Forest Ecology and Management 479 (2021) 118548

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Structural diversity and development in active fire regime mixed-conifer forests

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ARTICLE INFO

Keywords:
Forest structure
Mixed-conifer forest
Mixed-severity fire
Wilderness
Heterogeneity
Forest stand dynamics

ABSTRACT

Nearly a century of fire suppression in most forested land of the United States has limited researchers' ability to construct and rigorously test conceptual models of forest structural development in mixed-conifer ecosystems. As a result, land managers must rely on conceptual models of forest development that may overemphasize idealized stand structures and developmental pathways, which ultimately hampers management of many forest systems for resilience to future climate change impacts. We sought to determine the relative importance of fire history (frequency, severity, and time since fire) and biophysical variables on forest structural diversity and development. Importantly, we conducted our study in an ecosystem with a contemporary active fire regime where wildland fire has been managed as an ecosystem process for four decades. Using data from unburned (≥80 years since fire), once-burned and twice-burned mixed-conifer forests in the Bob Marshall Wilderness of Northwest Montana, we conducted a hierarchical clustering analysis to identify forest stand structure classes. We then used a Classification and Regression Tree analysis, combined with other post-hoc analyses, to elucidate the biophysical and disturbance history drivers that lead to each structure class. The cluster analysis revealed six forest structure classes. The CART analysis indicated that time since fire plays a large role in determining forest structure, but at intermediate time scales structure is further shaped by repeat fires and interactions with biophysical variables. The CART and post-hoc analyses did not, however, indicate a singular fire history or biophysical pathway to any one structure class. We synthesize our results in a conceptual model of forest structural development under an active fire regime. This model supports existing theory that succession following severe fire plays a large role in shaping forest structure. It also recognizes the role of fire at variable severities and frequencies, the physical environment, and tree community composition in influencing forest structural development. The complexity of forest structure and development generated by an active fire regime points to the need to incorporate a process-based view of wildfire if the goal is to manage for improved resiliency and adaptive capacity to future climate change impacts.

1. Introduction

Wildland fire is one of the main drivers of patch- and landscape-scale structural diversity in coniferous forest ecosystems of western North America (Habeck and Mutch, 1973, Franklin et al., 2002, Hessburg et al., 2005). A large proportion of these coniferous forests are classified as mixed-conifer, or forests in which no one species dominates the tree composition (Arno et al., 2000; North, 2008). The wide range of fire severities and frequencies typical of many mixed-conifer forests (i.e., a mixed-severity fire regime), as well as the differences amongst individual tree species in terms of fire adaptations, leads to complex and variable forest structures and structural development pathways (Arno, 1980, McNicoll, 1994, Agee, 1998, Linder, 1998, Belote et al., 2015, Hessburg et al., 2016). Structural development is further complicated by interactions among topography, geology, micro-climate, and non-fire disturbance history (Battaglia et al., 2002; Hessburg et al., 2015; Lydersen and North, 2012; Ng et al., 2020; North, 2008; Whipple and Dix, 1979).

Existing theory of mixed-conifer structural development relies heavily on two archetypal fire regimes and associated structural development pathways (Franklin et al., 2018). First, there is the frequent, low-severity fire regime that maintains open stands of large-diameter trees (Reynolds et al., 1992, Covington and Moore, 1994, Larson and Churchill, 2012). Second, there is the model of successional development from a simple, even-aged forest structure to a structurally

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https://doi.org/10.1016/j.foreco.2020.118548
Received 1 July 2020; Received in revised form 25 August 2020; Accepted 29 August 2020
Available online 11 September 2020

complex old-growth forest following a stand-replacement fire (Oliver, 1980, Romme, 1982, Spies and Franklin, 1991, Larson et al., 2008). Such models, however, largely ignore or minimize the role of intermediate fire intensities and frequencies, as well as other environmental variables that are likely contributing to forest structure development.

While recent reviews have increased the prominence of mixed-severity fire regimes in the literature (Hessburg et al., 2016, 2019), small sample sizes (Aplet et al., 1988, Goslin, 1997, Linder et al., 1997, Zenner, 2005, Beaty and Taylor, 2007, Hopkins et al., 2014) or a focus on only a few tree species (Weisberg, 2004, Poage et al., 2009) have limited the applicability of past empirical studies. The few studies that have undertaken a comprehensive investigation of the role of mixed-severity fire in forest structural development are further limited by the past century of timber harvest and aggressive fire suppression (Tepley et al., 2013, Reilly and Spies, 2015), which have altered the distribution, abundance, and configuration of forest structure across large portions of the western US. As a result, the high- and low-severity endmembers of the fire regime continuum tend to be overrepresented in the body of theory underpinning ecological forest management, forest restoration, and climate change adaptation for mixed-conifer forests.

Improved understanding of the structures created by the full range of fire severities and histories in mixed-conifer forests is necessary because fire suppression and past land use has led to a profound homogenization of forest structure (Everett et al., 1997, Naficy et al., 2010, Hessburg et al., 2015, LeFevre et al., 2020). This loss of forest heterogeneity has decreased resilience to disturbances such as drought, bark beetle attack, and fire, and is partly responsible for the increasing frequency of widespread and severe disturbance events (Prichard et al., 2010, Lydersen et al., 2014, Hessburg et al., 2019, Restaino et al., 2019).

With the uncertainty associated with climate change, forest resilience to future disturbances has become an increasingly common goal in forest management (Bone et al., 2016; Rist and Moen, 2013; Stephens et al., 2016, 2020). As a result, managers are recognizing the need to manage forests as complex adaptive systems, in which forested systems are capable of adapting and modifying structure and composition while maintaining essential functions under changing environmental conditions (Gunderson, 2000, Puettmann et al., 2008, Messier et al., 2015). Doing so, however, will require shifting forest management away from a paradigm that aims to achieve top-down construction of specified forest structures towards management that instead emphasizes process-driven heterogeneity and diversity within a system (Holling and Meffe, 1996, Beechie et al., 2010, Falk et al., 2011, Messier et al., 2015).

Managing forests for resiliency and adaptive capacity, however, is hindered by the limited understanding of the range of forest structures and pathways of structural development in mixed-conifer ecosystems. An improved understanding, therefore, of the range of forest structures and the conditions that give rise to them would allow land managers to promote the forest patterns produced by an active disturbance regime (Churchill et al., 2013, Hessburg et al., 2015). In doing so, managers can increase forest heterogeneity, adaptability, and resiliency as fire, insect infestations, and pathogens are less able to spread across the landscape (Rodriguez and Torres-Sorando, 2001, Drever et al., 2006, Messier et al., 2015, Restaino et al., 2019).

The best contemporary source of information about forest structure and dynamics produced by an active fire regime are the wilderness areas and other protected areas that have a long history of managing fire for resource benefit (Collins and Stephens, 2007, Hunter et al., 2014, Rollins et al., 2011, Parks et al., 2016). In such areas, fire has been managed for an active ecosystem role for decades. These areas therefore experience a wider range of burning conditions in terms of frequency of burning and the weather conditions under which wildfires burn relative to non-wilderness areas (Collins et al., 2007, van Wagtendonk, 2007, Larson et al., 2013). This allows for the potential range of fire effects and post-fire development to be more fully expressed (Hunter et al., 2011, Holden et al., 2006, Stevens-Rumann and Morgan, 2016).

Here, we investigate forest structural diversity and development under a contemporary, active mixed-severity fire regime in mixed-conifer forests in the US Northern Rocky Mountains. We sampled forest structural conditions in a large, forested wilderness area in which wildfires have been managed for resource benefit for the last four decades. Our study was guided by three research questions:

(1) What forest structural classes are generated by an active fire regime?
(2) What is the role and relative importance of fire history, topography, geology, and local climate in the developmental pathways to different forest structure classes?
(3) Does live tree species composition differ between forest structure classes, and do differences in fire history explain variation in species composition within each structural class?

2. Materials and methods

2.1. Study area and site selection

All data were collected from lower slope and valley bottom sites within the South Fork Flathead River watershed of the Bob Marshall Wilderness in Northwest Montana, USA. Elevations range from 1,266 to 1,697 m. The study area is dominated by mixed-conifer forest, with forest composition consisting primarily of lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*, Belote et al., 2015). Ponderosa pine (*Pinus ponderosa*) is also present at low densities, primarily in low-elevation valley bottoms on well-drained soils (Keane et al., 2006, Larson et al., 2013).

The study area was historically characterized by a mixed-severity fire regime, with a mean fire return interval of approximately 20–80 years (Hopkins et al., 2014). Most fires were suppressed from 1935 to 1982; beginning in the early 1980s, however, fire management plans changed to allow for management of naturally ignited fires for resource benefit. Since then, the area has experienced an active fire regime, with the fire rotation period for the wilderness decreasing from 9,230 years during 1935–1982 to 29 years from 1983 to 2017 (Berkey, 2020, Larson et al., 2020). Due to its wilderness designation, it is also free from confounding factors on forest structure and fire spread, such as road construction or vegetation management.

A total of 224 sites were sampled between the summers of 2015 and 2017. Plots were selected using a stratified random sampling design with a factorial combination of number of fires in the modern period (1984–2013), first fire severity, and topographic classes. Plot burn history fell into one of three categories: unburned (no fire since at least 1935, n = 15 plots), once-burned (one fire sometime between 1985 and 2013, n = 89 plots) and twice-burned (two fires between 1985 and 2013, n = 120 plots). We aspired to a balanced sample of once-burned and twice-burned sites in our design, but some sample locations were abandoned due to safety concerns and access limitations. Our field sampling was further limited by the active fire season of 2015, which truncated the field season and necessitated evacuation of the field crew.

For plot selection, number of burns in the modern period and burn severity were determined using the fire atlas published by Parks et al. (2015) for the years 1972–2012, updated to 2013 using data from the MTBS project (Eidenshink et al., 2007). To ensure we sampled the full range of fire severities, plot-level fire severity was grouped into four classes based on dNBR values extracted from the Parks et al. (2015) atlas, which were bilinearly interpolated for each plot center point (dNBR ≤ 76, 76 < dNBR ≤ 216, 216 < dNBR ≤ 486, and dNBR > 486, Parks et al., 2014). Topographic classes for the plots included flat, north-east facing, and south-west facing and were bilinearly interpolated using a 30-m DEM of the study area. Minimum distance between plots was 150 m, while average distance between plots was 344 m.

2.2. Field methods

To sample tree regeneration, live saplings, which we defined as regeneration ≥ 1.37 m tall with a diameter at breast height (dbh) of < 10 cm, were tallied by species and sampled in a circular plot. Sapling plot radius was 5 m at unburned sites and 17.84 m at burned sites. Live seedlings (< 1.37 m tall with a dbh of < 10 cm) were tallied by species within a nested 4 × 20 m rectangular plot, which shared a plot center with the circular plot. Standing trees with a dbh of less than 80 cm but greater than 10 cm were also sampled within the 17.84 m radius plot. We recorded all trees with ≥ 80 cm dbh within a 43.7 m radius plot to capture the density of relatively rare, large trees on the landscape. The species, status (live or dead), and dbh was recorded for all standing trees.

2.3. Data reduction and analysis

2.3.1. Forest structure classes

To investigate the structure classes generated by an active fire regime, we defined forest structure as the densities of live and dead standing trees and regeneration in a forest stand. This definition, while not accounting for other structural elements such as species composition or downed woody debris, allows for parsimonious representation of fundamental ecological structure-function relationships (Latham et al., 1998). Furthermore, excluding species composition facilitates the generation of forest structure classes that are applicable to a range of mixed-conifer forest types beyond those we measured in this study.

We reduced the field data for the 224 plots down to an eight-column data matrix quantifying the size distribution and abundance of live trees, dead standing trees, and regeneration stems at each site. The eight forest structure variables included in the data matrix were stem density of live seedlings (< 1.37 m tall with a dbh of < 10 cm) and live saplings (≥1.37 m tall with dbh of < 10 cm), and basal area of live and dead trees stratified into three dbh classes: small trees (≥10–30 cm), medium trees (≥30–60 cm), and large trees (≥60 cm). Seedling and sapling stem densities (stems·ha^{-1}) were log-transformed to better meet assumptions of normality, after adding a value of 1 to account for plots with no regeneration. For the tree data, the total basal area per hectare ($m^2 \cdot ha^{-1}$) was calculated for both live and dead trees within the three dbh size classes (small, medium, and large). Each column in the data matrix was then standardized to a mean of 0 and a standard deviation of 1 (i.e., z-scores) to equalize variance among the variables.

We conducted a hierarchical clustering analysis on the resulting data matrix using Euclidean distance and Ward's linkage method (Ward, 1963). The cluster analysis allowed for empirical identification of forest structure classes among the 224 plots based on distinctions in regeneration densities and tree basal area within the eight size-status variables. The final number of clusters was decided using the CH index, which determines the optimal number of clusters by the ratio of between cluster distance to within-cluster distance (Caliński and Harabasz, 1974).

The clusters, as well as their underlying structural differences, were represented graphically with a non-metric multi-dimensional scaling (NMDS) analysis of the vegetation data matrix using the Bray-Curtis measure of dissimilarity (Bray and Curtis, 1957). An NMDS was used because it allows for a visual display of distance between the clusters in multi-dimensional space in such a way that only assumes monotonicity of the underlying data (McCune and Grace, 2002, Legendre and Legendre, 2012). In addition, NMDS better preserves the distance between plots in ordination space than other methods. The final NMDS was conducted in three dimensions to minimize stress while maintaining interpretability (McCune and Grace, 2002).

To verify that the resulting clusters represented different structure classes, a multi-response permutation procedure (MRPP) analysis was conducted to determine if the forest structure variables were significantly different across all clusters. MRPP analysis is preferred for vegetation data because it is a non-parametric test of differences between groups (McCune and Grace, 2002). For this analysis, we again used the Bray-Curtis distance metric. Both the NMDS and the MRPP were conducted within the Vegan package in R (R Core and Team, 2017, Oksanen et al., 2019).

A post-hoc analysis using descriptive statistics was conducted after hierarchical clustering to investigate differences in vegetation structure across the identified forest structure classes. Descriptive rather than inferential statistics were used for this analysis because the data-driven delineation of classes using the clustering approach maximizes the ratio of among-cluster to within-cluster variability, and therefore invalidates formal significance testing of class-to-class differences (Huang et al., 2015).

2.3.2. Relative importance of environmental variables to structure classes

A classification and regression tree (CART) analysis was conducted to investigate the relative importance of fire history and biophysical variables in the development of the forest structure classes identified by the cluster analysis (question 2). CART was chosen because it is a non-parametric method that can handle a combination of continuous and categorical data (De'ath and Fabricius, 2000). In addition, it provides an easily interpretable way to display interactions amongst variables. The CART was run as a classification analysis, in which the forest structure classes identified in the cluster analysis were the response variable. Tree pruning was conducted using cost-complexity pruning, which attempts to minimize misclassification within a terminal node while simultaneously selecting for the smallest possible tree.

Explanatory variables fell into four categories: climatic, topographic, geologic, and fire history. Climate variables included 30-year average temperature and rainfall in the 4-km^2 pixel containing each plot, bilinearly interpolated from plot center using PRISM monthly data (PRISM climate group, 2004). Topographic variables were bilinearly interpolated from plot center using a 30-m DEM for the study area and included elevation and topographic wetness index (TWI). TWI serves as a proxy for shallow soil moisture levels and accounts for local controls on water movement as well as upslope water contributions (Beven and Kirkby, 1979, Western et al., 1999). In addition, a heatload value for each plot was calculated using the McCune and Keon (2002) formula. Heatload is an estimate of solar radiation that incorporates plot latitude, slope, and aspect (McCune and Keon, 2002).

Geologic parent material was derived using simple extraction from a 30-m dataset for the Bob Marshall Wilderness containing dominant landform and parent material groupings (J. Skovlin, USDA-NRCS, Missoula Soil Survey Office, personal communication, March 12, 2020). Parent material classification included five classes: alluvial valley bottoms, cirque basins, glacial till and colluvial slopes, non-calcareous residual bedrock-controlled slopes, and calcareous residual bedrock-controlled slopes. Fire history variables included the number of burns since 1935 (0, 1, or 2) and the burn severity of each fire (first and second) as a continuous variable. We also included the time since the most recent burn, calculated as the number of years between the most recent fire and the sampling date, as well as the time between fires for twice-burned plots. All data extraction was performed in the program R (R Core and Team 2017).

2.3.3. Role of fire history in development of structure classes

We used descriptive statistics to evaluate the role of fire history in the development of forest structure (question 2). For each structure class, we investigated the proportion of plots that experienced zero, one, or two burns. In addition, we divided the time-since-burn variable into four classes, where unburned plots remained classified as unburned and all other plots were classified as short (< 10 years), medium (10–20 years), or long (> 20 years) time since fire. Similarly, the fire severity variable was broken down into five classes based on field data and dNBR values: unburned plots remained classified as unburned, plots where the most recent fire resulted in a dNBR value of < 200 were classified as unchanged, plots with a dNBR value between 200 and 400 were classified as low severity, 400–600 was classified as moderate

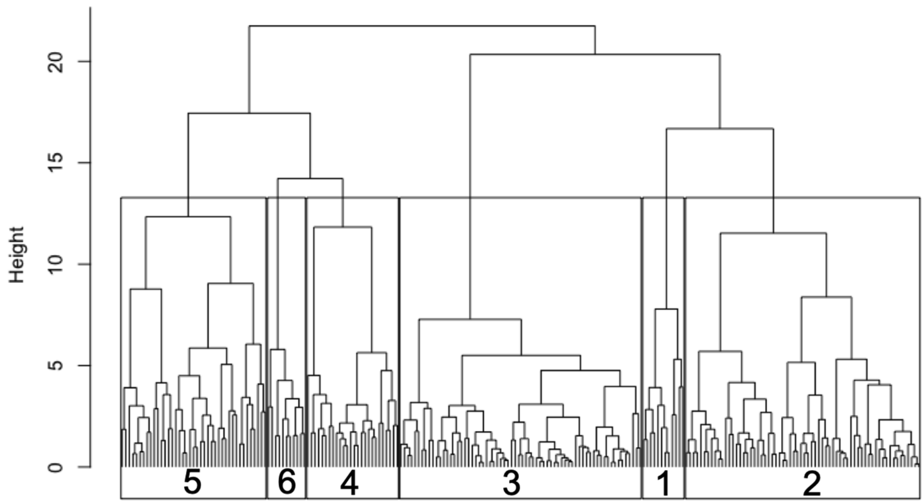


Fig. 1. A dendrogram depicting the six forest structure classes resulting from the hierarchical clustering of 224 mixed-conifer forest sites on stem density of live tree regeneration and basal area of live and dead small, medium, and large trees. The height variable on the y-axis represents dissimilarity, while each of the terminal nodes represents one of the 224 plots. Earlier (higher) branches in the dendrogram indicates plots that are more dissimilar than plots that branch apart at lower heights.

severity, and > 600 was classified as high severity (Belote et al., 2015). These dNBR cut-offs differ from the cut-offs used during plot selection in order to remain consistent with other analyses conducted in this area (Belote et al., 2015).

We also investigated the breakdown of the forest structure classes using a classifier that combined number of burns and burn severity. Plots were categorized as unburned, once-burned at either low (dNBR < 400) or moderate to high severity (dNBR ≥ 400), and then all possible combinations of reburns: low followed by low, low followed by mod/high, mod/high followed mod/high, and mod/high followed by low (Stevens-Rumann and Morgan, 2016).

2.3.4. *Vegetation composition of forest structure classes*

Further post-hoc analysis was conducted to compare live species composition and structure across the forest structure classes identified in the hierarchical cluster analysis (question 3). First, because live tree structure is largely shaped by fire, the small, medium, and large live trees were classified in three groups based on species traits that confer fire tolerance: highly fire-tolerant ponderosa pine and western larch, moderately fire-tolerant Douglas-fir, and all other (comparably fire-intolerant) species, following the fire resistance classification for our study area developed by Belote et al. (2015). Seedlings and saplings were also split into three groups on the basis of traits relevant to post-fire regeneration and shade tolerance: serotinous lodgepole pine, shade-tolerant species (subalpine fir, Engelmann spruce, Douglas fir, and Pacific yew (*Taxus brevifolia*)), and all other, shade-intolerant species. Basal area of trees and regeneration density for these species' groupings were than compared across the six structure classes.

We also evaluated the role of fire history in shaping vegetation composition within the six structure classes. Live vegetation structure was again classified on the basis of traits that confer fire resistance for trees, and serotiny/shade tolerance for regeneration. For this analysis, however, the live trees and regeneration were grouped into two classes: regeneration (< 10 cm dbh) or trees (≥10 cm dbh). The plots assigned to each structure class were then subdivided along the same breakdown of fire history used in Section 2.3.3, in which plots were classified by number, order, and severity of burns. This allowed for comparisons of average stem density (stems·ha^{-1}) per plot for each species grouping across fire histories within each forest structure class.

3. Results

3.1. *Forest structure classes*

The hierarchical cluster analysis conducted on the vegetation size-status data matrix resulted in six distinct forest structure classes (Fig. 1). The MRPP indicated that vegetation structure between each of these six forest structure classes was significantly different (A = 0.25, p value of delta = 0.001, Appendix A).

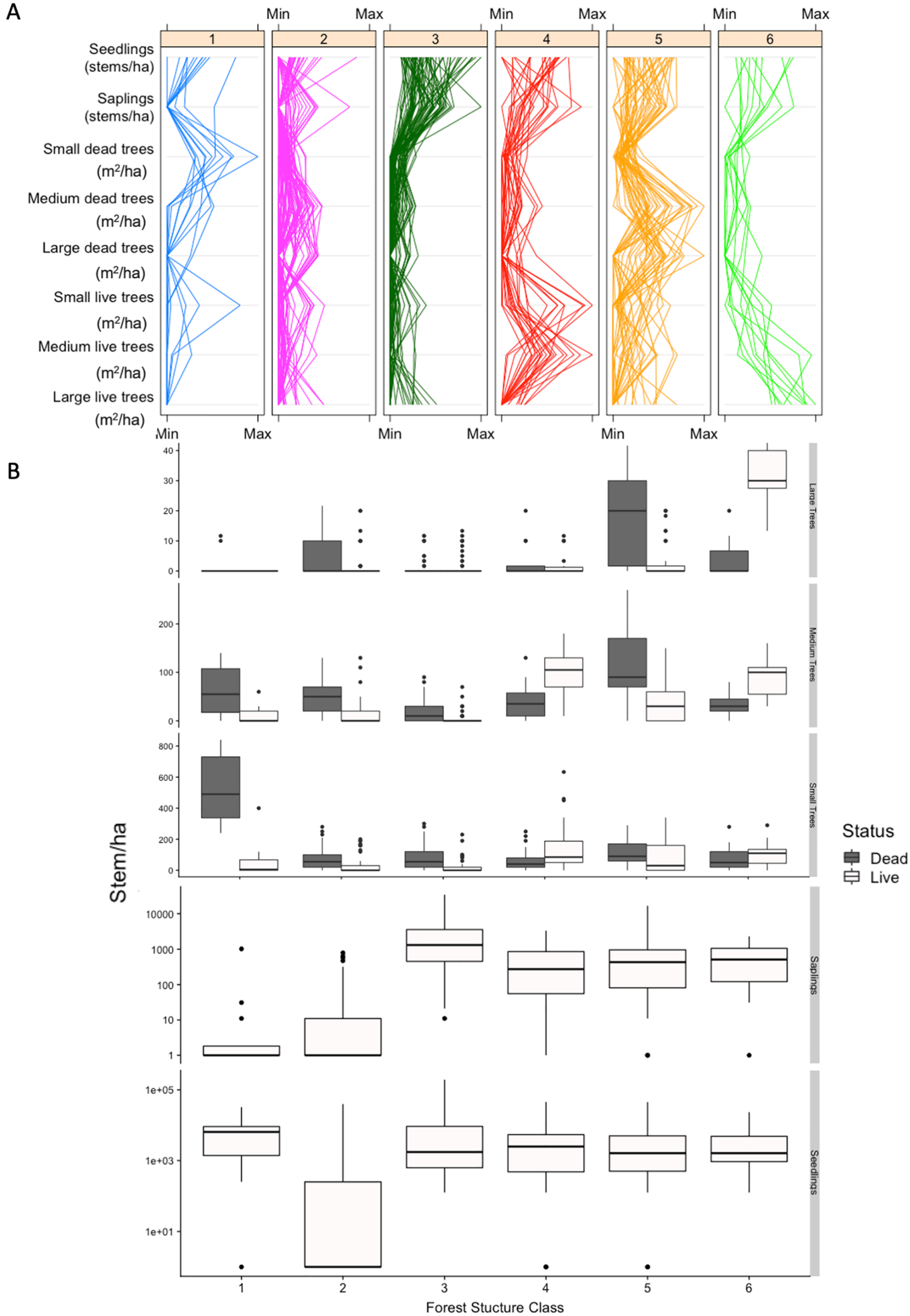
The NMDS and the descriptive statistics for the eight size-status variables used in the clustering analysis revealed the structural components that defined each forest structure class. Forest structure class 1, for example, was identified as a unique cluster on the basis of relatively high densities of small dead trees, whereas forest structure class 2 tends to have plots with relatively low to moderate densities of all trees and regeneration (Appendix A, Fig. 2). Forest structure class 3 is defined by high density tree regeneration, both in the seedling and sapling size classes (Fig. 2). Plots assigned to forest structure class 4 were clustered on the basis of greater small and medium live tree densities than the other classes, whereas forest structure class 5 was defined by high densities of dead trees, either in the medium or large size class. Finally, forest structure class 6 was defined by plots with large, live trees present (Fig. 2).

3.2. *Relative importance of environmental variables to structural development*

The CART analysis revealed that time since fire plays a large role in determining forest structure classes (Fig. 3). Plots that burned within five years tended to fall into forest structure class 2, whereas plots that have not burned since at least 1935 tended to fall into forest structure class 4. In the CART analysis, this is indicated by the branch determined by ≥ 68 years since fire (Fig. 3).

In the plots that have burned since 1985 but have not burned within the past five years, environmental factors beyond time since fire begin to shape forest structure. These plots, which are identified in the CART tree as having burned most recently in the past 6–67 years, are classified into forest structure class 2, 3, or 5 depending on the number of burns, 30-year average temperature, and heatload, in addition to time since fire. Forest structure classes 1 and 6 were not assigned a pathway to development within the CART analysis, likely because they have the fewest number of plots and therefore do not dominate any one terminal node of the classification tree.

The CART model reveals a number of pathways to development for each forest structure class. In particular, structure class 2 is identified as the predicted class in four of the seven terminal nodes (Fig. 3). This structure class predominated in the plots that were burned 5 years prior to sampling, or those that burned in the past 6–67 years and experienced a second burn, high heatload, or high mean annual temperature (Fig. 3). The overall misclassification rate for this CART model was 41.1%.



(caption on next page)

Fig. 2. The vegetation structure of the six forest structure classes identified by hierarchical clustering analysis based on eight size-status levels (live seedlings and saplings and live and dead trees in three dbh classes). Panel A displays structure relative to the minimum and maximum values of attributes (categorical y-axis) across all plots within each structure class, where each line represents the forest structure of a single plot. Panel B displays the vegetation structure of the six forest structure classes identified by hierarchical clustering analysis based on eight size-status levels (live seedlings and saplings and live and dead trees in three dbh classes). Boxplot vertical lines display the range (minimum and maximum) of stem densities, the box includes first quartile, median, and third quartile values, and points represent outliers for each of the six structure classes.

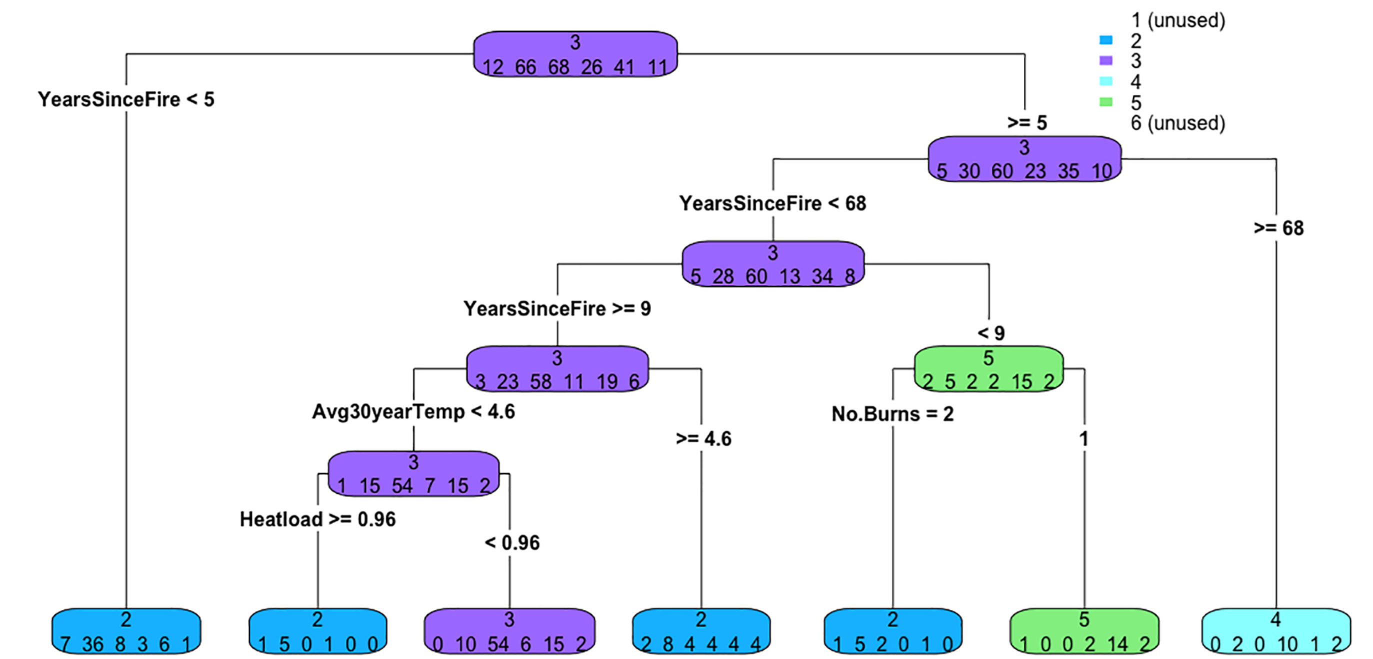


Fig. 3. Results of CART model, indicating the most likely forest structure class for a given combination of fire history and biophysical variables. The top number of each box represents the predicted forest structure class, while the numbers at the bottom of the box represent the number of plots within each structural class, ordered 1 through 6.

3.3. Role of fire history in development of structure classes

The fire history analysis revealed that many possible fire history pathways can lead to a given forest structure class. Forest structure classes 1, 2, 3, and 5 have the greatest fire activity, with only three unburned plots among these structure classes (Fig. 4a). In addition, over a third of the plots in these structure classes burned at high to moderate severities at least once since 1985 (Fig. 4d). Forest structure classes 4 and 6, by comparison, have a higher proportion of plots that were unburned, as well as a higher proportion of plots burning only at low severities.

Plots in forest structure class 1 have all experienced at least one fire and tend to have burned within the past 10 years (Fig. 4). Plots in forest structure class 2 have also burned at least once, with the exception of one plot. This structure class also had one of the highest proportion of plots experiencing reburns (Fig. 4a). These plots tend to be classified as “short time since fire” and burned at a range of severities, although over 20% of plots in structure class 2 have experienced at least one high to moderate severity burn (Fig. 4d).

No plot in forest structure class 3 was unburned, as in class 1, but these plots tended to have more time since fire than class 1 (most commonly 10–20 years removed from the most recent fire; Fig. 4). Forest structure class 5 has the greatest proportion of once-burned plots, with most of those plots burning at low severities. Only two of these plots are unburned or are classified as long time since fire.

Forest structure class 4 has the greatest proportion of unburned plots, with only three plots experiencing a high or moderate severity burn. Forest structure class 6 is similar in that it has a relatively high proportion of plots that are unburned. All structure class 6 plots that have burned did so within the past 20 years, and at severities classified as low or unchanged (Fig. 4).

3.4. Vegetation composition

The post-hoc analysis of species composition and tree densities within each of the six forest structure classes revealed several distinct patterns. Forest structure classes 1, 2, and 3, for example, all have low live tree densities (Fig. 5a). In forest structure class 3, the high regeneration densities are primarily caused by serotinous, lodgepole pine stems, although the densities of both shade-tolerant and -intolerant species are relatively high in the seedling size class (Fig. 5b).

Forest structure classes 4, 5, and 6, in contrast, have a much larger live tree component. In structure classes 4 and 6, the live species composition is similar for the small and medium live tree variables, with relatively low densities of fire-tolerant species in the small tree size class, and relatively high densities of these species and the moderately fire-tolerant Douglas-fir in the medium tree size class (Fig. 5a). In forest class 6, the live, large trees are dominated by fire-tolerant ponderosa pine and western larch, with moderately high densities of Douglas-fir. Plots in forest structure class 5 also contain moderate densities of medium and small live trees, mostly Douglas-fir (Fig. 5a). Regeneration in these three forest structure classes is dominated by shade-tolerant species, especially in the sapling size class (Fig. 5b).

There were some common trends across all forest structure classes in relation to burn history and vegetation composition (Fig. 6). For live tree structure, fire-intolerant species tended to have their highest densities in plots that were unburned or burned once at unchanged to low severities (Fig. 6a). The greatest densities of the highly fire-tolerant ponderosa pine and western larch species were located in plots that burned at unchanged to low severities (Fig. 5a).

Forest structure classes 4, 5, and 6 show the greatest within-class diversity in live tree species composition (Fig. 6a). In forest structure class 4, repeat burns or a single, higher severity burn generally reduced

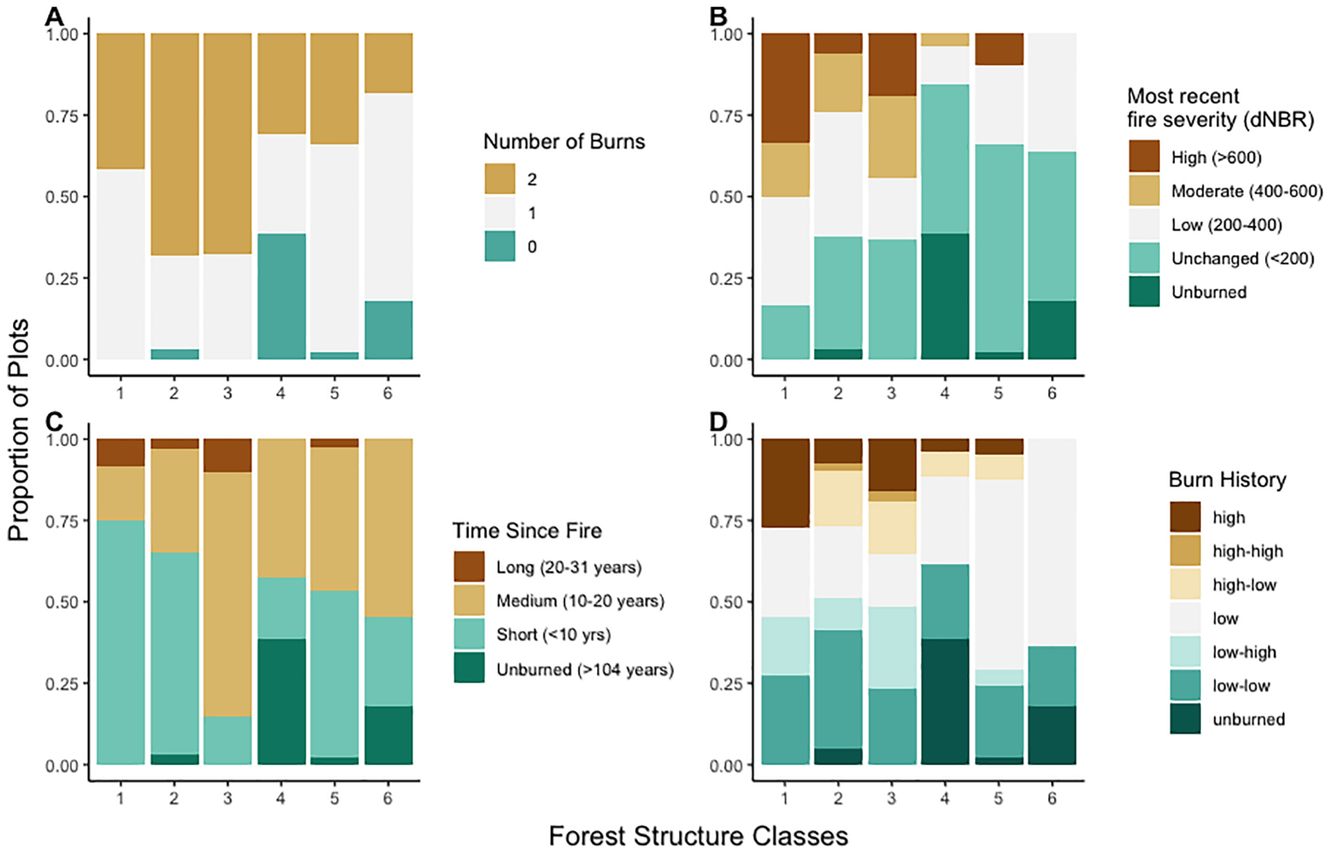


Fig. 4. Fire history, including a) number of burns, b) the severity of the most recent fire, c) the time since fire, and d) the sequence of burn severities for each forest structure class. In panel D, the cut-off between low and high severity was a dNBR value of 400.

live tree densities by removing fire-intolerant species. A similar pattern is evident in forest structure class 5. Finally, in forest structure class 6, Douglas-fir dominated in plots that burned once at an unchanged to low severity, western larch and ponderosa pine dominated in the plots that burned twice at unchanged to low severities, and the fire-intolerant species dominated in the unburned plots.

The species composition of regeneration showed less variation between fire histories as compared to live tree species composition. Instead, regeneration composition tended to vary more between forest structure classes (Fig. 6b). In structure class 3, for example, regeneration density is high across all plot burn histories. The greatest densities of serotinous, lodgepole pine regeneration, however, were found in plots that burned once at a moderate to high severity or in the low–high reburn plots.

4. Discussion

4.1. Conceptual model of forest structural development

The results from these analyses point to a new conceptual model of stand development in mixed-conifer ecosystems across a range of fire severities (Fig. 7). This model is not intended to capture all of the possible pathways to structural development supported by our analyses, or all possible forest structures in a mixed-conifer forest. Instead, this model is intended to describe how a range of fire disturbances, successional pathways, tree species compositions, and physical environmental variables may interact to produce a mosaic of forest structure classes over space and through time.

From a successional standpoint, a high-severity fire “resets” forest structure to class 1 or 2. These structure classes, with their lack of live vegetation, correspond well with the early seral stages following a stand-replacing disturbance event described by other forest classifications (Fig. 8; O’Hara et al., 1996, Foster et al., 1998, Franklin et al., 2002, Reilly et al., 2018). Whether the forest patch arrives at class 1 or 2 appears to largely depend on the pre-existing vegetation conditions. Structure class 1 requires a high density of small diameter trees prior to the fire, and therefore likely results from a high-severity burn of a relatively young, probably even-aged forest patch. The potential pathways to structure class 2, however, are more numerous (Fig. 7).

The many possible pathways to structure class 2 results in a highly heterogenous structure class (Figs. 2 & 5). The variability of forest structure in class 2 points to evidence for multiple pathways in early-successional forest development following a natural disturbance (Donato et al., 2012). Rather than a single dominant successional pathway in which tree regeneration establishes promptly after a high-severity fire (e.g., Oliver, 1980, Franklin et al., 2002), structure class 2 is consistent with a protracted period of conifer tree establishment (Gabriel, 1976, Donato et al., 2012, Freund et al., 2014). This complexity likely results from the range of disturbance histories operating on this landscape, in combination with the potential range of interactions with the biophysical environment (Fig. 3).

Without further fire activity, successional development from structure classes 1 or 2 will likely lead to structure class 3. This structure class includes the dense regeneration patches, typically dominated by lodgepole pine, that often result from succession and re-establishment following stand-replacing disturbance events (Turner et al., 1997, 1999, 2004). However, forest patches in structure class 2 containing low-density tree regeneration may develop directly into structure class 4, bypassing the high-density, closed-canopy stage of structure class 3 (Donato et al., 2012). Similarly, burned plots on low-productivity sites may remain in structure class 2 rather than progressing to structure classes 3 or 4 due to biophysical limitations to forest structure development (Larson et al., 2008).

If structure class 3 burns, it will likely reset to class 1, especially if that forest patch contained high densities of lodgepole pine that had reached

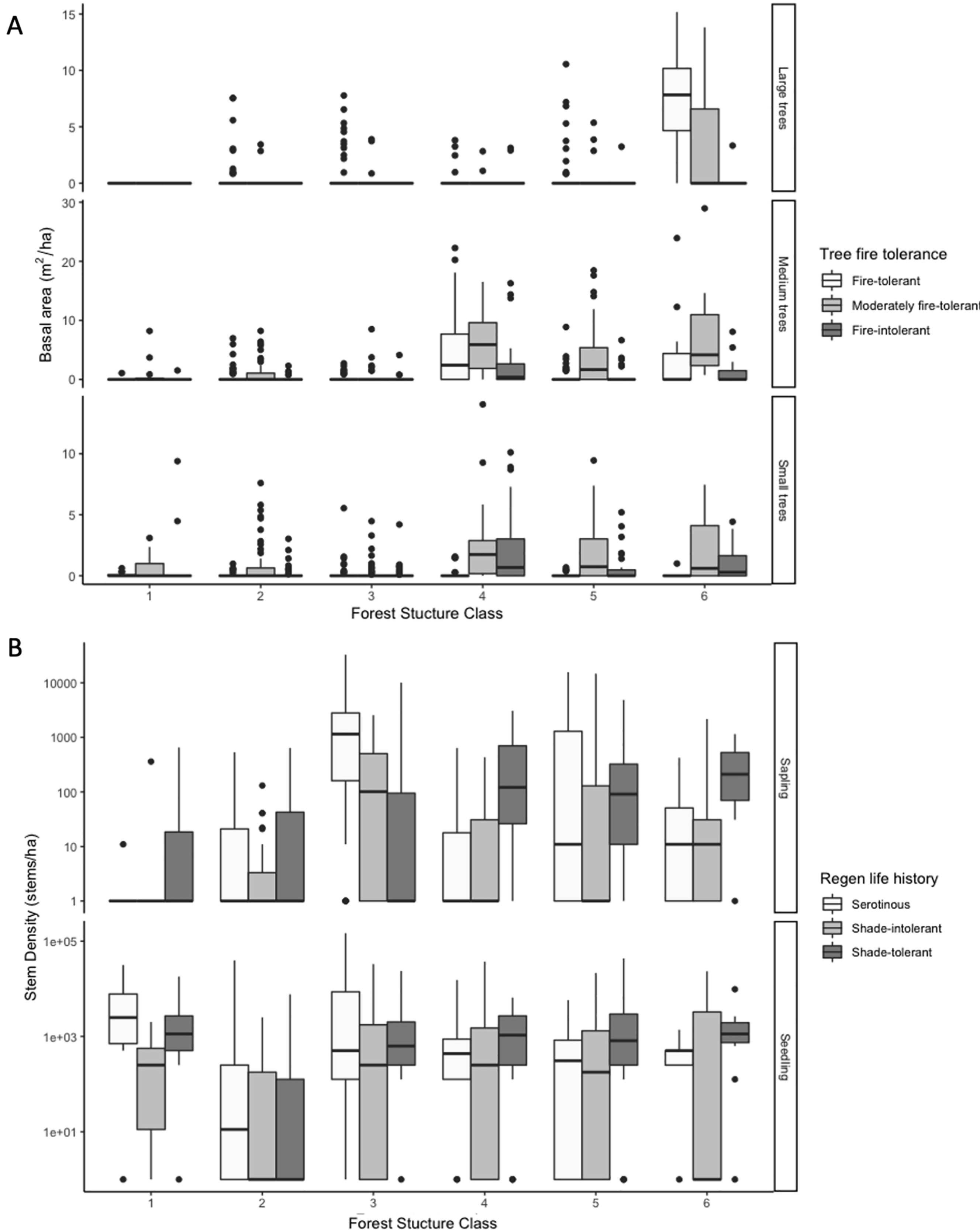


Fig. 5. Live tree species composition and structure of the six forest structure classes identified in the hierarchical cluster analysis. Boxplot vertical lines display the range (minimum and maximum) of stem densities, the box includes first quartile, median, and third quartile values, and points represent stem density outliers for each of the six structure classes. Tree species were classified as fire-tolerant (ponderosa pine or western larch), moderately fire-tolerant (Douglas-fir), or fire-intolerant (all other species). Regeneration species were classified as serotinous (lodgepole pine), shade-tolerant (subalpine fir, Engelmann spruce, Douglas fir, and Pacific yew), and shade-intolerant (all other species). Note the differences in density measurements between A) trees and B) regeneration plots, which is reflective of the variables used for the clustering analysis. Regeneration stem density is displayed in log-transformed space.

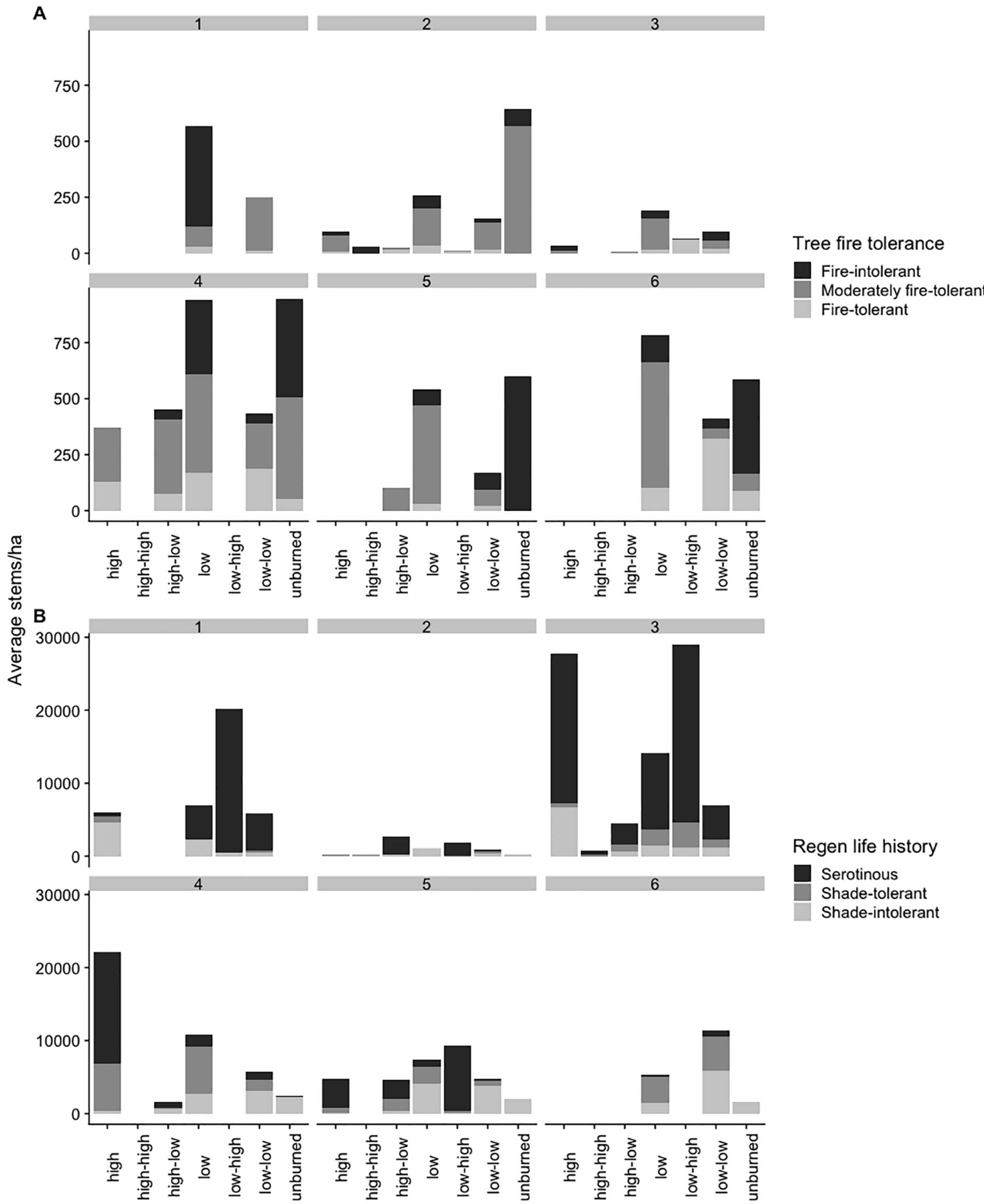


Fig. 6. Live vegetation composition for A) trees and B) regeneration for each forest structure class, broken down by fire history. Fire history was determined by the dNBR value for the plot, with 400 serving as the cutoff between a low and high severity fire. Multiple fires are indicated by hyphenated severity categories (e.g., high-low indicating a high severity fire followed by a low severity fire).

reproductive maturity. If the patch burns again, or as the small, dead trees fall and becomes downed woody debris, structure class 3 could easily reset to class 2 as well. In a landscape with an active fire regime, this "reverting" back to class 1 or 2 is highly likely given the predominance of fire-intolerant, lodgepole pine in structure class 3. If forest structure class 3 remains unburned long enough, however, it will likely develop into forest structure class 4 (Franklin et al., 2002, Turner et al., 2016). The species composition of any given forest patch in structure class 4 will vary given the density and species composition of regeneration, the climate and topographic conditions, and subsequent fire activity (Larson, 1992).

Fire activity in forest structure class 4 can lead to a number of structural changes. If it burns at high severity, the patch may return to structure class 1 or 2. A single, low-severity fire in the forest patch may maintain the patch in structure class 4 at lower stem densities or begin a transition towards class 6. If that fire activity is followed by a bark beetle attack, however, the trees that survived the fire may die due to

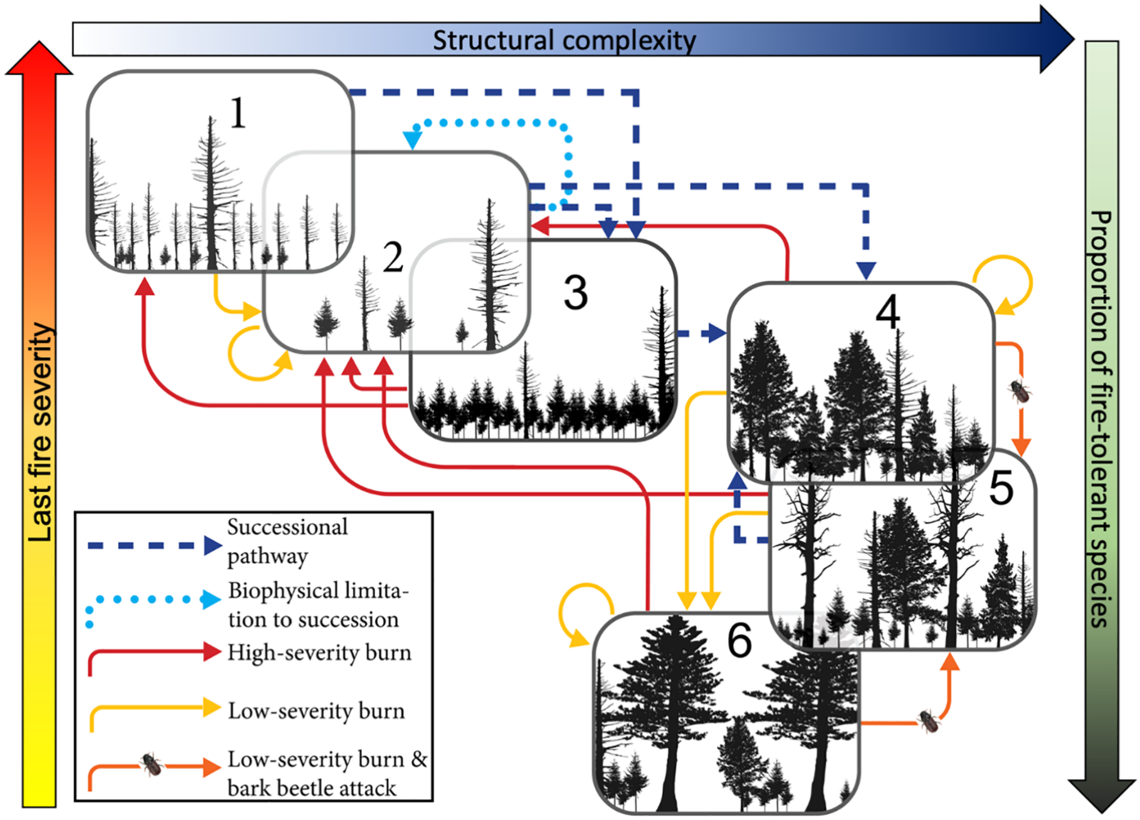


Fig. 7. Conceptual model of stand development between six empirically-defined forest structure classes in a mixed-conifer ecosystem with an active fire disturbance regime. The darker, foliated trees represent live trees in this model. For each axis, the variable increases towards the head of arrow- i.e., the last fire severity increases going up vertically, the structural complexity increases from left to right, and the proportion of fire-tolerant species increases going down vertically. High structural complexity was defined as having greater densities of large trees (live or dead) and multiple live canopy layers, indicated by high densities across many live stem size classes (Zenner and Hibbs, 2000, Franklin et al., 2002, Larson et al., 2008). Bark beetle activity, while not explicitly measured in this study, is included in the model on the basis of the findings of Ryan and Amman (1994), McCullough et al. (1998), and Hood and Bentz (2007).

beetle activity, thereby switching to structure class 5. Although this study did not explicitly measure beetle activity, this disturbance interaction and associated developmental pathway is well established for this region (Ryan and Amman, 1994, McCullough et al., 1998, Hood and Bentz, 2007, Belote et al., 2015). It is also consistent with the prevalence of low-severity fire in the development of a structure class dominated by large diameter, dead trees and abundant live small and medium diameter trees (Figs. 2 & 4). Finally, repeat, low-severity fires in structure class 4, especially if the patch has more fire-tolerant species present, could cause a switch to structure class 6.

If a fire did convert a forest patch to structure class 6, this class is then maintained by subsequent, low-severity fires (Fig. 4). This is a well-documented disturbance history that allows for large diameter, fire-resistant species such as western larch and ponderosa pine to outcompete other shade-tolerant, fire-intolerant species (Leirfallom and Keane, 2010, Larson et al., 2013, Hopkins et al., 2014). A high severity fire in this class, however, could kill the large, fire-resistant trees and convert this class to structure class 2 (Larson et al., 2013). Additionally, as with structure class 4, conversion to class 5 could occur with a low-severity fire followed by a bark beetle attack (McHugh and Kolb, 2003, Hood and Bentz, 2007).

4.2. Relative importance of environmental variables to structural development

The CART analysis highlights the relatively strong influence of post-disturbance successional dynamics in this landscape, as time since fire is particularly important in determining structure classifications (Fig. 3). It also reveals, however, that the physical environment plays a role in structure development in patches with intermediate time-since-fire values. For example, forest structure class 3 is most likely to develop in a stand ≥ 9 years after a fire (Fig. 3), likely because nine years of post-fire development allows for dense regeneration to occur at suitable sites. If, however, the forest patch has higher annual temperatures or receives higher levels of solar radiation, then the CART model predicts it will remain in the lower stem density condition typical of structure class 2 due to conditions unfavorable to regeneration and dense tree growth.

These results suggest that traditional successional theory in which a structurally simple young forest develops into a structurally diverse old forest (Oliver and Larson, 1996) are oversimplified for mixed-conifer ecosystems. Biophysical factors and complex fire histories of variable frequency and severity do not allow for such a predictable trajectory of forest structural development. Instead, recently burned plots can contain high levels of structural complexity, and unburned plots span several forest structure classes.

Overall, the CART model provides evidence for a system in which succession plays a large role, but structural diversity is maximized by intermediate levels of disturbance interacting with the physical environment (Roxburgh et al., 2004, Zinck et al., 2010, Hessburg et al., 2015). These results agree with existing theory that identifies succession and disturbance as broad controls over ecosystem structure and function, while topography influences vegetation patterns at the patch scale (Hessburg et al., 2015). Furthermore, the relatively high misclassification rate results from the fact that nearly every developmental pathway described by the CART analysis contains at least four structure classes, not just the single structure class predicted by the model (Fig. 3). This underscores the complexity of this mixed-conifer system, as it indicates that there are factors besides the biophysical and fire

Fig. 8. Plot level photographic representations of each empirically-defined forest structural class, 1–6, taken in the field.

history variables central to our analyses, such as chance seed dispersal events (Shibata et al., 2010), patch dynamics (Kemp et al., 2016), and climate change effects (Davis et al., 2019), that play a role in determining forest structure.

4.3. Vegetation composition

There are high levels of compositional diversity within each forest structure class. The post-hoc analysis of vegetation composition indicates that this diversity appears to be largely driven by fire history (Fig. 6). This is important in that it further informs our understanding of within-class heterogeneity and may have implications for future forest developmental trajectory and future fire effects. For example, the higher densities of fire-intolerant species in the unburned forest class 6 plots suggest that these plots have experienced a buildup of ladder fuels in the understory (Fig. 6). As a result, these unburned structure class 6 patches may be at greater risk of a high severity fire and subsequent conversion to a different structure class in the future (Larson et al., 2013).

There are also plots that have not burned in the last 20 years that were classified as forest structure class 2, a supposedly early development structure class. The resulting forest patches tend to have higher densities of live trees, particularly Douglas-fir, when compared to other stands in structure class 2 (Fig. 6). In this case, it is likely an interaction of fire history and physical environmental variables that maintains species heterogeneity within a single structure class (Fig. 3).

4.4. Management implications

The findings of this study underscore the complexity of managing mixed-conifer forest landscapes subject to mixed-severity fire regimes. Increasingly, land managers aim to restore heterogeneity in these systems in order to confer forest resilience to future climate change impacts (Drever et al., 2006, North et al., 2009, Messier et al., 2015). What heterogenous forest structure looks like in a mixed-conifer system with an active fire regime, as well as how these forest structures are dispersed across the landscape, is often unclear due to over a century of fire suppression and the legacy of past timber harvest and other land uses. As a result, forest structural development is often simplified to the archetypal models of structure resulting from either non-lethal surface fire or high-severity, stand replacement fire (Oliver, 1980, Covington

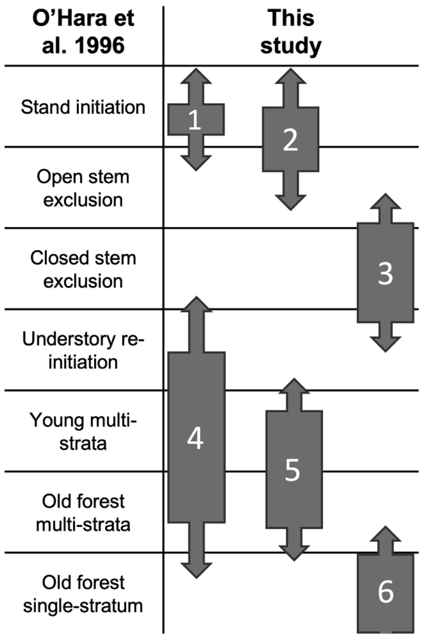


Fig. 9. Comparison of our structure classes to those of O'Hara et al. (1996), which is frequently used to guide forest management decisions. The diversity captured within our structure classes (i.e., class 4) combined with the overlap of multiple of our structure classes within the framework of the O'Hara model (i.e., classes 1 and 2), highlights the potential pitfalls of attempting to capture the diverse forest structures, such as those occurring under a mixed-conifer, active fire regime, to discrete forest bins.

and Moore, 1994, Franklin et al., 2002). The results from this study, which includes environmental variables beyond these archetypal fire regimes, can therefore contribute to guiding management for heterogeneity and resiliency on multiple scales.

It is particularly useful to examine how the forest structure classes revealed in this analysis correspond to the structural classification guide developed by O'Hara et al. (1996), which is frequently used by land managers of the Inland Northwest and US Northern Rocky Mountains (Reynolds and Hessburg, 2005, Gärtner et al., 2008, O'Hara, 2014). The comparison shows that each of the forest structure classes identified in this analysis span multiple classes in the O'Hara system, with forest structure classes 4 and 5 demonstrating the greatest diversity (Fig. 9). Some forest structure classes, however, do map more directly onto the existing classification system. Structure class 1, for example, corresponds well to the stand initiation stage in which a stand replacing disturbance allows for establishment of early-successional species. Forest structure class 6 similarly overlaps relatively cleanly to the old forest single-stratum class from the O'Hara model.

The overlap of multiple of our classes within the O'Hara classification system is partially due to the relative importance that our model places on dead, standing structure. Forest structure class 1 differs from class 2 in part due to the high densities of small, dead trees in class 1 plots. Similarly, structure class 5 is distinguished from structure class 4 in our analysis due to differences in large, dead stem densities. The differences in dead structure between these classes will have implications for future fire activity (Larson et al., 2020) as well as wildlife habitat for animal species (Hutto, 1995, Hoyt and Hannon, 2002).

The lack of clean correspondence between our data-driven forest structure classes and the O'Hara classification system points to potential shortcomings of using forest classifications to guide management. The O'Hara model categorizes forest structure into discrete bins developed through expert opinion and is predicated on classical stand development theory (i.e., resource availability, competition, and successional replacement processes; Oliver and Larson, 1996). It therefore largely ignores the role of wildfire in determining forest structural conditions.

In contrast, our results indicate that fire history largely controls structure in mixed-conifer forests of the Inland Northwest and Northern Rockies region. Furthermore, the structures generated by this active fire regime do not fit cleanly into the distinct structure classes that correspond well to stand development theory and conventional silvicultural systems. The diversity of structures apparent in our dataset, and the multiple developmental and fire history pathways leading to each structure class, point to the need to manage forests as complex adaptive systems. Such a management approach allows for greater resiliency of essential forest ecosystem functions to unknown future conditions (Gunderson, 2000, Puettmann et al., 2008, Messier et al., 2015). This could be achieved by emphasizing ecosystem processes, especially wildfire, rather than taking the top-down approach of engineering idealized forest structures.

In the future, a wider variety of forest structures across a larger spatial extent could potentially be captured using LiDAR technology, with potential to inform management of fire-prone mixed-conifer forests (Moran et al., 2018, Jeronimo et al., 2018). Although this approach would not capture some of the elements included in this analysis, such as species composition or below-canopy tree regeneration, a LiDAR based approach would permit cost-effective quantification of other forest attributes, such as spatial aspects of structural complexity created by wildfire (Wiggins et al., 2019, Kane et al., 2019).

5. Conclusion

This study offers new insight into the complexity of mixed-conifer ecosystems experiencing a contemporary, active fire regime. The frequent focus on certain archetypes of fire-forest dynamics, such as infrequent stand replacing fire or frequent surface fire, makes this study particularly important to management of fire-driven landscapes that fall somewhere in the middle of that continuum (Agee, 1993, Hessburg et al., 2016). Our results highlight the complexity of fire history and how it interacts with the biophysical environment to shape forest structure. This complexity underscores the necessity of managing these forests in the context of a system in which succession following a high-severity fire event is heavily shaped by the physical environment in combination with subsequent, non-stand replacing disturbance events (Hood and Bentz, 2007, Lydersen and North, 2012, Hessburg et al., 2015, Merschel et al., 2018).

Ultimately, our results do not offer prescriptive restoration targets. The inherent complexity of this system makes that goal difficult, as there is no way to precisely predict the appropriate forest structure or composition from easily measurable environmental variables. Instead, our results highlight the importance of a general strategy to manage fire as an integral ecosystem process across the full range of biophysical conditions, rather than attempting to create idealized or archetypal forest structures through silvicultural approaches while continuing to largely exclude wildfire.

CRediT authorship contribution statement

Julia K. Berkey: Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **R. Travis Belote:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - review & editing, Supervision, Funding acquisition. **Colin T. Maher:** Validation, Formal analysis, Data curation, Writing - review & editing. **Andrew J. Larson:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

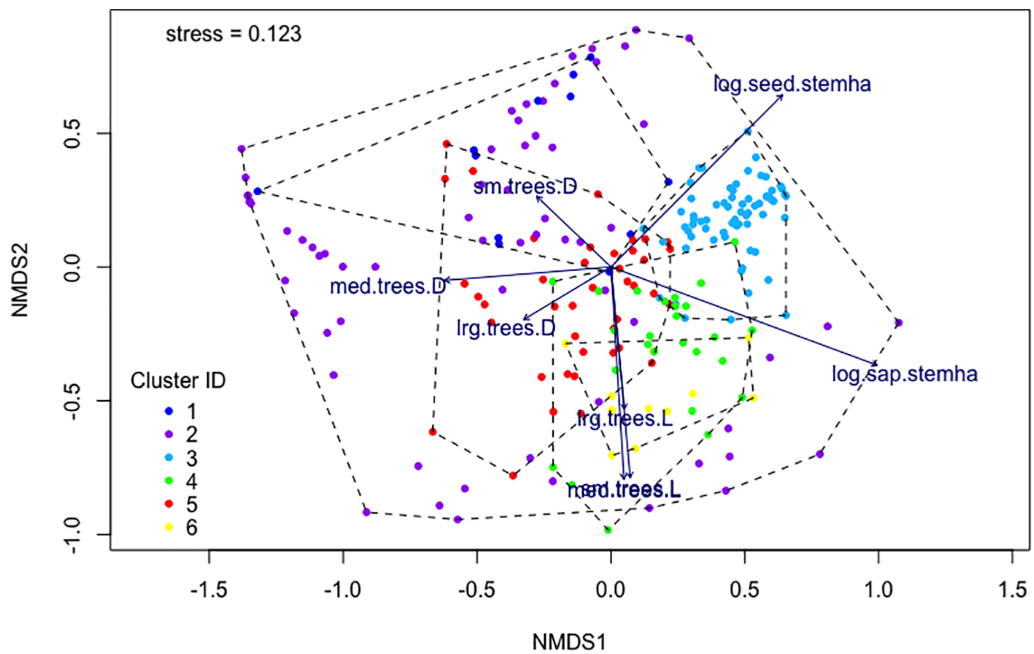
Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the Joint Fire Science Program [project number 14-1-02-9]. Jay Skovlin of the NRCS Soil Survey provided us with the dominant landform and parent material data for the entirety of the Bob Marshall Wilderness, for which we are very grateful. We thank the Spotted Bear Ranger District of the Flathead National Forest for facilitating our field research, especially Deb Mucklow, Tad Wehunt, Seth Carbonari, and Jim Flint. Thanks also to Phil Higuera and Dave Affleck and two anonymous reviewers, who provided constructive feedback on earlier versions of the manuscript.

Appendix A



The NMDS for the 224 plots, conducted on the vegetation data matrix of eight vegetation size-status variables in three dimensions. The final NDMS solution was centered and rotated orthogonally to its principal components (Legendre and Legendre, 2012), resulting in a display of the data in two dimensions. In this plot, the first axis contains the highest dispersion of points and the second axis contains the next greatest dispersion (Oksanen et al., 2019). Arrows depict the magnitude and direction of the correlation between each size-status variable and the ordination axes.

Appendix B

Summary table of mean and standard deviation of vegetation densities for each size-status variable used in the clustering analysis, by forest structure class. Vegetation density was measured using basal area (BA) per hectare for trees and stems per hectare for regeneration.

Cluster	No. plots	Tree Size Class	BA (live, m^2/ha)	Std. dev.	BA (dead, m^2/ha)	Std. dev.	Regen Size Class	Stem/ha	Std. dev.
1	12	Large	0.0	0.0	0.8	1.8	Sapling	88	293
		Medium	1.3	2.5	8.3	7.2	Seedling	8,469	9,797
		Small	2.0	3.6	15.9	6.8			
2	66	Large	0.6	1.6	1.8	2.6	Sapling	62	160
		Medium	1.5	2.6	6.7	5.1	Seedling	1,274	5,204
		Small	1.0	1.8	2.5	2.0			
3	68	Large	0.8	1.8	0.5	1.3	Sapling	4523	7776
		Medium	0.6	1.6	2.4	3.1	Seedling	11,869	28,707
		Small	0.6	1.2	2.3	2.2			
4	26	Large	0.8	1.4	0.9	1.7	Sapling	627	903
		Medium	13.8	7.0	5.1	4.7	Seedling	5,538	9,595
		Small	4.9	4.6	2.4	2.2			
5	41	Large	1.4	2.7	6.1	4.8	Sapling	1,851	3,938
		Medium	5.1	5.9	16.8	9.8	Seedling	4,585	8,307
		Small	2.4	2.7	3.5	2.5			
6	11	Large	11.4	2.5	1.5	2.4	Sapling	662	706
		Medium	13.6	7.6	5.0	3.8	Seedling	5034	7,167
		Small	3.3	2.4	2.6	2.7			

Appendix C

Summary data, broken down by forest structure class, for the live species of our study area. Species data was calculated for the five most common species, with all other species grouped into "other." Live tree (dbh ≥ 10 cm) and regeneration (dbh < 10 cm) species data includes the number of plots with the species present and the average and standard deviation for the stem density (stems/hectare) across all plots assigned to that structure class. Live tree data also includes the average and standard deviation for the basal area (m^2/ha) per plot across all plots assigned to that structure class.

		Live Trees					Regeneration		
Species	Forest Structure Class	Number of plots	Avg. stem density/plot	SD stem density/ plot	Avg. BA/plot	SD BA/plot	Number of plots	Avg. stem density/plot	SD stem density/plot
Subalpine fir (*Abies lasiocarpa*)	1	0	–	–	–	–	1	10	–
	2	1	20	–	0.01	–	1	50	–
	3	1	10	–	0.03	–	16	671	829
	4	6	37	26.6	0.03	0.02	12	447	644
	5	11	36	41.8	0.03	0.02	23	395	464
	6	4	83	87.7	0.03	0.01	11	318	357
Western larch (*Larix occidentalis*)	1	3	13	5.8	0.05	0.02	6	643	688
	2	15	22	19.0	0.32	0.23	10	297	302
	3	14	46	46.0	0.34	0.23	43	1,959	5,210
	4	15	63	47.3	0.17	0.08	18	3,372	8,662
	5	11	30	21.0	0.35	0.17	34	2,065	4,466
	6	9	63	65.4	0.47	0.40	8	4,246	7,815
Lodgepole pine (*Pinus contorta*)	1	2	225	148.5	0.04	0.02	10	7,076	9,787
	2	8	30	27.8	0.06	0.05	22	2,670	8,654
	3	9	41	35.5	0.03	0.02	103	8,381	20,401
	4	9	101	82.4	0.07	0.04	22	1,699	3,662
	5	5	18	13.0	0.07	0.06	26	2,247	3,746
	6	2	20	0	0.02	0.02	7	444	457
Engelmann spruce (*Picea engelmannii*)	1	0	–	–	–	–	4	539	607
	2	4	48	45.0	0.03	0.01	7	574	856
	3	1	20	–	0.07	–	35	2,646	4,680
	4	7	99	126.7	0.06	0.04	18	386	300
	5	10	51	53.8	0.04	0.03	26	2,341	6,747
	6	4	58	51.2	0.07	0.06	7	1,341	2,520
Douglas-fir (*Pseudotsuga menziesii*)	1	5	66	59.0	0.05	0.02	6	4,317	6,532
	2	26	80	77.4	0.08	0.06	22	823	1,707
	3	16	49	58.5	0.07	0.07	50	667	1,154
	4	24	135	105.9	0.09	0.05	41	1,197	1,730
	5	27	143	108.0	0.09	0.08	50	1,288	2,247
	6	11	125	120.8	0.12	0.04	14	861	1,002
Other species	1	0	–	–	–	–	0	–	–
	2	6	17	8.2	0.17	0.17	13	332	488
	3	4	18	9.6	0.21	0.37	38	802	1,028
	4	3	27	28.9	0.04	0.02	4	211	154
	5	4	15	10.0	0.21	0.21	4	229	208
	6	1	20	–	0.49	NA	3	215	252

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