13 ± 4	1115 ± 626	2 ± 8	0.4 ± 2	6 ± 8	26 ± 19
5.2	25 ± 11	12 ± 4	30 ± 12	23 ± 9	389 ± 306	22 ± 25	2 ± 4	7 ± 8	24 ± 21
5.3	79 ± 48	26 ± 11	61 ± 18	21 ± 8	923 ± 557	42 ± 57	8 ± 13	13 ± 18	0.3 ± 1
6	69 ± 41	21 ± 9	42 ± 16	32 ± 14	359 ± 287	115 ± 156	23 ± 37	13 ± 14	47 ± 31
6.1	73 ± 40	22 ± 9	45 ± 14	31 ± 11	363 ± 222	73 ± 64	12 ± 11	12 ± 11	47 ± 30
6.2	43 ± 36	11 ± 8	23 ± 17	42 ± 27	329 ± 563	413 ± 251	96 ± 62	25 ± 23	45 ± 38
7	69 ± 38	27 ± 11	70 ± 16	16 ± 6	1926 ± 1528	19 ± 23	2 ± 4	10 ± 11	55 ± 34
7.1	70 ± 29	25 ± 8	62 ± 14	20 ± 4	838 ± 305	15 ± 21	2 ± 3	7 ± 7	57 ± 34
7.2	86 ± 41	31 ± 10	76 ± 13	14 ± 3	2060 ± 777	27 ± 23	3 ± 4	13 ± 12	53 ± 30
7.3	46 ± 37	23 ± 13	78 ± 14	9 ± 2	3701 ± 1849	15 ± 23	2 ± 5	13 ± 13	55 ± 40
8	157 ± 80	37 ± 13	69 ± 15	32 ± 11	584 ± 374	28 ± 34	5 ± 11	29 ± 36	83 ± 40
8.1	123 ± 47	33 ± 10	67 ± 14	28 ± 7	624 ± 316	22 ± 21	3 ± 3	10 ± 9	89 ± 40
8.2	139 ± 68	34 ± 12	69 ± 16	29 ± 9	684 ± 467	39 ± 46	9 ± 16	65 ± 42	68 ± 38
8.3	234 ± 83	46 ± 15	71 ± 14	43 ± 12	399 ± 243	26 ± 28	5 ± 8	17 ± 18	92 ± 38
9	157 ± 82	44 ± 16	80 ± 13	20 ± 6	1757 ± 1138	79 ± 73	13 ± 14	21 ± 26	39 ± 32
9.1	98 ± 50	32 ± 11	71 ± 14	18 ± 6	1555 ± 1005	97 ± 50	14 ± 11	20 ± 16	57 ± 30
9.2	194 ± 79	51 ± 13	82 ± 11	23 ± 6	1527 ± 907	44 ± 34	7 ± 7	10 ± 9	28 ± 25
9.3	163 ± 72	47 ± 15	87 ± 10	16 ± 4	2681 ± 1388	134 ± 120	26 ± 22	49 ± 42	36 ± 36
10	262 ± 130	55 ± 19	77 ± 13	33 ± 12	820 ± 515	120 ± 98	33 ± 32	29 ± 25	29 ± 33
10.1	206 ± 97	46 ± 16	72 ± 15	31 ± 10	769 ± 514	163 ± 111	38 ± 27	31 ± 21	61 ± 33
10.2	266 ± 123	56 ± 18	79 ± 12	33 ± 12	834 ± 497	74 ± 64	19 ± 17	25 ± 19	10 ± 12
10.3	383 ± 131	71 ± 18	85 ± 9	36 ± 11	900 ± 558	155 ± 90	62 ± 47	39 ± 43	12 ± 16
11	482 ± 165	75 ± 22	83 ± 12	46 ± 18	647 ± 537	73 ± 57	40 ± 37	67 ± 57	73 ± 39
11.1	483 ± 163	76 ± 23	85 ± 13	41 ± 15	825 ± 620	87 ± 63	53 ± 41	90 ± 63	57 ± 31
11.2	482 ± 169	73 ± 20	80 ± 9	54 ± 18	406 ± 240	54 ± 38	21 ± 18	35 ± 26	94 ± 39

† BPH = Live Tree Biomass, BA = Basal Area, CC = Canopy Cover, TPH = Live Tree Density, SDPH = Snag Density, SBPH = Biomass of Snags, BDW = Biomass of Dead and Downed Wood, and USC = Understory Cover.

ment, but is based on a limited range of structural variation and disturbance history, potentially biasing findings and missing structural conditions that don't fit into the simple stand development models. The strength of our approach is the ability to characterize the full range of structural conditions as it exists whether or not the types fit into preconceived models. We view the two approaches as complimentary. An unbiased regional sample of the diversity and abundance of different structural conditions can detect structural types that arise from both common and relatively rare (limited by the intensity of the sample) ecological patterns and processes including different environment and disturbance regimes. An unbiased characterization of forest structure can be used to generate hypotheses on putative processes inferred from

structural pattern that more traditional, intensive localized studies can test with better control for environment and disturbance history.

Patterns in ecological systems are often the result of multiple processes, and any prediction regarding pattern must be derived not only from the patterns themselves, but from an understanding of the variety of processes that might be operating to create them (Cale et al. 1989). Past conceptual models of structural development have embraced pattern and process and described similar stages based on the dominant processes and resulting structural conditions that occur during a particular range of stand ages (e.g., Bormann and Likens 1979, Oliver and Larson 1990, Franklin et al. 2002). Many of our structural classes and types correspond well with previously described stages (Fig. 6) and provide

Table 3. Relative abundance (%) of eleven major structural classes and twenty-five structural types by vegetation zone† (Simpson 2013) in Oregon, Washington, and inland Northern California, USA.

Class type	SS-RW	DF-TO	WH	SF	MH	WJ	PP	DF	GF/WF	SA	All
1	1.7	2.2	2.4	0.8	0.9	1.1	2.3	2.2	2.1	7.0	2.5
1.1	0.0	1.9	0.1	0.1	0.9	0.0	0.4	1.1	0.9	5.8	0.8
1.2	1.7	0.3	2.3	0.6	0.0	1.1	1.9	1.1	1.2	1.2	1.6
2	0.3	2.2	1.9	1.3	1.3	54.6	15.3	5.3	4.3	2.3	7.4
2.1	0.3	1.3	0.4	0.5	1.1	41.6	12.2	3.0	2.9	1.7	5.0
2.2	0.0	0.9	1.5	0.8	0.2	13.0	3.2	2.3	1.5	0.6	2.3
3	5.5	1.6	7.5	5.7	1.6	0.0	2.9	6.7	3.2	3.2	4.9
4	1.7	0.9	2.6	1.3	1.3	18.6	21.6	11.0	9.9	4.4	8.9
5	5.9	4.1	5.8	3.3	5.9	21.2	27.3	12.0	12.5	7.6	11.0
5.1	2.1	0.3	2.6	1.4	1.1	8.9	11.4	2.8	3.3	2.3	3.6
5.2	0.7	0.6	0.4	0.5	1.4	11.9	12.9	4.5	5.2	2.3	4.1
5.3	3.1	3.1	2.8	1.4	3.4	0.4	3.0	4.6	4.0	2.9	3.2
6	2.4	2.5	2.7	0.5	4.5	2.6	8.7	7.7	11.3	14.0	6.3
6.1	2.4	1.3	2.5	0.5	3.2	2.6	8.6	7.2	9.7	8.2	5.5
6.2	0.0	1.3	0.1	0.0	1.3	0.0	0.1	0.5	1.6	5.8	0.8
7	15.9	19.7	12.2	14.4	12.7	1.5	15.7	20.4	14.2	20.7	14.8
7.1	4.8	3.8	5.4	5.1	2.9	0.7	8.7	9.8	6.6	6.4	6.4
7.2	6.6	7.8	3.7	4.6	6.5	0.0	3.6	6.4	5.3	7.3	4.8
7.3	4.5	8.1	3.1	4.7	3.4	0.7	3.3	4.2	2.3	7.0	3.6
8	26.9	8.4	25.9	12.4	5.4	0.4	2.3	10.8	10.2	7.6	12.5
8.1	10.0	1.9	8.3	4.6	2.5	0.4	1.9	5.8	5.1	2.9	5.2
8.2	9.7	5.0	10.1	5.4	1.4	0.0	0.4	1.8	3.1	4.4	4.0
8.3	7.2	1.6	7.6	2.4	1.4	0.0	0.0	3.2	2.0	0.3	3.3
9	13.4	35.6	13.5	16.7	31.9	0.0	3.6	14.0	14.8	19.2	14.2
9.1	4.8	4.1	3.8	4.2	9.3	0.0	1.6	4.2	5.9	13.4	4.7
9.2	5.2	25.6	6.3	7.4	12.9	0.0	1.9	8.9	6.6	1.5	6.8
9.3	3.4	5.9	3.4	5.1	9.7	0.0	0.1	1.0	2.3	4.4	2.7
10	15.5	19.7	13.4	20.9	29.0	0.0	0.1	8.0	15.2	14.0	12.1
10.1	4.1	2.5	5.7	7.0	10.8	0.0	0.0	2.0	6.0	10.8	4.4
10.2	8.3	14.7	5.6	6.3	11.8	0.0	0.1	5.6	7.6	3.2	5.7
10.3	3.1	2.5	2.1	7.7	6.5	0.0	0.0	0.5	1.7	0.0	1.9
11	10.7	3.1	12.1	22.7	5.6	0.0	0.0	1.9	2.1	0.0	5.5
11.1	4.5	1.6	6.2	17.1	4.1	0.0	0.0	0.7	1.1	0.0	3.2
11.2	6.2	1.6	5.9	5.6	1.4	0.0	0.0	1.2	1.0	0.0	2.3

† WJ = Western Juniper, PP = Ponderosa Pine, GF/WF = Grand Fir/White Fir, DF = Douglas-fir, SS-RW = Sitka Spruce–Redwood, DF-TO = Douglas-fir–Tanoak, WH = Western Hemlock, SF = Silver Fir, and MH = Mountain Hemlock.

some support for these models in forests where stand-replacing disturbance has been common historically and biomass tends to accumulate monotonically with age. However, broad overlap in age among structural classes in dry vegetation zones indicates that "stand" age is a poor surrogate for structure in forests where disturbance regimes include low-severity or partial stand-replacing disturbance and age structure is far more complex (Muir 1993, Taylor and Skinner 2003, Taylor 2010).

Differences in productivity, the range of variation in individual components of structure (e.g., live biomass), and the timing of several ecological processes among different vegetation zones limit the generalizability of process- and age-based conceptual models of structural development at a regional scale. Our structure-based classification offers an alternative framework for

conceptualizing structural development, but structure alone may be equivocal since many structural types potentially developed through multiple pathways and often represent different stages of development in any given vegetation zones. An age- or process-based understanding is evidently still necessary to provide an ecological interpretation of structural patterns in terms of development (e.g., early vs. old-growth; Tables 4–6; Appendix D). These are inevitably contingent on subjectively binning a continuous process into a discreet stage-based framework with some implicit temporal progression, but can still be applied with explicit recognition that development may proceed in a multi-directional, non-linear fashion.

Most structural classes and types in the low biomass group correspond well with previously described early developmental stages (Fig. 6)
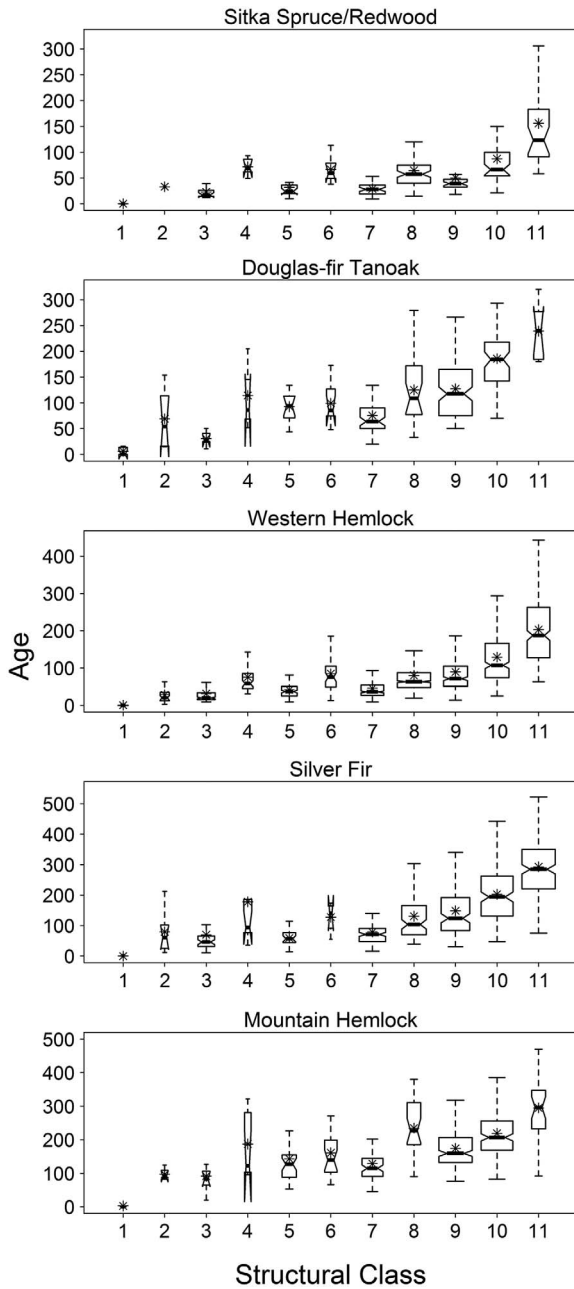
Fig. 4. Boxplots of mean age of all dominant and co-dominant trees by structural class for wet vegetation zones in Oregon, Washington, and inland Northern California: Sitka-spruce/redwood, Douglas-fir tanoak, western hemlock, silver fir, and mountain hemlock. The width of each boxplot is proportional to the square root of the sample size and means are represented by an asterisk.
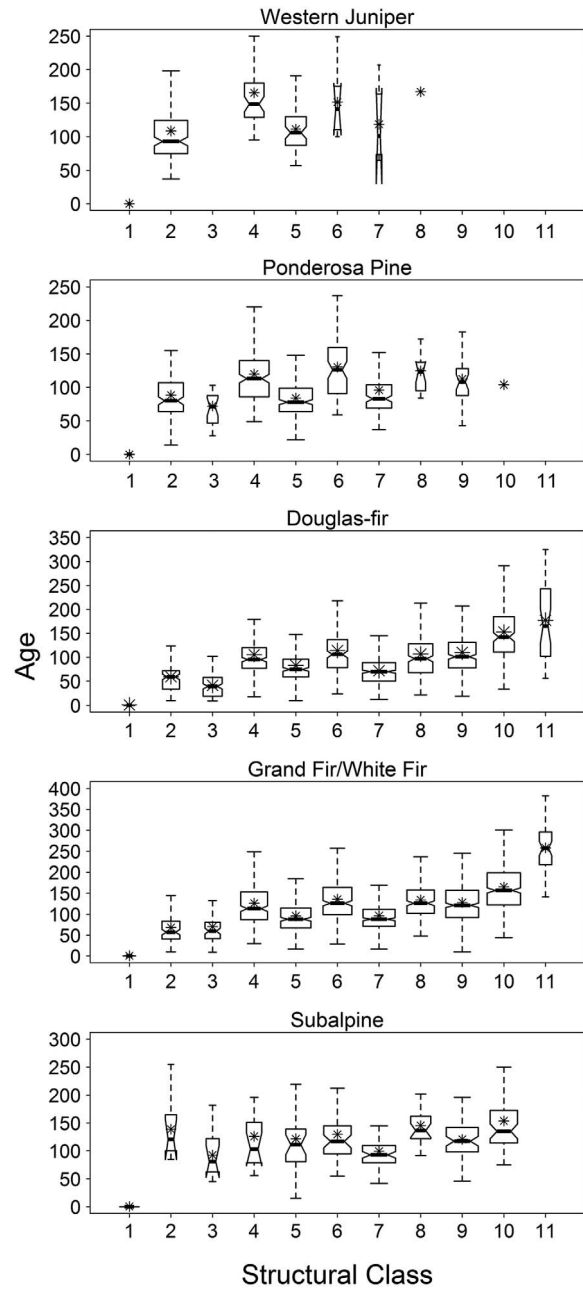
Fig. 5. Boxplots of mean age of all dominant and co-dominant trees by structural class for dry vegetation zones in Oregon, Washington, and inland Northern California: western juniper, ponderosa pine, Douglas-fir, grand fir/white fir, and subalpine forests. The width of each boxplot is proportional to the square root of the sample size and means are represented by an asterisk.
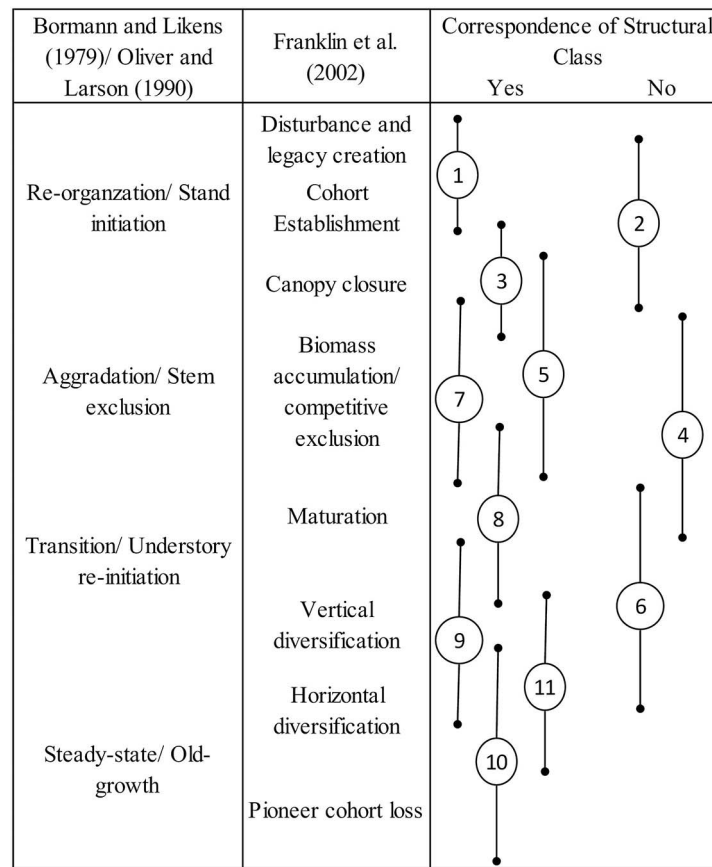
Fig. 6. Correspondence of traditional conceptual models of strucural development with empirically based structural classes in this study.

Table 4. Characterization of developmental stage, potential developmental pathways, and supporting lines of evidence† for low biomass structural types in Oregon, Washington, and inland Northern California, USA, by vegetation zone‡ (Simpson 2013).

Structural type	Developmental stage	Potential developmental pathways	Vegetation zone	Evidence
(1.1) Very Low Live Biomass and Density w/ Very High Snag Density	early	stand-replacing fire and/or epidemic pathogen	all	AGE, RFH
(1.2) Very Low Live Biomass and Density w/out Snags	early	recent clearcutting, salvage following recent fire and/or epidemic pathogen, forest expansion	all	AGE, RFH, CMP
(2.1) Low Live Biomass and Density w/ Medium Trees, (2.2) Low Biomass and Low Density	early	recent clearcutting, forest expansion	SS-RW, DF-TO, WH, SF, MH, PP, GF/WF, DF, SA	AGE, PROD, CMP
	mid	forest expansion	WJ	AGE, PROD
(3.0) Low Live Biomass and High Density	early	forest expansion	SS-RW, DF-TO, WH, SF, MH, PP, GF/WF, DF, SA	AGE, PROD
		clearcutting		AGE, HIST

† Lines of evidence include stand age (AGE), recent fire history since 1984 (RFH), productivity (PROD), disturbance and management history (HIST), and current management practices (CMP).
‡ WJ = Western Juniper, PP = Ponderosa Pine, GF/WF = Grand Fir/White Fir, DF = Douglas-fir, SS-RW = Sitka Spruce–Redwood, DF-TO = Douglas-fir–Tanoak, WH = Western Hemlock, SF = Silver Fir, and MH = Mountain Hemlock.

Table 5. Characterization of developmental stage, potential developmental pathways, and supporting lines of evidence† for moderate biomass structural types in Oregon, Washington, and inland Northern California, USA, by vegetation zone‡ (Simpson 2013).

Structural type	Stage	Potential developmental pathways	Vegetation zone	Evidence
(4.0) Moderate Live Biomass and Low Density w/ Big Trees	mid	variable retention harvest	SS-RW, DF-TO, WH	CMP
		forest expansion	SF	AGE, PROD
	mature	forest expansion, low-severity fire	MH, PP, GF/WF, DF, SA	
	late	forest expansion	WJ	
(5.1) Moderate Live Biomass and Very High Density	mid	mid/late 20th century clearcutting	SS-RW, DF-TO, WH	AGE, HIST
		forest expansion	SF, MH, SA	AGE
		infilling from fire exclusion and high grading, early 20th century stand-replacing fire	GF/WF, DF	AGE, HIST
		infilling from fire exclusion and high grading	PP	
	mature	forest expansion, infilling	WJ	
(5.2) Moderate Live Biomass and Density	mid	mid/late 20th century clearcutting and thinning	SS-RW, DF-TO, WH	AGE, HIST
		late 19th/early 20th century stand-replacing fire, forest expansion	SF, MH, SA	
		infilling from fire exclusion and high grading, early 20th century stand-replacing fire, recent thinning or prescribed fire	GF/WF, DF	AGE, HIST, CMP
		infilling from fire exclusion and high grading, recent thinning or prescribed fire	PP	
	mature	forest expansion, infilling	WJ	AGE
(5.3) Moderate Live Biomass and High Density w/ Big Trees	mid	mid/late 20th century clearcutting	SS-RW, DF-TO, WH	AGE
		late 19th/early 20th century stand-replacing fire, forest expansion	SF	
	mature	late 19th/early 20th century stand-replacing fire, forest expansion	MH, SA	
		infilling from fire exclusion and high grading, early 20th century stand-replacing fire	GF/WF, DF	AGE, HIST
		infilling from fire exclusion and high grading	PP	
	old-growth	forest expansion, infilling	WJ	
(6.1) Moderate Live Biomass and Density w/ Big Trees and High Snag Density	mature	recent low-severity fire, endemic insect and/or pathogen	SS-RW, DF-TO, WH, SF	AGE, RFH
	late		MH, SA, GF/WF, DF, PP	
	old-growth		WJ	
(6.2) Moderate Live Biomass and Density w/ Big Trees and Very High Snag Density	early	recent partial stand-replacing fire and/or epidemic insect, pathogen	ALL	RFH
(7.1) Moderate Live Biomass and High Density, (7.2) Moderate Live Biomass and Very High Density	mid	mid/late 20th century clearcutting	SS-RW, DF-TO, WH	AGE, HIST
		late 19th/early 20th century stand-replacing fire, forest expansion	SF	
	mature	late 19th/early 20th century stand-replacing fire, forest expansion	MH, SA	
		infilling from fire exclusion and high grading, early 20th century stand-replacing fire	GF/WF, DF	
		infilling from fire exclusion and high grading	PP	

Table 5. Continued.

Structural type	Stage	Potential developmental pathways	Vegetation zone	Evidence
(7.3) Moderate Live Biomass and Extremely High Density	mid	mid/late 20th century clearcutting	SS-RW, DF-TO, WH	AGE, HIST
		late 19th/early 20th century stand-replacing fire, forest expansion	SF, MH, SA	AGE, PROD
		infilling from fire exclusion and high grading, early 20th century stand-replacing fire	GF/WF, DF	AGE, HIST
		infilling from fire exclusion and high grading	PP	
	old-growth	forest expansion, infilling	WJ	AGE, HIST

† Lines of evidence include stand age (AGE), recent fire history since 1984 (RFH), productivity (PROD), disturbance and management history (HIST), and current management practices (CMP).
‡ WJ = Western Juniper, PP = Ponderosa Pine, GF/WF = Grand Fir/White Fir, DF = Douglas-fir, SS-RW = Sitka Spruce–Redwood, DF-TO = Douglas-fir–Tanoak, WH = Western Hemlock, SF = Silver Fir, and MH = Mountain Hemlock.

and have characteristics of early-seral habitats including sparse canopy cover and low basal area (Swanson et al. 2010). Variation in the density of live trees, snags, and dead and downed wood are indicative not only of the potential diversity of structural conditions in early developmental stages (Fig. 3) depending on recent disturbance history (Table 4), but also variation in the role of different ecological processes during early developmental stages depending on productivity. Snags and dead and downed wood may be abundant following legacy creation in wildfires in Type 1.1 (90% burned since 1984), but are absent during stand initiation and cohort establishment following logging or expansion into previously non-forested areas (Type 1.2). Differences in live tree density, canopy cover, and age between Structural Classes 2 (Low Live Biomass and Density) and 3 (Low Live Biomass and High Density) suggest variation in the roles of several ecological processes and a major dichotomy in early developmental pathways. Canopy closure may occur relatively rapidly as in Structural Class 3 where rapid growth and continuous recruitment offset high levels of density-dependent mortality in smaller, less competitive trees (Lutz and Halpern 2006). These processes are likely less important in Structural Class 2 where trees are older and density and canopy cover are much lower. This stage represents a period of protracted recruitment either not described or less emphasized in traditional models of structural development. Cohort establishment may be episodic from recruitment limitation related to climatic fluctuations (Brown and Wu 2005, Zald et al. 2012), competition from shrubs or herba-

ceous vegetation (Putz and Canham 1992, Riginos 2009), frequent fire (Taylor 2010), dispersal limitation (Agee and Smith 1984), or a combination of these factors (Acacio et al. 2007). While competition may play an important role in rapidly regenerating stands at high density, facilitation may be more important to overcome recruitment limitation in harsh environments (Berkowitz et al. 1995, Callaway 1998, Calder and St. Clair 2012, Rice et al. 2012).

Structural types in the moderate live biomass group generally lack dead wood and represent a wide array mid, mature, and late developmental stages that have resulted from a variety of developmental pathways in different vegetation zones (Table 5). Structural Classes 5 (Moderate Live Biomass and High Density) and 7 (Moderate Live Biomass and Very High Density) resemble previously described stages (Fig. 6) that are characterized by rapid growth and biomass accumulation following stand-replacing disturbance (Franklin et al. 2002). Tremendous variation in density among the types that make up these classes reflect differences in productivity and management practices in the vegetation zones where they occur. Structural Classes 4 (Moderate Live Biomass and Low Density with Big Trees) and 6 (Moderate Live Biomass and Density with Big Trees and Snags) resemble woodlands and savannahs with sparse canopy and big trees. These lack analogs in current models of stand development, but are recognized as important alternative stable states across much of the world (Staver et al. 2011). The geographic distribution of Structural Class 4 across the drier, hotter eastern part of the study region (Appendix: Fig. A2) suggests slow growth and low

Table 6. Characterization of developmental status, potential developmental pathways, and supporting lines of evidence† for high biomass structural types in Oregon, Washington, and inland Northern California, USA, by vegetation zone‡ (Simpson 2013).

Structural type	Stage	Potential developmental pathways	Vegetation zone	Evidence
(8.1) High Live Biomass and Density w/ Big Trees and Low Dead Biomass	mature	early/mid 20th clearcutting	SS-RW, DF-TO, WH	AGE, HIST
		late 19th century stand-replacing fire, forest expansion	SF	
	late	late 19th century stand-replacing fire, forest expansion	MH, SA	
		frequent pre-20th century fire, infilling from fire exclusion and high grading, late 19th century stand-replacing fire	GF/WF, DF	
	old-growth	frequent pre-20th century fire, infilling from fire exclusion	PP	
(8.2) High Biomass and Density w/ Big Trees and Very High Biomass of Dead and Downed Wood	mature	early/mid 20th century stand-replacing fire	SS-RW, DF-TO, WH	AGE, HIST
		late 19th century stand-replacing fire	SF	
	late	late 19th century stand-replacing fire	MH, SA	AGE, PROD
		frequent pre-20th century fire, infilling from fire exclusion and high grading, late 19th century stand-replacing fire	GF/WF, DF	AGE, HIST
	old-growth	frequent pre-20th century fire, infilling from fire exclusion	PP	
(8.3) High Live Biomass and Moderate Density w/ Big Trees	late	mid 20th century clearcutting, recent thinning	SS-RW, DF-TO, WH	AGE, HIST, CMP
		late 19th century stand-replacing fire, forest expansion	SF, MH, SA	AGE, HIST
	old-growth	frequent pre-20th century fire, late 19th century stand-replacing fire	GF/WF, DF	
(9.1) High Live Biomass and Very High Density w/ Big Trees and Moderate Dead Biomass	mature	early 20th century stand-replacing fire	SS-RW, DF-TO, WH	AGE, HIST
		19th century stand-replacing fire, forest expansion	SF, MH, SA	
		infilling from fire exclusion and high grading, late 19th century stand-replacing fire	GF/WF, DF	
	late	frequent pre-20th century fire, infilling from fire exclusion and high grading	PP	
(9.2) High Live Biomass and Very High Density w/ Big Trees and Low Dead Biomass	late	early 20th century stand-replacing fire	SS-RW, DF-TO, WH	
		19th century stand-replacing fire, forest expansion	SF	
	old-growth	19th century stand-replacing fire, forest expansion	MH, SA	
		frequent pre-20th century fire, infilling from fire exclusion	GF/WF, DF, PP	
(9.3) High Live Biomass and Extremely High Density w/ Big Trees and High Dead Biomass	late	early 20th century stand-replacing fire	SS-RW, DF-TO, WH	
		19th century stand-replacing fire, forest expansion	SF, MH, SA	
		frequent pre-20th century fire, infilling from fire exclusion	GF/WF, DF	
	old-growth	frequent pre-20th century fire, infilling from fire exclusion	PP	

Table 6. Continued.

Structural type	Stage	Potential developmental pathways	Vegetation zone	Evidence
(10.1) Very High Live Biomass and High Density w/ Large Trees and High Dead Biomass and Understory Cover	late	centuries since stand-replacing disturbance	SS-RW, DF-TO, WH, SF	
	old-growth		MH, SA, GF/WF, DF	
(10.2) Very High Live Biomass and High Density w/ Large Trees and Moderate Dead Biomass	late		SS-RW, DF-TO, WH, SF	
	old-growth		MH, GF/WF, DF, SA, PP	
(10.3) Extremely High Live Biomass w/ Large Trees and High Dead Biomass			MH, GF/WF, DF, SA	
(11.1) Extremely High Live Biomass w/ Giant Trees and High Density, (11.2) Extremely High Live Biomass w/ Giant Trees and Moderate Density			SS-RW, DF-TO, WH, SF, MH, GF/WF, DF	

† Lines of evidence include stand age (AGE), recent fire history since 1984 (RFH), productivity (PROD), disturbance and management history (HIST), and current management practices (CMP).

‡ WJ = Western Juniper, PP = Ponderosa Pine, GF/WF = Grand Fir/White Fir, DF = Douglas-fir, SS-RW = Sitka Spruce–Redwood, DF-TO = Douglas-fir–Tanoak, WH = Western Hemlock, SF = Silver Fir, and MH = Mountain Hemlock.

recruitment while lack of snags and low density indicate very little competition related mortality. In contrast, Structural Class 6 represents an alternative stage where very high but variable snag density reveals a gradient in recent levels of mortality suggestive of low- or moderate-severity partial stand-replacing disturbances (10% burned since 1984) which decrease live tree biomass and density, but increase the dominance of bigger trees. Structural Type 6.2 (Moderate Live Biomass and Density with Big Trees and Very High Snag Density and Biomass) is emblematic of the diverse structural conditions created by wildfire (70% burned since 1984) in later stages of development where elements of both early (e.g., high snag density, sparse canopy cover) and later developmental stages (e.g., big, old remnant trees, big snags, abundant dead wood) can be found.

Structural classes in the high live biomass group generally resemble later developmental stages (Table 6) described in previous models of stand development (Fig. 6) and corroborate the diversity of structural conditions that can be found in mature and old-growth stages (Franklin et al. 2002). Mortality during these stages is hypothesized to shift towards density-indepen-

dent sources such as wind, insects, and disease (Franklin et al. 2002), but results supporting this have been mixed (see Lutz et al. 2014). Large differences in the density of live trees and small snags among high biomass structural classes (Appendix B) indicate that the role of density-dependent mortality may vary considerably during later developmental stages, especially in different vegetation zones where density in later stages may also be variable (Table 2). Very high density of small trees and snags in Structural Class 9 (High Live Biomass and Very High Density with Big Trees) indicate that density-dependent mortality can be very high during understory re-initiation or vertical diversification. On the contrary, low density of small snags and trees in Structural Class 8 (High Live Biomass and Density with Big Trees) indicate little density-dependent mortality where understory re-initiation has been either been delayed by dispersal limitation (Wimberly and Spies 2001) or prevented by dense understory vegetation (George and Bazazz 1999), browsing (Rooney and Waller 2003), or frequent low-severity fire (Platt et al. 1988). Although high levels of density-dependent mortality may operate at fine scales where aggregated recruitment occurs in
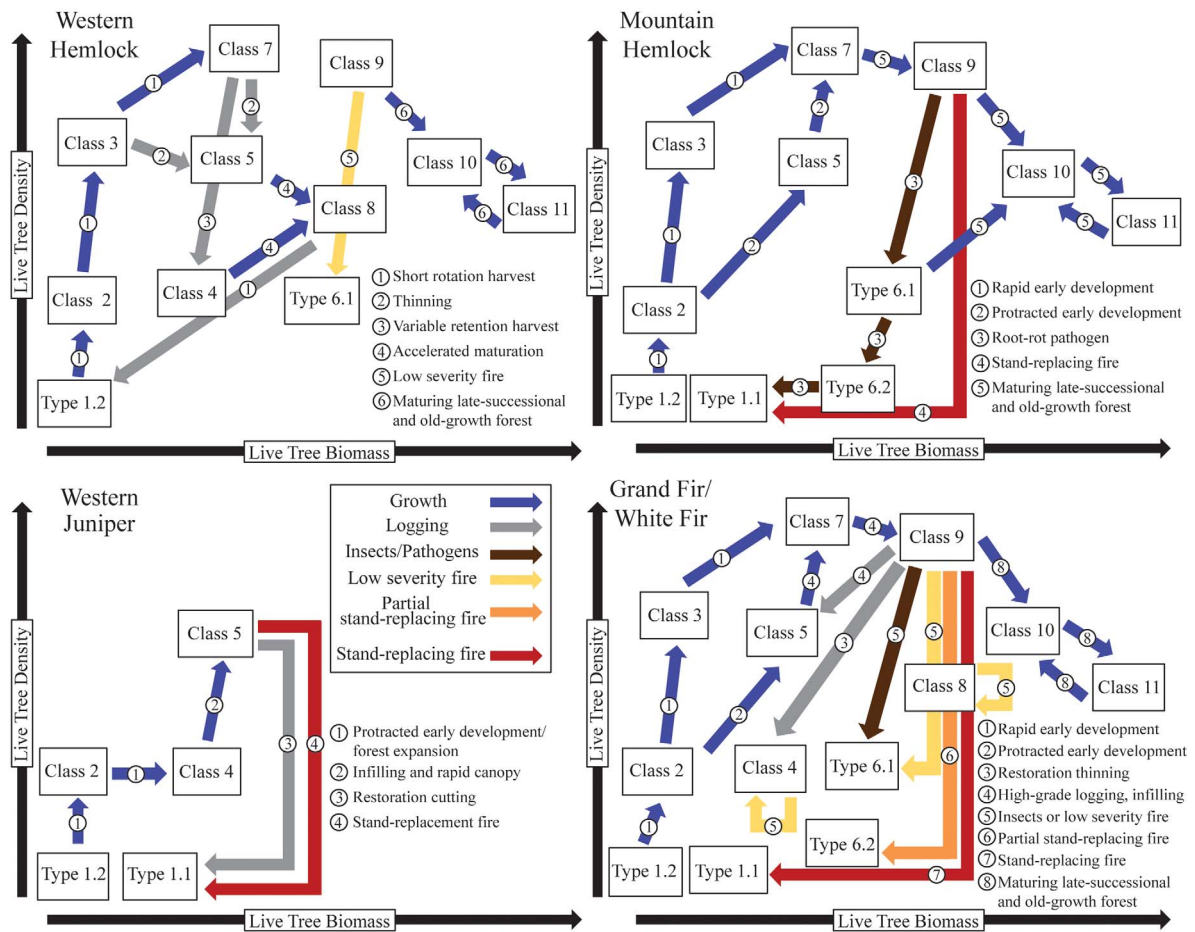
Fig. 7. Conceptual models of potential pathways of structural development in western hemlock, mountain hemlock, western juniper, and grand fir/white fir vegetation zones in Oregon, Washington, and inland Northern California.

gaps, it may have little effect on structural change (Lutz et al. 2014). Instead, low levels of density-independent mortality of big trees from windthrow and endemic infestations of insects and disease (Franklin et al. 2002) that increase biomass of snags and dead and downed wood have greater implications for structural development in Structural Classes 10 (Very High Live Biomass with Large Trees) and 11 (Extremely High Live Biomass with Giant Trees).

Potential pathways of structural development

While many of our structural classes fit into some stages of existing models of stand development, it is clear that there is a great deal of variation in structure within any of these existing stages of development. It is also clear that the pathways of development and expression of different structural types varies greatly across the region. The relative abundance of structural classes and types in individual vegetation zones corresponds with major gradients in climate and productivity but also reflects legacies of historical and contemporary management practices and disturbance regimes. Together, productivity and disturbance regimes interact to constrain the abundance and diversity of structural conditions and developmental pathways in an individual vegetation zone. Below, we present conceptual models of four of the major types of structural development that we hypothesize have given rise to the some structural classes and types observed

in the region (Fig. 7). We limit discussion to a few dominant pathways supported by the abundance of structural classes or types by vegetation zone and the available literature. The proposed pathway types are distinguished based on the range of variation along various components of structure (e.g., biomass and density), the rate and timing of transitions among stages, the relative importance of different disturbance types, and complexity of pathways.

Structural classes and potential pathways of development in the western hemlock zone correspond with existing models of development for infrequent, stand-replacing disturbance regimes (e.g. Douglas-fir/western hemlock, Franklin et al. 2002; Fig. 7). Regeneration, live biomass, and density may develop rapidly during early stand development (Lutz and Halpern 2006). The dead wood component can reach its peak following fire (Spies et al. 1988), but was most abundant in later developmental stages as logging and infrequent fire during the 20th century (Curtis et al. 1998, Healey et al. 2008, Johnson and Swanson 2009,) have limited the occurrence of diverse early-seral conditions with live and dead legacies which made up a very small proportion of this vegetation zone (~0.2%). Although protracted establishment (~40 years to end of establishment stages) was common in the past (Winter et al. 2002, Tepley et al. 2014), management practices and current policy (Oregon Revised Statutes 527.745; http://www.oregonlaws.org/ors/527.745) have reduced the duration of early development stages (Hansen et al. 1991). Application of silvicultural treatments like pre-commercial thinning, thinning (Chan et al. 2006), or variable retention harvest (Aubry et al. 2009) may alter developmental trajectories by decreasing density, increasing dominance of big trees, and accelerating the development of structural development (Bailey and Tappeiner 1998). Low- and moderate-severity wildfire played an historic role during later developmental stages in some parts of the western hemlock zone (Tepley et al. 2013), but these have affected only a small proportion of the vegetation zone during the 20th century. Current dynamics in later stages may be driven primarily by stand-level processes rather than external disturbance agents (Lutz et al. 2014). Multiple old-growth structural conditions and stages are possible as live biomass may fluctuate from mortality of individual large trees or loss of founding cohorts, increasing dead and downed wood and density through gap phase recruitment (Gray and Spies 1996).

In contrast to the western hemlock zone, forest management has been minimal in the mountain hemlock zone and structural types and pathways development are primarily the result of natural processes (Fig. 7). Live biomass and density rise to levels similar to in the western hemlock zone, but at a much slower rate. Early stand development may be initiated following stand-replacing fire (Bekker and Taylor 2010), prolonged pathogen exposure (Matson and Waring 1984), or expansion into meadows (Taylor 1995, Zald et al. 2012) and can be rapid or protracted. Biomass development and density may continue to increase until later stages of development when partial stand-replacing disturbance from a root rot pathogen (laminated root rot, Phellinus weirii Murr.; Matson and Waring 1984) or stand-replacing wildfire (Agee 1993) may occur. Live biomass decreases as waves of mortality create localized patches of complete stand-replacement over time (Matson and Boone 1984, Hansen and Goheen 2000) or the stand may recover and regain live biomass on a trajectory towards old-growth stages. In the absence of root disease development may continue towards old-growth.

Structural variation in western juniper suggests that development operates within a very low range of biomass and density, both of which are primarily limited by climate. Early developmental stages may be initiated following high-severity wildfire (Campbell et al. 2012) or complete mechanical removal of live trees (Bates et al. 2005). Expansion into non-forested grasslands or shrublands, however, has been more common over the last century and accounts for a ~900% increase in western juniper (Miller and Rose 1995). Expansion may be rapid, but growth is slow and establishment is protracted with big trees developing prior to canopy closure. An abrupt shift towards an old-growth stage with closed canopy (Waichler et al. 2001) may occur from infilling associated with changing disturbance regimes or favorable climate (Soule et al. 2004). Old-growth juniper was historically restricted to sites offering refuge from fire, but has encroached on sagebrush steppe over the last few

centuries following grazing, decreased fire occurrence, and relatively moist climatic conditions (Miller and Rose 1999). In the absence of disturbance the old-growth stage may persist for centuries (Romme et al. 2009).

Structural patterns in the grand fir/white fir vegetation zone suggest that these developmental pathways are among the most complex in the region. Early developmental stages may have been initiated by stand-replacing fire, logging (Adams and Latta 2007), or expansion into meadows or shrublands (Halpern et al. 2010). Early developmental stages in the late 20th century have been truncated and with rapid canopy closure following planting for timber management (Seidel 1979, Sensenig et al. 2013), but our data suggest that pathways of protracted development have also been common. Most late developmental stages are associated with a different pathway which includes repeated removal of large trees and fire exclusion followed by recruitment and infilling of shade tolerant trees dating to late 19th and early 20th centuries (Youngblood et al. 2004, Merschel et al. 2014) and current basal area and density are much higher than in the late 19th and early 20th century (Baker 2012, Hagmann et al. 2013, Hagmann et al. 2014). Current pathways in later developmental stages may include mechanical thinning for restoration and reduction of risk of high-severity fire (Harrod et al. 2009), but natural disturbance including fire (Littell et al. 2009, Wimberly and Liu 2014, Cansler and McKenzie 2014) and insects (Meigs et al. 2015) have been more common in recent years. Some stand-replacement fire has occurred in a small proportion of this vegetation zone (~0.9%), but partial stand-replacement fire has been more common (1.6%) and both are rare compared to the total extent of the vegetation zone in late and old-growth developmental stages (~46%). Old-growth stages with extremely high biomass and dead wood may persist in topographically related fire refugia or other remote areas that were not logged (Camp 1999), but are uncommon (2.1%).

Implications for conservation and management

Our study represents the first empirical characterization of early developmental stages and can serve as a reference and for assessing the contribution of early-seral forests to landscape diversity and for developing strategies aimed at conserving or creating them. Declines in early-seral forests around the world (Angelstam 1998, Trani et al. 2001) have been linked with corresponding losses in biodiversity (Pimm and Askins 1995, Betts et al. 2010) and are a focus of some recent forest restoration proposals in the Pacific Northwest (Franklin and Johnson 2012). The large degree of variation in the structure of early developmental stages that we found substantiates the need to differentiate among early-seral forests for conservation purposes. Dead biological legacies have the potential to increase structural complexity in early developmental stages and provide important habitat elements for a variety of organisms that may not be present in all early-seral forests (Hutto 2008, Swanson et al. 2014). In addition, although the scale and frequency of disturbance affects the extent of early successional habitats (Lorimer and White 2003), variation in productivity and rates of seedling establishment and regrowth will also affect the extent of early-seral habitats which may be ephemeral in productive vegetation zones but persist for much longer where it is cold or dry. Diverse early-seral forests are still one of the rarest habitats in the region, but the amount of this habitat varies tremendously with scale and differs among vegetation zones and geographical locations. Most diverse early-seral forests are located in a few "hotspots" associated with very large wildfires in the Klamath (Biscuit Fire 2002), Eastern Cascades/Cascades (B and B Fire 2003), and North Cascades (Tripod Fire 2007) ecoregions (Appendix A1).

High density moderate biomass plantations are a major source of timber in many regions of the world (Hartley 2002). Although they are not often the focus of conservation, their management has important implications for biodiversity since they comprise the majority of non-reserve forest lands (Franklin and Lindenmayer 2009) but typically lack habitat elements (e.g., dead wood, large remnant trees) that many species may depend on (Johnson and O'Neil 2001). A mesofilter conservation approach aimed at conserving specific elements in managed forests (Hunter 2005) could enhance structural diversity and habitat function in managed forests. Other moderate biomass structural classes with lower density of live trees pertain to conservation issues

in drier forests where savannahs and woodlands around the world have gone through recent rapid structural change from either mortality (Allen and Breshears 1998, Williams et al. 2010, Vila-Cabrera et al. 2011) or expansion (Weltzin and McPherson 1999, Archer 2010, Gimeno et al. 2012) with important consequences for ecosystem function (Sala and Maestre 2014) and biodiversity (Ratajczak et al. 2012). Our results indicate that western juniper has experienced very little recent change related to mortality, but some woodland types with big trees and high densities of snags in the ponderosa pine, Douglas-fir, and grand fir/white fir vegetation zones are evidence of recent episodes of mortality that have affected anywhere from ~8–11 % of these vegetation zones. Our results suggest that many dry forests in the Pacific Northwest are going through a period of thinning from mortality, but decreases in overall density and increases the dominance of big trees may be restoring some aspects of historical structure.

The number of structural classes in the high live biomass group demonstrate the diversity of later developmental stages across environments and vegetation zones in a region that still supports millions of hectares of old-growth forest (Moeur et al. 2011). Late successional and old-growth have been the focus of considerable conservation efforts and around the world (Woodgate et al. 1996, Kimmins 2003, Spies and Duncan 2009; Davis et al., *in press*) due to their unique contribution to biodiversity and role they play in global carbon storage (Luyssaert et al. 2008). High densities of big trees and snags and large amounts of dead and downed wood are shared attributes of old-growth forests around the world (D'Amato et al. 2008, Burrascano et al. 2013), but these attributes may not be present in late developmental stages of all vegetation zones where environment or disturbance constrain development of one or more components of structure (e.g., frequent fire consumes dead wood). Refined definitions based on regional inventories incorporating the full range of potential structural conditions have the potential to avoid confusion that has occurred in the past regarding policy and management (Parker et al. 2000, Spies 2004). Our results also clearly show that the relationship between stand age and structural development does not apply to all "old" forests, especially those in low productivity or frequently disturbed environments (O'Hara et al. 1996). The general model of stand development from the western hemlock zone that emphasizes development of high live and dead biomass and canopy layering is not necessarily a good basis for assessment and conservation of "older" forest in other vegetation zones. Rates of development differ along regional gradients in productivity and complex age structures can result from both partial stand-replacing disturbance and protracted development dry or cold environments. Finally, despite the numerous ecological roles of forests in later developmental stages, perhaps one of the least recognized is that they are the only source of the unique habitat elements capable of creating highly diverse early-seral habitats.

Conclusion

This study provides the first empirically based regional-scale characterization of forest structure and how it varies in relation to age, vegetation zone, and disturbance history. Although most of variation in forest structure was accounted for by live tree biomass, other components related to tree size and density, dead wood, and understory vegetation cumulatively accounted for as much variation. Our results indicate that structural development across regional gradients in environment, species composition, and disturbance history include more complex pathways than the monotonic accumulation of live biomass often depicted in simple conceptual models of stand development following stand-replacing disturbance in relatively productive environments. Indicative of the variation in importance and timing of the various ecological processes operating during development, some components of structure may act independently or emerge at multiple points during development. As a result, models of structural development based only on live biomass are inadequate to account for dynamics at a regional scale.

The regional scale classification of structural types reveals the diversity of ways that interactions among individual structural components may be expressed at the stand-scale. We identified twenty-five structural types with unique combinations of live tree biomass, density, and size, snag and dead wood abundance, and

understory cover. High levels of structural diversity occurred at all levels of live biomass, but diverse low biomass structural types were far less common than diverse types with high live biomass. Although age typically increased with biomass across structural classes in wet forests, the relationship between age and structural class was much weaker in dry forests where a history of mixed-severity fire regimes and pathogen and insect outbreaks have created a complex mosaic of forest structure and wide range of tree ages on a site.

Most structural types corresponded well with stages described in current models of stand development, but some types associated with protracted early development, transitions between woodland/savannah and closed canopied forest conditions, and partial stand-replacing disturbance substantiate the need for a broader framework for conceptualizing structural development and tracking regional forest dynamics. Structural development in woodlands and savannahs includes many of the same processes (e.g., self-thinning, infilling or understory re-initiation) that occur in closed canopy forests, but they may occur repeatedly or at different times. Development may be slow, but transitions can happen rapidly as infilling trees approach percolation thresholds for canopy closure (Abades et al. 2014) or partial stand-replacing disturbances reduce density of smaller trees. Thus, woodlands and savannah dynamics can be characterized by a persistent structural backbone of big trees where the density of smaller trees fluctuates depending on climatic conditions and the frequency and severity of disturbance. We propose several general models using a multiple pathway framework based on interpretation of structural patterns, recent fire history, and general knowledge of disturbance and management history across the region. General models can be distinguished based on the range of variation along various components of structure (e.g., biomass and density), the rate and timing of transitions among stages, and complexity of pathways and relative importance of different disturbance types. These models can serve as a conceptual framework for developing more comprehensive models of structural development that apply to a wider variety of vegetation zones with different environments and disturbance regimes.

Future research and application

Our study provides a complimentary approach to the traditional chronosequence approach of sampling of a small number of subjectively selected stands. Despite incorporating and characterizing the wide range of structural conditions across a diverse region, our inferences regarding ecological processes are based primarily on observations of structural patterns and knowledge of management and disturbance history with support from a rich literature on dynamics of forests, woodlands, and savannahs around the world. There is a need for future studies to explicitly test many of our findings, particularly those regarding the role of mortality in various developmental stages. Intensive plot-based studies have the potential to elucidate the roles of these processes by explicitly quantifying them and incorporating finer scale spatial pattern to provide a more mechanistic understanding of their consequence on structural development. Proposed conceptual models of structural development can be tested in other vegetation zones to assess their generality and limitations. Finally, this study provides a reference and framework with which to evaluate historical and potential future trajectories of landscape diversity related to changes in climate, disturbance, and management.

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Supplemental Material

Ecological Archives

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