Long-Term Effects of Fire Severity, Time Since Fire, and Topography on Douglas-Fir Canopy Complexity in the Western Cascades, Oregon, USA

by

Clayton Sodergren

A PROJECT

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Forestry in Forest Ecosystems and Society

Presented March 17th, 2023
Commencement June 2023

ABSTRACT OF THE PROJECT OF

Clayton Sodergren for the degree of Master of Forestry presented on March 17th, 2023. Title: Long-Term Effects of Fire Severity, Time Since Fire, and Topography on Douglas-Fir Canopy Complexity in the Western Cascades, Oregon, USA.

The patterns of forest structure are inextricably linked to ecosystem function. Forest canopy complexity, while nebulously defined as a concept, generally increases through time as forests develop and is associated with late successional and old growth Pacific Northwest forests. Fire and topography are thought to be drivers of canopy complexity, particularly in coastal Douglas-fir/western hemlock forests that experience non-stand-replacing fire. This study sought to understand how patterns of canopy complexity are associated with patterns of topography and the processes of fire and post-fire successional recovery. Building on previous research conducted near the H.J Andrews Experimental Forest and Long-Term Ecological Research site, I linked lidar data to field data to look for associations between canopy complexity, time since fire, fire severity, and potential relative radiation. My findings of no associations between these variables differed from much of the literature. Reasons for these results may include chosen metrics, stand dynamics, simplified models, and/or data constraints.

Corresponding e-mail address: clayton.sodergren@gmail.com

Introduction

Forest structural complexity

In Simon Levin's much-cited lecture "The Problem of Pattern and Scale in Ecology," he argued that "understanding patterns in terms of the processes that produce them is the essence of science" (Levin 1992). The patterns of structure in a forest ecosystem are inextricably linked to its function (Spies 1998, Franklin et al. 2002, Franklin and Van Pelt 2004, Ishii et al. 2004, Kane et al. 2010a). Structure affects and is affected by species composition, age distribution, and site productivity (Franklin et al. 1981). For instance, more structurally complex forests are generally more productive (Ishii et al. 2004). Forest structural complexity does not have a single agreed-upon definition (Spies 1998, McElhinny et al. 2005) and can vary according to forest type; this study will focus on structural complexity in Pacific Northwest (PNW) Douglas-fir forests. Typically, structural complexity focuses on forest trees (as opposed to including understory) and describes size and distribution of spatial, horizontal and vertical measures of trees, wood, and leaf area in a stand (Kane et al. 2010a). More generally, structural complexity is a measure of heterogeneity in the three-dimensional arrangement of biomass (Ehbrecht et al. 2021), and in some forests is associated with biodiversity (Lindenmayer et al. 2000). Definitions of structural complexity can include a high degree of variability in tree size; presence of standing dead trees and dead and down wood; vertically continuous canopy or multiple layers of foliage; and irregular horizontal distribution of structures, often apparent as canopy gaps and dense patches of saplings and poles (Franklin and Van Pelt 2004). Forest structure is dynamic through time, and is affected by the processes of succession and disturbance (Spies 1998). This study seeks to understand patterns of forest structure, how these patterns are affected by the processes of fire and post-fire successional recovery, and how those processes are modulated by patterns of topography.

In PNW coastal Douglas-fir forest ecosystems, forest complexity generally increases as forests move towards late-successional and old growth (LSOG) ages, but can also vary widely in LSOG forests (Spies 2004, Reilly and Spies 2015). Complexity also influences ecosystem function (Reilly and Spies 2015); for example, higher levels of forest structural complexity are correlated with increased habitat quality and rates of primary production (Gough et al. 2019), and lower average summer temperatures compared to younger, less structurally complex forests (Frey et al. 2016). More complex forests may also act as climate microrefugia (Frey et al. 2016). Structural complexity is one of the key features of LSOG forests of the Pacific Northwest, USA (PNW) (Franklin and Spies 1983, Franklin et al. 2002, Franklin and Van Pelt 2004). LSOG forests in the Pacific Northwest are characterized by large trees, large dead wood, and complex, multi-layered canopies (Spies 2004, Davis et al. 2015). These forests are a focus of research, monitoring, and conservation for PNW forest managers (Davis et al. 2015), have the highest rates of potential carbon capture of any forest type in the world (Franklin and Waring 1980), and take hundreds of years to develop complexity (Spies et al. 2018). These forests are on a continuum of LSOG traits—the Northwest Forest Plan uses an index of traits called old growth structure index (OGSI), which uses thresholds at 80 years of age to generally describe forests that start to mature and display stand structures associated with older forests, and at 200 years of age to generally describe forests that are deemed to have old growth features (Davis et al. 2015).

Structural complexity in LSOG coastal variety Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) forests contributes to their ability to provide habitat for a diverse group of organisms, including the northern spotted owl (Mouer et al. 2005), endangered marbled murrelet (Lorenz et al. 2021), and other vertebrates (Franklin et al. 2002). Less than 5% of LSOG Douglas-fir/western hemlock forests remain from what existed pre-settlement (Franklin et al. 1981). Additionally, the Northwest Forest Plan defines "'classic' Douglas-fir old growth" as having multiple canopy layers (Mouer et al. 2005), and notes that fire is one of the biggest factors leading to losses in this forest category (Spies et al. 2018). While fire can lead to losses in LSOG forest coverage, it is also an intrinsic part of succession and development in PNW Douglas-fir forests.

Role of fire in Douglas-fir forests

Fire effects on forest ecosystems are diverse and depend on the forest's fire regime as well as the characteristics of individual fires. A fire regime describes an ecosystem's long-term patterns in fire seasonality, return intervals, size, severity, intensity, complexity, and type (Sugihara et al. 2006). Different definitions exist for fire severity; this study will use a definition based on percent of mature trees killed: I define high severity fires as those that kill >70% of mature trees. In forests with low-severity, high-frequency fire regimes, fires usually kill understory shrubs, seedlings and saplings, but not mature trees, reducing competition for mature trees and leading to low-density forests (Allen et al. 2002, Turner et al. 2003, Sugihara et al. 2006). In forests with high-severity, low-frequency fire regimes, fires usually kill at least 70% of mature trees (according to the definition of high severity used in this study) and clear space for new seedlings and early seral species (Turner et al. 2003, Perry et al. 2011). These high-severity fires are often stand-replacing (SR), and this study refers to them as such. Mixed-severity fire regimes are more complex—these can be regimes with moderate severity fires, or regimes that include a range of fire effects between low-severity and high-severity, in which the typical fire creates a complex patchwork of fire-caused mortality (Agee 2005).

Coastal Douglas-fir (hereafter referred to as Douglas-fir) forests exist in a variety of ecosystems from California to British Columbia. This study will focus on coastal Douglas-fir in the western Cascades of Oregon. Historically, research on these forests focused on high severity fire regimes and succession that could only occur after high severity, stand-replacing (SR) fire, which certainly applies to some Douglas-fir forests (Tepley 2010, Franklin et al. 2002). Fire's role in these forests was viewed as a creator of open canopy patches, generating what was considered as necessary open conditions for shade-intolerant Douglas-fir seedlings to germinate. Though Douglas-fir is relatively shade-intolerant and germinates more readily in canopy gaps, germination also occurs in shade, though at much lower densities (Gray and Spies 1996). These Douglas-fir forests also include shade-tolerant trees, namely western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Non-stand replacing (NSR) fires in these forests typically kill many of the fire-susceptible shade-tolerant species, while the adult Douglas-fir trees survive (Tepley et al. 2013). Though the traditional SR fire and subsequent successional model applies to many PNW Douglas-fir forests, NSR fires are also part of these forests' complex mixed-severity fire regimes.

Recent decades have seen an increase in research into Douglas-fir mixed-severity fires and fire regimes (e.g., Perry et al. 2011, Tepley et al. 2013, Hessberg et al. 2016). Complex structures can result from non-stand replacing disturbance, such as high variability in tree diameter, multiple age cohorts, and small canopy gaps that shade-tolerant species colonize (Weisberg 2004). Fire may also lead to increased canopy complexity in surviving Douglas-fir trees by triggering creation of additional branches in the canopy (Johnston et al. 2018). Mixed-severity fire regimes are also the most variable category of fire regimes, and can include low, moderate and high-severity fires (Agee 2005). Additionally, fire exclusion in moist Pacific Northwest forests has altered the patchwork distribution of seral stages that was historically created by fires (Spies et al. 2018).

In relatively productive Douglas-fir environments with stand replacing (SR) fire, there's a wide variety of successional pathways towards higher structural complexity. In environments with non-stand replacing (NSR) fire as well, there's an even wider variety (Reilly and Spies 2015). Using Tepley and colleagues' (2013) study in this ecosystem as an example, stands that experienced SR fire and no subsequent NSR fires tended to have shade-tolerant species regenerating continuously. This led to an initial shade-intolerant cohort and numerous cohorts of shade-tolerant trees, and in the absence of fire, fine-scale non-fire disturbances and gap dynamics drove further succession (Tepley et. al 2013). In contrast, stands that experienced NSR fire may have experienced either episodic or chronic NSR fires, both of which led to multiple age cohorts in both shade-intolerant and -tolerant species due to NSR fires creating canopy gaps in which shade-intolerant species could regenerate (Tepley et al. 2013). These results highlight the large number of different pathways towards complexity in these Douglas-fir forests.

Structural Complexity, Topography and Scale

Structural complexity after a disturbance can range from simple to highly complex, but stands are generally considered less structurally diverse during early and mid-development stages and higher during later development stages (Reilly and Spies 2015, Spies and Franklin 1988, though see Donato et al. 2012). Canopy structural complexity metrics derived from field and lidar measurements, such as crown height, rumple index, and proportion of canopy gaps, generally increase with stand age (Ogunjemiyo et al. 2005).

Topography affects many aspects of forests, such as composition, productivity, germination, and fire risk (Dyer 2009). Complexity is also influenced by topography, which has more of an influence in mixed severity fire regimes than in SR fire regimes (Tepley 2010). I use topography as a proxy for water availability in this study. I chose water availability under the assumption that stands with greater water availability have higher site productivity, and are able to mature and build structural complexity more quickly compared to drier stands. Additionally, drier forests are more prone to fires in general.

While some conifer forests can have high structural complexity in early regrowth after stand-replacing fire (Harvey and Holzman 2014), complexity generally is relatively low after SR fires and increases as recovery from fire proceeds (Reilly and Spies 2015). Evidence of multiple successional pathways has been observed in some coniferous forests post-fire (Spies 1998, Poage et al. 2009, Tepley et al. 2013), including diverging successional pathways for which topography (i.e., aspect and slope steepness) was the strongest abiotic association (Harvey and Holzman 2014). Poage et al. (2009) found a weak association between the distributions of tree ages and landscape-level topographic variables in western Oregon Douglas-fir forests, and a strong association between distributions of tree ages and landscape-level fire variables. However, previously cited studies (e.g., Poage et al. 2009, Harvey and Holzman 2014) did not examine a finer scale of topographic variables; studies examining stand- or smaller scale topography (1s to 10s of ha) and Douglas-fir forest structure are rarer than studies involving larger-scale topography (100s-1000s of ha) (but see Tepley 2010, which examined the association between topography and age structure on a <1 ha scale).

The finer scale (30 m resolution) of the topographic data I use in this study is useful for numerous reasons. It allows for effective use of the fine resolution of remotely sensed data. Topographic heterogeneity is associated with forest hydrological conditions at fine scales (Muscarella et al. 2019), which in turn is correlated with forest canopy height heterogeneity. Forest fires can be spatially variable, with patches of different severity (Agee et al. 2005, Sugihara et al. 2006). A finer scale of topographic data allows for more directly relating topography to fire effects on forest canopy. Finally, topography influences fire behavior (Sugihara et al. 2006). For example, fires generally spread faster on steeper slopes, and aspect affects soil moisture and thus vegetation flammability (Agee 1993). Certain areas of fire-prone forests can be less likely to burn at high severity than their surroundings, known as fire refugia (Meddens et al. 2018); fire refugia can be associated with certain topographies (Krawchuk et al. 2016). Therefore, interactive effects of topography and fire on canopy complexity are possible.

It's important to note that, although neither have an agreed-upon definition and they are often correlated (Kane et al. 2010b), canopy complexity and structural complexity are not necessarily the same thing. Spies (1998) lists four essential components of forest structure: distribution of tree ages/sizes; vertical distribution of foliage; distribution of horizontal canopy; and dead wood. Definitions of forest structure also sometimes include species composition (McElhinny et al. 2005). Canopy complexity generally focuses on canopy height, canopy density, and variability in horizontal and vertical distribution of trees (Kane et al. 2010a, Kane et al. 2010b) but can also include leaf area index (Parker and Russ 2004). Consider a hypothetical stand with a diverse species composition and a wide distribution of diameters and ages, but a relatively uniform height distribution. This stand would have a high degree of structural complexity but not canopy complexity. This study will focus on canopy complexity.

Knowledge Gap

Questions remain regarding differences between mixed-severity and high-severity fire regimes as ecological processes contributing to LSOG Douglas-fir forests (Spies et al. 2018). Studying the effects of historical fires, relatively fine-scale topography, and their potential interactions on Douglas-fir canopy complexity may help clarify those differences. The 2018 Northwest Forest Plan (NWFP) Science Synthesis notes both a lack of remote sensing methods to detect non-high-severity disturbance in LSOG forests, and that "future monitoring work will pursue approaches that tie the plot-based and mapped data sets together more closely" (Spies et al. 2018). Factors influencing spatial variability in forest conditions are poorly understood in mixed-severity fire regime Douglas-fir/western hemlock forests (Tepley 2010). Using lidar-based measurements of the forest canopy enables analysis of canopy structure, including tree and stand height, horizontal density, and height variability on a larger spatial scale than can be achieved by field methodology in the same amount of time (Beland et al. 2019). Lidar data has been shown to be effective in directly assessing forest structural complexity, particularly when assessing changes in forest structure as they relate to succession in Pacific Northwest forests (Kane et al. 2010b). Additionally, Spies (1998) argues that the position of the observer affects the ecological observation made; examining this study site from above the canopy may reveal different insights than *in situ* observations. Research examining long-term dynamics in forest structural complexity in LSOG Douglas-fir forests and how they are impacted by fire and topography can help forest managers understand the importance of fire for succession, conservation, and future adaptation, as well as how to respond to current or future fires.

Research Question and Hypotheses

In this study, I examined canopy complexity in two Douglas-fir/western hemlock forests in the western Cascades mountains of Oregon, and how it is related to topography, time since last fire, and severity of the last fire. I completed this analysis to test in order to test three hypotheses arising from a single conceptual model of post-fire forest structural development (Figure 1). First, I hypothesized that canopy complexity immediately post-fire would be higher in sites that experienced NSR fire than sites that experienced SR fire. I reasoned that because NSR fires leave more mature trees alive than SR fires, the remnant trees in the post-fire canopy would contribute to higher heterogeneity than a canopy comprised of mostly or virtually all standing dead trees.

Secondly, I hypothesized that these differences in canopy complexity between SR and NSR post-fire stands diminish over time as the burned areas are recolonized and succession proceeds, and that over time, this difference in canopy complexity would diminish until eventually both pathways converge on an asymptote of maximum canopy complexity, and there was no longer a difference in canopy complexity between SR and NSR sites. It’s important to note that this study only examines recovery after the most recent fire.

Finally, I hypothesized that stands in relatively drier topographic conditions would take longer to develop canopy complexity because they have less access to water than stands in relatively wetter topographic conditions, and that this slower development would prolong the time taken for both NSR and SR stands to converge upon maximum canopy complexity. This assumes that growth in stands is at least somewhat constrained by water availability. This also assumes that topography can be used as a proxy for water availability.

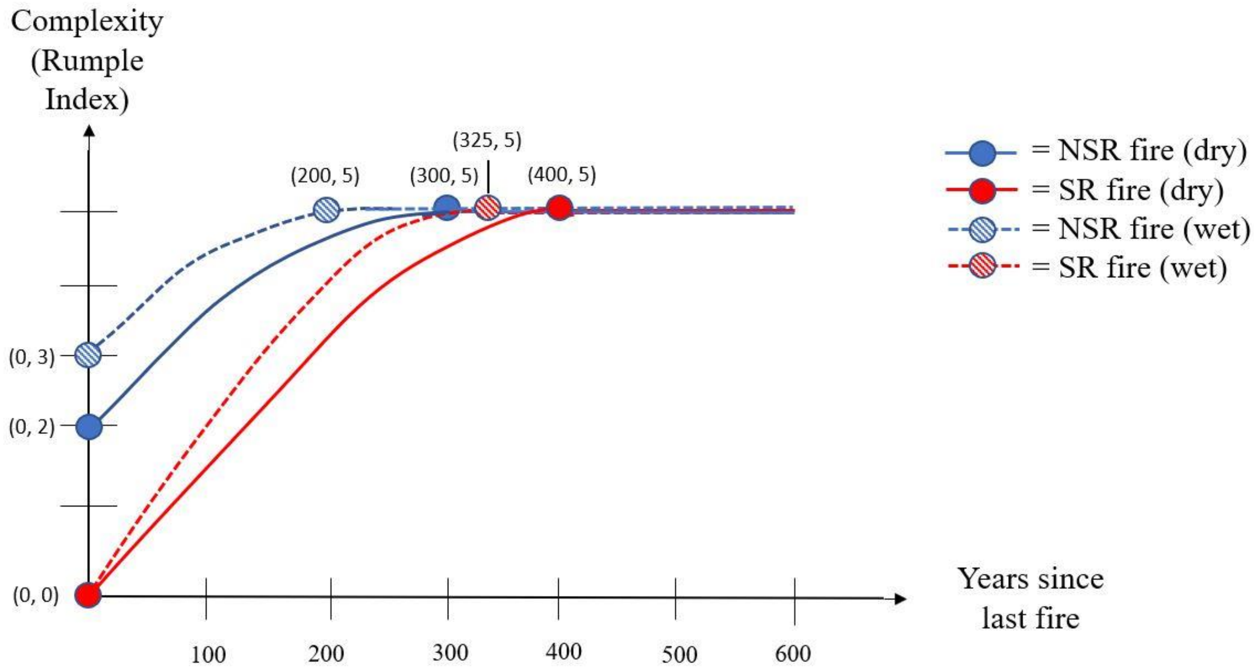


Figure 1. Conceptual diagram of hypothesized relationships between years since last fire, relative moisture (PRR) and rumple index (RI) in moist Douglas-fir/western hemlock forests in the central western Cascades in Oregon. In this study, I use topography as a proxy measure of water availability; PRR stands in for relative moisture. Hypothetical values, shown as points, are meant to show conjectured trends, not to predict actual values. Numbers are included in parentheses next to points for clarity. Numbers on RI axis are used only conceptually, meant to be compared relative to one another to show hypothesized trends.

Methods

The sites in this study are in the central western Cascades in Oregon, USA, and were originally established by Alan Tepley (Tepley 2010). These sites were chosen to represent Douglas-fir/western hemlock forests across a variety of topographies in the central western Cascades. This study region was chosen because these Douglas-fir/western hemlock forests have a mixed-severity fire regime, meaning they experience both stand replacing (SR) and non-stand replacing (NSR) fires (Tepley et al. 2013). These sites are located in two watersheds: the Blue River watershed and the Fall Creek watershed (Figure 2). The Blue River watershed contains the H.J. Andrews Experimental Forest, part of the NSF Long-Term Ecological Research network. The Blue River study area includes the 240 km^2 Blue River watershed as well as an additional 33 km^2 to the north of the watershed. The Fall Creek study area consists of the easternmost 330 km^2 in the Fall Creek watershed.

Field data

In this study, I used the same slope facets, slope positions, transects, and plots as Tepley et al. (2010; 2013). The following describes that study design and field collection completed by Dr.

Alan Tepley. 124 stands were sampled in the original study—71 in the Blue River study area and 53 in the Fall Creek study area (Figure 2). A slope facet is defined as an area of common aspect extending from ridgetop to valley bottom. According to Tepley's sampling design (2010; 2013), facets were selected from within each of the two study areas (Blue River and Fall Creek) using stratified random sampling. A 5x5 km grid was superimposed over each study area and one slope facet was randomly selected in each of these 25 km^2 grid cells. Slope facets were randomly selected by generating a random number corresponding with a single 1 km^2 square within the 25 km^2 grid cell, then selecting the slope facet that made up the majority of that 1 km^2 square. Within each selected slope facet, the total elevational range was divided into three equal segments—upper, lower, and middle—called slope positions. In each slope position, a randomly selected point within the forested area that was at least 100 m away from roads, streams or previously harvested areas was used as the midpoint of a 120 m transect that ran parallel to the slope contours. Each 120 m transect was divided into five 0.02-ha plots spaced evenly at 30 m intervals along the transect. In this nested structure, the different levels of spatial units, arranged from largest to smallest, are as follows: study area > slope facet > slope position > transect > plot. To take advantage of the availability of lidar data, I increased the area of the Tepley field transects by extending a 30-m buffer on either side of each transect, so that each transect had an area of approximately 7200 m^2. These 7200 m^2 transects are the unit of analysis for this study.

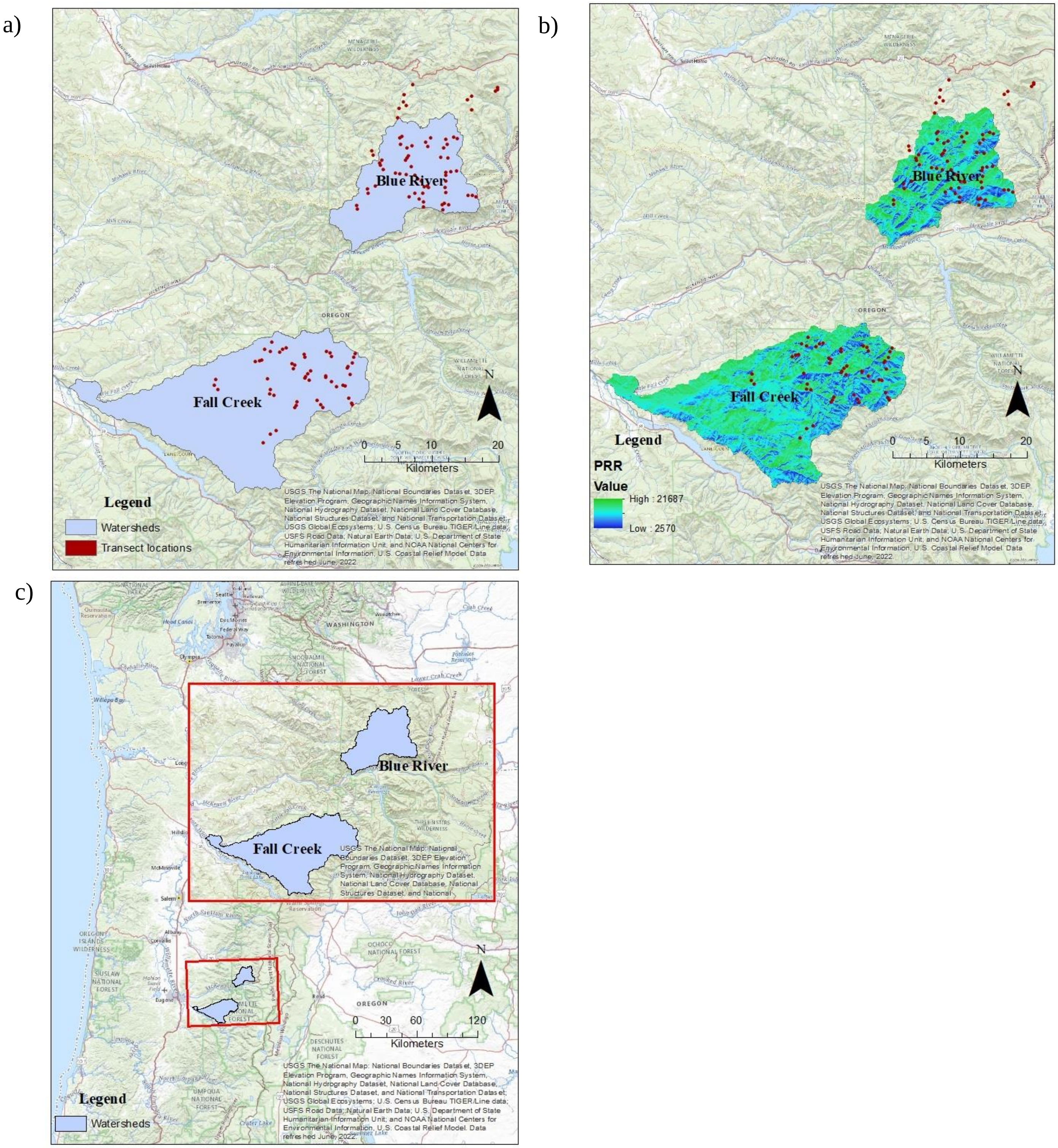
The field-measured stand and age structure data were collected in each plot. For each living or standing dead tree >15 cm, diameter at breast height (DBH) and evidence of fire (i.e. charred bark or catfaces) were recorded. To measure tree ages within each transect, Tepley et al. (2013) split each plot into four quadrats and took an increment core of the largest-diameter living tree of each species in each quadrat. A total of 3277 trees over all transects were cored using this method, with an average of 27 trees sampled per transect (this was 76% of live trees in the transects). Sampling the largest tree of each species in each quadrat was done under the assumption that that was the largest tree, and including each species was done to also include smaller trees in the dataset. Tree cores were sanded and inspected under a microscope, then read to estimate establishment date. 85% of the cores were cross-dated, and establishment date was estimated for 89% of cores (3,046 trees). These data were used to create the age-structure classes described in the next section.

Defining stand-replacing and non-stand-replacing fire

In order to estimate the severity (stand replacing vs. non-stand replacing) and time since historical fires on each transect, Tepley et al. (2013) used the age structure of fire tolerant and intolerant tree species, presence of multiple age cohorts, and presence of fire scars and catfaces on living trees in any given transect to infer that the most recent fire was a NSR fire. The logic used was that if a given stand experienced NSR fire, some trees would die and others would survive. Shade-tolerant trees can be killed by low- to moderate-intensity fires such as surface fires, due to their thin bark, low crown heights and shallow roots (Hood et al. 2008). The shade intolerant trees in this ecosystem, Douglas-fir, are less likely to die in a surface fire once the trees become large. So, after an NSR fire, the oldest cohort of shade tolerant trees is younger than the oldest cohort of shade intolerant trees, and the distribution of establishment dates of shade tolerant trees gets narrower as older shade tolerant trees are killed by fire. If the oldest cohort of shade tolerant trees is noticeably younger than the oldest cohort of shade intolerant trees, this is not by itself necessarily indicative of a NSR fire (because of other potential factors affecting mortality, like insects or disease that target western hemlock or western redcedar), but is one piece of evidence used to detect NSR fire.

Additionally, burn scars and catfaces on surviving trees would indicate that there had been a fire there that did not kill every tree. Conversely, if the last fire a given stand had experienced was a SR fire, then the resulting oldest cohort would be made up of trees that germinated post-fire and thus establishment dates of both the shade intolerant cohort and the oldest shade tolerant cohorts should be similar. The SR label was assigned to a transect when the tree mortality in the transect was estimated to be greater than or equal to 70%, while transects were identified as NSR when mortality was less than 70% (Tepley et al. 2013). In addition to the mortality threshold, each transect was designated as SR or NSR based on the combination of the multiple indicative factors listed above.

To measure age structure, Tepley et al. (2013) used four variables for both shade tolerant and intolerant species to describe the distribution of establishment dates for shade tolerant and intolerant species separately. Some of the variables for shade tolerant and intolerant species differed because of the higher likelihood of shade intolerant trees' mortality in the event of fire; to reduce the influence of non-fire factors on analysis of age structure at the chosen scale; and to account for the potential differences between shade tolerant and intolerant age structures resulting from differences in post-fire regeneration patterns. Specifically, in this study environment, shade intolerant species like Douglas-fir have higher resistance to fire mortality but tend to regenerate between the immediate post-disturbance phase and the canopy closure phase. In contrast, shade tolerant species in the study environment tend to regenerate continuously, but are more prone to fire mortality. Variables were chosen to identify trends in forest age structure development post-fire regardless of the years (and thus year-based trends) in which each stand established, in order to compare stands that burned in different fires. Because of two historical periods of relatively high fire activity from the late 1400s to ~1650 and ~1800 to ~1925, Tepley et al. used the year 1780 as the cutoff between the two periods to help elucidate the background levels of fire when a tree germinated (Weisberg and Swanson 2003, Tepley et al. 2013). The 4 variables used in a transect to identify age structure of shade-intolerant species were 1) proportion of trees that germinated before 1780, 2) total age range in a transect, 3) age range of trees germinated before 1780, and 4) proportion of trees with char marks on bark. The 4 variables used for shade-tolerant species were 1) proportion of trees that germinated before 1780, 2) total age range of the transect, 3) average age of sampled oldest living trees, and 4) standard deviation of sampled oldest living tree ages (Tepley et al. 2013). Tepley et al. (2013) used these metrics to assign each transect as either SR or NSR, which I used as an explanatory variable in my analysis.



<u>Figure 2.</u> a) The two watersheds in the study, Blue River and Fall Creek, and locations of the transects in the study area. b) Potential relative radiation values across the watersheds used in the study. c) Inset map showing the two watersheds' location within Oregon and the greater Pacific Northwest.

Lidar data

As Tepley et al. 2013 used only field metrics, I used lidar data to further investigate the forest canopy structure of the same field sites. Often, forest canopy structure that's been measured with lidar is described using three categories of lidar metrics: height, variability of height, and density metrics of vegetation structures in the canopy (Lefsky et al. 2005, Kane et al. 2010a, Kane et al. 2010b). My study used vertical structural complexity, which is related to variability in height. I chose a single metric to represent canopy complexity as the response variable: lidar-measured rumple index (RI), which is a 3D measure of canopy surface heterogeneity (Kane et al. 2010a). Kane et al. (2010a) found that most field-measured forest canopy structure variables in western Cascades coniferous forests were correlated with similar lidar-measured metrics. Lidar-measured RI specifically correlates well with standard deviation of canopy height and mean DBH (Kane et al. 2008, Kane et al. 2010a). Rumple index is defined as the ratio of canopy surface area to ground surface area for a given extent (Kane et al. 2010a); in this study, the extent used was approximately 7200 m^2. Because rumple index measures both horizontal and vertical heterogeneity in the canopy surface, it is sensitive to both forest canopy gaps and variation in tree heights. Rumple index can also be thought of as crown roughness, and generally increases as the age of the stand increases (Ogunjemiyo et al. 2005). I chose rumple index as my response variable due to its correlation with a number of other forest canopy measurements and forest age, and ability to describe 3D variability.

The scale of the 7200 m^2 (0.72 ha) transect area allows assessment of canopy complexity over a larger area than the transects of Tepley et al.'s original 2013 study. However, if a hypothetical mixed-severity fire had a complex patchwork of fire severities, which sometimes occurs in this fire regime, then the resolution of a transect at this scale may be too coarse to capture that. The rumple index was calculated using the R package "lidR" (Roussel et al. 2020), which uses Jenness' algorithm (2004). This algorithm calculates canopy surface area by calculating the vertical and horizontal distances between the cell in question's centerpoint and the centerpoint of the 8 surrounding cells, then calculating the canopy surface area of the 8 triangles created by connecting the centerpoint of the central cell to each surrounding cell's centerpoint (Jenness 2004). Since these centerpoints of the 8 surrounding cells extend beyond the area of the cell in question, the lengths of the created triangles are divided by 2 to only cover the area within the cell. This algorithm does this process for cells in the canopy surface model and the digital elevation model, then divides the two to get the ratio, deemed rumple index. In this study, rumple index was calculated over each transect as a whole by summing the total surface area of the canopy in the transect, then dividing by the sum of the total surface area of the ground under that canopy. When surface area was calculated for the cells at the edge of the polygons, it used cells outside the polygon as needed to calculate the horizontal and vertical distances required. Each transect had one centerpoint, one summation of surface area, and one division to obtain the rumple index ratio. In ecological terms, if rumple were calculated at a 5x5 m pixel, for example, the ecological unit would be about the scale of an individual tree and its neighbors. At the 0.72 ha scale of the transects, the ecological unit being described can be thought of as the canopy roughness on a stand scale—as noted before, this scale may not be able to assess a potentially fine-scale mosaic of burn severity.

I assumed that the differences in tree size between 2010, when the field data were collected, and 2008-2016, when the lidar data were collected (Table 1), would have a negligible effect on measurements of rumple index. The ages of the oldest trees in each transect range from 100 to 850 years, and I generally used the lidar acquisition closest to 2010, so the maximum gap between field measurements and lidar measurements is 6 years. All trees were at least 100 years old when measured. Height growth slows as coastal Douglas-fir trees age and get larger (Bond et al. 2006); coastal Douglas-fir trees can grow more than 1.5 m in height per year under ideal conditions, but that growth slows by an average of 2 cm per year of tree age (Bond et al. 2006). By 100 years of age, the trees in these transects have slowed their height growth per year considerably. Additionally, Tepley et al. (2013) did not measure tree heights. Therefore, I felt justified in assuming the effects of the difference in growth between field and lidar measurements on rumple index could be ignored.

Table 1. Details of the lidar acquisitions used in this study. Acquisition refers to the general area covered. Sensor refers to the name of the instrument used. Field of view refers to the angle at which the sensor emits light. First return point density refers to the number of points in a given area that are returned after bouncing off the first object the light hits. Vertical accuracy is the smallest difference in height that the lidar can detect.

Acquisition	Year	Sensor	Field of View	First Return Point Density (points/m^2)	Vertical Accuracy (cm)
H. J. Andrews	2008	Leica ALS50 Phase II	28°	9.1	2
Blue River	2011	Leica ALS60 Phase II	28°	10.4	5
Lane County	2014	Leica ALS80	30°	18.1	3
Sweethome & Timber Ridge	2016	Leica ALS80	30°	12.5	2

Topographic data

I used a topographic variable as a proxy for moisture limitation. Potential relative radiation (PRR) was used as this proxy: it measures incoming solar radiation, which also indirectly measures water availability based on evapotranspiration and slope steepness (Pierce et al. 2005). In this study system, water is an important limiting factor for growth (Chen et al. 2010, Littell et al. 2008). Lidar-based studies of forest structure at the H.J. Andrews Experimental Forest (HJA) found that temperature, precipitation, and elevation were highly correlated with each other as well as with live forest carbon stocks (measured as aboveground live carbon) (Seidl et al. 2012, Zald et al. 2016). Another study done partly in the HJA suggests that, in this environment and other topographically complex environments in the western USA, PRR is better correlated with vegetation patterns than other measures of radiation (Pierce et al. 2005). Seidl et al. (2012) found that solar radiation was also an important driver of growth (measured as aboveground live carbon) at the HJA. PRR is calculated at the scale of the transect by averaging the PRR value of each 30x30 m cell within the transect, but does not account for topographic position relative to surrounding forest.

Explanatory and response variables

The explanatory variables used in this study were potential relative radiation (PRR, a dimensionless measure of averaged relative radiation, used as a proxy for moisture limitation), time since most recent fire (TSF, measured in years), and fire severity (either SR or NSR, NSR defined as mature tree mortality less than 70% and SR as mature tree mortality greater than or equal to 70%). Fire severity was a categorical variable, with transects being either SR or NSR depending on the severity of the most recent fire in that transect. PRR was initially measured at a 30 m resolution, but was averaged across each transect (approximately 7200 m^2). TSF and fire severity did not vary at the 7200 m^2 scale of each transect, so only one value for each was needed per transect. Rumple index was calculated at the scale of the transect.

Modeling

I used evidence from multiple linear regression to test my hypotheses. Because I hypothesized that complexity would reach an asymptote within the study's temporal scale, violating the linear model assumption that every explanatory variable has a linear relationship with the response variable, I used the logarithm of each transect's rumple index as the response variable. This converts the hypothesized nonlinear relationship into a relationship that can be described with a linear model. I checked the regression model assumptions of constant variance, and symmetric distribution of residuals, visually by plotting estimated residuals versus fitted values and normal quantile-quantile plots of estimated residuals for each model.

Relationships among explanatory variables were initially visualized using pairwise scatterplots to ensure that the dataset had sufficient range across explanatory variables to support the inclusion of interaction terms in some regression models (Figure 3). Interactions between each explanatory variable were examined to assess whether changes in one explanatory variable were modulated by changes in another variable—for example, whether the relationship between PRR and RI depended on time since fire.

I fit a full model (Model 1) including all three variables (PRR, fire severity, time since fire) as well as all interactions between variables, including a three-way interaction between all of them (see Equation 1). I fit 12 additional models that contained subsets of these 7 terms. Differing combinations of variables and interactions were used to examine each hypothesis. Table 1 lists the explanatory variables included in each model. I used AIC to compare the support for each model relative to the other models (Akaike 1973). All analysis was done using R (R Core Team 2019), and plots were made using the "ggplot2" package (Wickham 2009) or with core R functions.

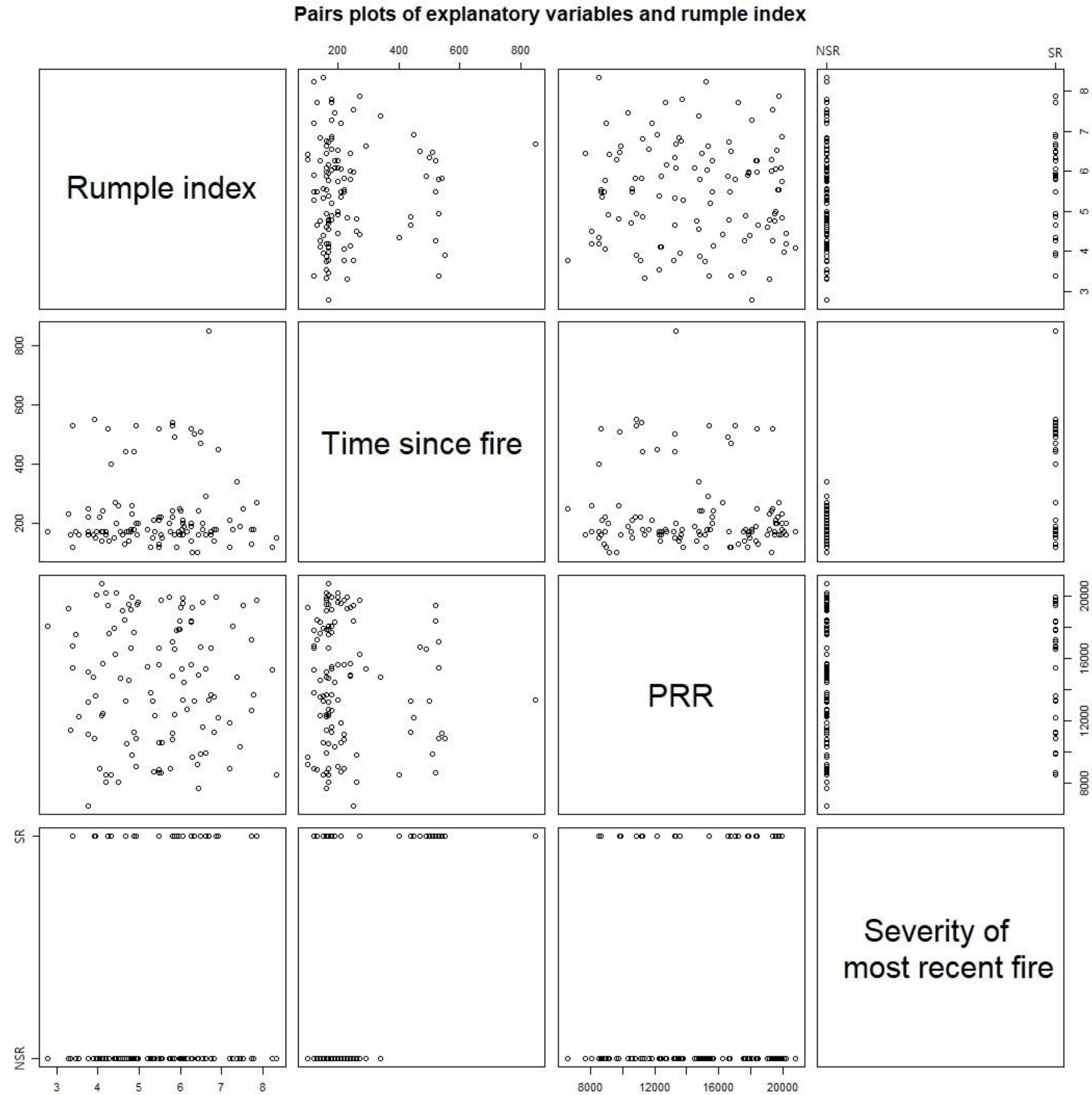


Figure 3. Pairs plot of response variable, rumple index, and all explanatory variables, showing range across all variables. Rumple index is the ratio of canopy surface area to ground surface area per transect. Time since fire is measured in years. PRR is a dimensionless metric representing incoming solar radiation and is averaged across each transect. Severity of the most recent fire in each transect is categorical and is either non-stand replacing fire (NSR, <70% mature tree mortality) or stand replacing fire (SR, ≥70% mature tree mortality).

Equation 1. Mathematical description of Model 1, the full model, including all variables and all interactions of variables. Because SR and NSR are represented by indicator variables, each transect is assigned to either group SR or group NSR depending on the severity of its most recent fire.

$Y_t = \beta_0 + \beta_1 * I.SR_t + \beta_2 * PRR + \beta_3 * TSF + \beta_4 * I.SR_t * PRR + \beta_5 * I.SR_t * TSF + \beta_6 * TSF * PRR + \beta_7 * TSF * PRR * I.SR_t + \varepsilon_t$

where:

Y_t is the logarithm of the average rumple index (RI) of the t^{th} transect; t = 1, 2, ..., 124

β_0 is the mean RI for a transect immediately after a fire (TSF = 0), with a PRR of 0

β_1 is the incremental change in the mean RI of group SR compared to group NSR

I.SR is 1 when a transect is in group SR and 0 when a transect is in group NSR,

β_2 is the incremental change in mean RI for a 1-unit increase in PRR,

β_3 is the incremental change in mean RI for a 1-year increase in time since fire compared to a transect that has just burned,

β_4 is the incremental change in the PRR slope (β_2) for the SR group compared to the NSR group,

β_5 is the is the incremental change in the TSF slope (β_3) for the SR group compared to the NSR group,

β_6 is the interactive effect of TSF and PRR,

β_7 is the is the incremental change in the TSF*PRR slope (β_6) for the SR group compared to the NSR group

ε_t is the random error associated with the t^{th} transect, where $\varepsilon_t \sim N(0, \sigma^2)$ and ε_t and $\varepsilon_{t'}$ are independent.

Modeling strategy and hypotheses

AIC analysis was used to determine which combination of explanatory variables was best supported by the data. AIC penalizes models as the number of parameters increases, and a lower AIC score means the data support that model better than other models considered (Akaike 1973). Delta AIC, or ΔAIC, is the difference between a model's AIC score and the minimum, or best, AIC score of the models it's being compared to. If the full model was found to be best supported, then it may suggest that time since fire, PRR, an interaction between fire severity and PRR, an interaction between fire severity and time since fire, an interaction between time since fire and PRR, and a three-way interaction between PRR, time since fire, and fire severity were associated with a transect's RI. The interactions being included in the best supported model could suggest that the relationship of PRR and time since fire on RI each are modulated also by the values of the other two explanatory variables (the second explanatory variable being fire severity, which as a categorical variable cannot have an association with RI).

If a model with the interaction between PRR and time since fire was selected as best supported, it could suggest that drier transects reached complexity at a different rate than wetter transects. If the best supported model included the interaction between PRR and fire severity, this could suggest that topographically mediated differences in fire severity may be associated with differing effects of both variables on RI. If the interaction between fire severity and time since fire was included in the best supported model, it could suggest that transects that burned at different severities were associated with different amounts of time to reach a given level of complexity.

If PRR was included in the model with the best support, it could suggest that moisture limitation is correlated with a transect's RI. If fire severity was included in the model with the best support, it could suggest that NSR and SR transects start at different levels of complexity, and if in conjunction with other evidence, may provide additional evidence that NSR and SR transects remain at different complexities through time. Whether time since fire is included in the model with the best support or not, I can use a plot of RI and TSF to look for evidence of a nonlinear association.

The estimated coefficients of each explanatory variable in whichever model is most supported can help determine the relative correlation and sign of correlation (positive or negative) with log RI after accounting for all the other variables in the model.

I also used a Kruskal-Wallis test of medians to assess whether there was a difference in log RI between age-structure types, in order to see if these RI data aligned with Tepley et al.'s (2013) findings. Tepley et al. (2013) used the age structure variables and evidence of past fires to classify each transect into one of six age-structure types. These data were then used to deduce a general fire regime of each age-structure type: Types 1 and 5 were classified as infrequent SR fire regimes; types 2, 3, and 4 as episodic NSR fire, and type 6 as chronic NSR fire. I tested medians in addition to means because I used logarithm of rumple index in my analysis, and, when backtransformed from a logarithmic scale to the original linear scale, the mean of the logarithm of rumple index is the median of rumple index.

Scope of Inference

The facets were randomly selected from all facets in the Blue River and Fall Creek study areas. Transects used in this study were selected randomly from the forested areas 100 m from roads, previously harvested stands, and streams within the facets in the Fall Creek and Blue River watersheds, and in a 33 km^2 area north of the Blue River watershed. Therefore, the findings of this study can be applied to the forested areas meeting the aforementioned criteria within the Fall Creek and Blue River watersheds, and the 33 km^2 area north of the Blue River watershed, during this study period. Further sampling and analysis would be required to determine whether the results apply to forests outside the studied areas or study period.

Results

I checked the linear model assumptions for each of the 13 models, and found them sound. The logarithm of rumple index and explanatory variables were expected to have a linear relationship, and a scatterplot did not show evidence to disprove this. Transects were independent and randomly selected for sampling. Estimated residuals were found to have constant variance by looking at residuals vs. fitted values. Explanatory variables were not strongly correlated with one another. A quantile-quantile plot did not show evidence that residuals deviated from a normal distribution.

Table 2. AIC scores, adjusted R^2 values, and terms in each model. An X means that this column's variable was included in this row's model. AIC values compare each model's relative level of support with each other included model, with lower scores being a higher level of support. Adjusted R^2 values measure how much of the variance in rumple index is explained by each model, penalizing models with relatively more terms. Explanations of each term's abbreviations can be found in Equation 1.

Model ID	AIC Value	ΔAIC From Best Supported Model	Adjusted R^2 Value	β0	β1*I.SRt	β2*PRR	β3*TSF	β4*I.SRt*PRR	β5* I.SRt * TSF	β6*TSF* PRR	β7*TSF* PRR*I.SRt
1	0.917	4.930	0.015	X	X	X	X	X	X	X	X
2	4.810	8.823	-0.027	X	X	X	X	X	X	X	
3	2.945	6.958	-0.019	X	X	X	X	X	X		
4	0.946	4.959	-0.009	X	X	X	X	X			
5	2.849	6.862	-0.026	X	X	X	X		X		
6	0.872	4.885	-0.017	X	X	X	X				
7	-0.181	3.832	-0.016	X		X	X				
8	-0.943	3.070	-0.010	X	X	X					
9	-1.002	3.010	-0.009	X	X		X				
10	-2.857	1.156	-0.001	X	X						
11	-2.086	1.927	-0.008	X		X					
12	-2.123	1.890	-0.008	X			X				
13	-4.013	0	N/A	X							

The logarithm of RI was not correlated with any of the explanatory variables by themselves, or with any interaction of explanatory variables. Each of the 12 estimated models had very low adjusted R^2 values, ranging from -0.027 (Model 2) to 0.015 (Model 1). Model 13, which includes no explanatory variables, had the best AIC score (-4.013), indicating that the best supported model for RI is the overall average. The AIC scores, difference from the best AIC scores (ΔAIC), and adjusted R^2 values can be found in Table 2.

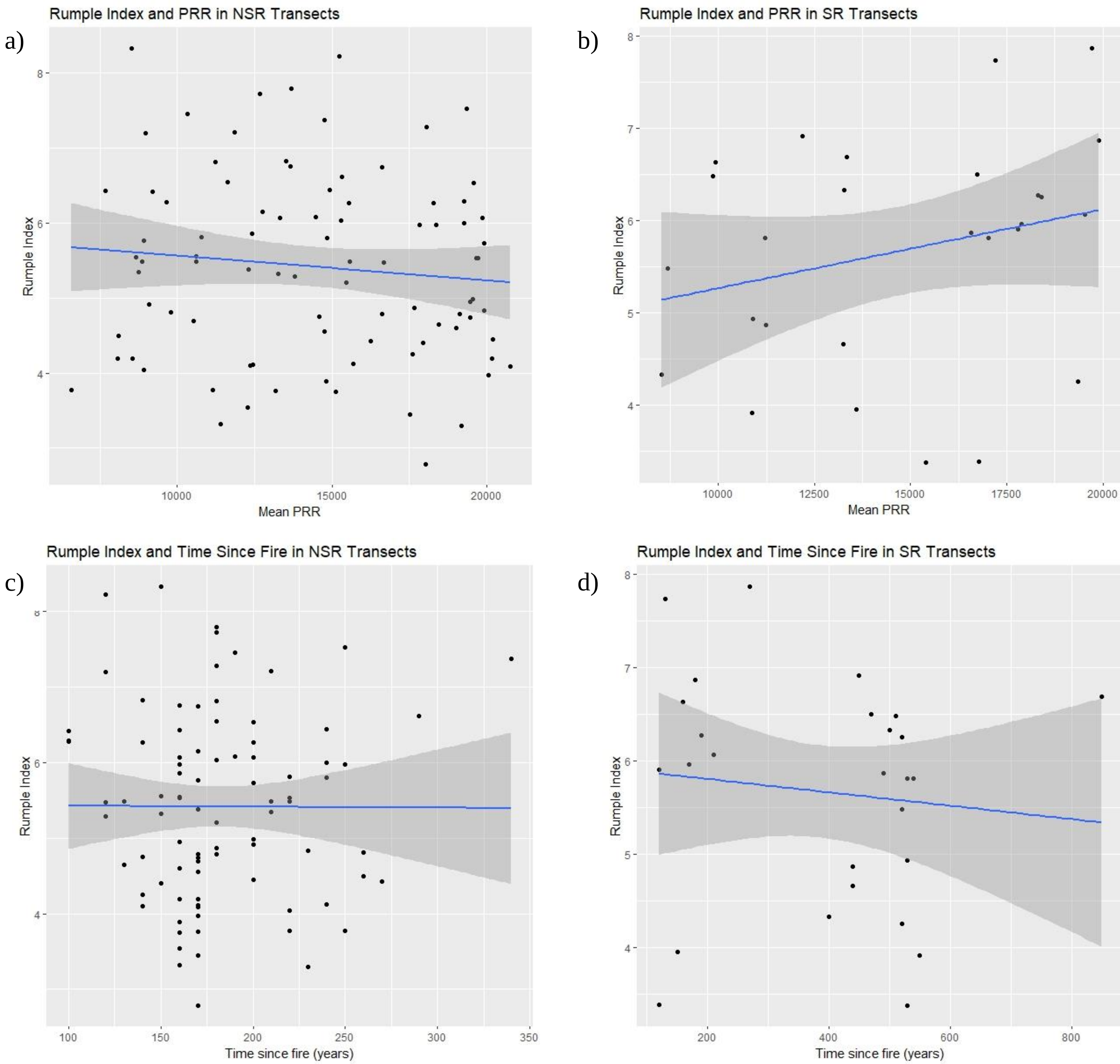


Figure 4. a) Visualization of the relationship between PRR and rumple index in transects in which the most recent fire was non-stand replacing. This graph includes the estimated regression of logarithm of rumple index and PRR with a 95% confidence interval. Both PRR and rumple index are averaged per transect. The regression line is curvilinear (logarithmic response variable), but because the correlation between variables is so low, the regression line looks linear. b) Visualization of the relationship between PRR and rumple index in transects in which the most recent fire was stand replacing. This graph includes the estimated regression of logarithm of rumple index and PRR with a 95% confidence interval. Both PRR and rumple index are averaged per transect. This regression line is also curvilinear (logarithmic response variable), but because the correlation between variables is so low, the regression line looks linear. c)

Visualization of the relationship between time since fire and rumple index in transects in which the most recent fire was non-stand replacing. This graph includes the estimated regression of logarithm of rumple index and time since fire with a 95% confidence interval. The regression is curvilinear because of the logarithmic response variable, but the line is virtually flat, showing extremely low correlation. d) Visualization of the relationship between time since fire and rumple index in transects in which the most recent fire was stand replacing. This graph includes the estimated regression of logarithm of rumple index and time since fire with a 95% confidence interval. The regression is curvilinear because of the logarithmic response variable, but looks linear. Again, this shows an extremely low correlation between these data. Visualizations c) and d) also show that the values of time since fire in NSR transects only range from approximately 100 to 340 years since fire, while in SR transects, time since fire values range from approximately 120 to 850 years since fire.

The AIC analysis done, in addition to the adjusted R^2 values of each model, failed to provide evidence for any of the hypotheses in the studied stands. As the model with no variables and only an intercept (Model 13) had the best AIC score, we did not find evidence that time since fire or PRR were associated with log rumple index, or that time since fire or PRR had an interaction with fire severity. Visualization of relationships between variables confirm a seeming lack of adherence to variables' hypothesized relationships. Figure 4 above shows the extremely low correlation between rumple index and mean PRR, and rumple index and time since fire, demonstrating a lack of correlation between assumed moisture stress, forest age, and canopy complexity.

The Kruskal-Wallis test of medians found, at a significance level of 0.05, there was suggestive but inconclusive evidence of a difference between the median rumple indices of the different age-structure types (chi-squared = 10.67, df = 5, p = 0.05834).

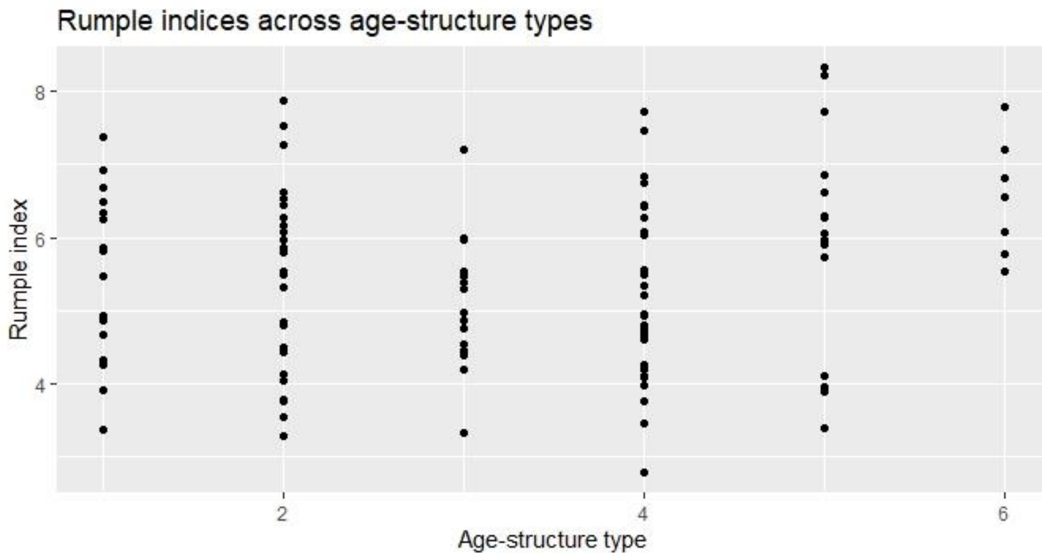


Figure 5. Visualization of each transect's average rumple index, grouped by age-structure types, indicates that the distribution of rumple index varied similarly across most age-structure types, with the exception of type 6. Age-structure types describe different pathways of stand development which are affected by the frequency and severity at which the stands have burned (Tepley et al. 2013). Shade tolerant and intolerant trees are described using separate metrics because of shade tolerant tree's higher chance of mortality after fire, as well as shade tolerant tree's tendency to regenerate continuously between fires, while shade intolerants tend to mostly regenerate between immediate post-disturbance and the canopy closure seral stage. The age structure of shade tolerant trees is based on 1) proportion of trees that germinated before 1780, 2) total age range of the transect, 3) average age of sampled trees, and 4) standard deviation of sampled tree ages (Tepley et al. 2013). Age structure of shade intolerant trees is based on 1) proportion of trees that germinated before 1780, 2) total age range in a transect, 3) age range of trees germinated before 1780, and 4) proportion of trees with char marks on bark (Tepley et al. 2013). Age-structure type 6 describes stands aged approximately 60-200 years that have experienced relatively regular non-stand replacing fires since germinating after a stand replacing fire. This is the only age-structure type in the study that has experienced frequent non-stand replacing fires.

Discussion

The results of this study did not provide evidence for any of the hypotheses. The models were designed to identify which explanatory variables and interactions between these variables were correlated with logarithm of rumple index. Each hypothesis was tested with a related variable or set of variables, but no variable or interaction was found to be associated with logarithm of rumple index. In other words, I found no evidence that suggests an association between logarithm of rumple index, time since fire, or PRR, and found no interaction between any combination of PRR, time since fire, and fire severity.

To reiterate, the hypotheses of this study were as follows:

1. There are differences in canopy complexity between transects that most recently experienced SR vs. NSR fire and these differences are at their maximum at year 0 post-fire and decline over time;

2. Given enough time, transects will converge on the same asymptote of canopy complexity, with transects that experienced SR fire take longer to reach this asymptote than transects that experienced NSR fire;

3. At drier sites, forest development is slower, and the convergence between NSR and SR transects takes longer than at wetter sites.

These findings conflict with much of the literature on forest structure and canopy structure, including literature specifically on forest canopy structure in PNW LSOG Douglas-fir forests. Topography was found to be associated with structural and canopy complexity in LSOG Douglas-fir forests in the western Cascades (Weisberg 2004, Tepley 2010, Seidl et al. 2012) and with coniferous forests in Yosemite National Park (Kane et al. 2014). Variability in forest carbon (related to structural and canopy complexity) in western Cascades LSOG Douglas-fir was also found to be correlated with topography, and topography and time since fire had an interactive effect in the same study (Zald et al. 2016), although time since fire had a low R^2 value in unlogged forests and the models had more than 10 explanatory variables. Zald et al. (2016) also found an asymptote of aboveground live carbon after 500 years since fire. Douglas-fir growth in the Pacific Northwest is correlated with moisture availability (Littel et al. 2008), and water balance is correlated with forest and canopy structure in coniferous forests in Yosemite National Park (Kane et al. 2014). Fire severity is correlated with subsequent structural and canopy complexity in PNW LSOG forests (Franklin et al. 2002, Franklin and Van Pelt 2004, Weisberg 2004, Tepley 2010, Tepley et al. 2013, Kane et al. 2014, Hessberg et al. 2016). Finally, time since fire is correlated with structural and canopy complexity in PNW LSOG Douglas-fir forests (Spies and Franklin 1991, Franklin et al. 2002, Franklin and Van Pelt 2004, Zald et al. 2016, but see Donato et al. 2012 and Reilly and Spies 2015).

This discussion will focus mainly on four potential explanations for these results:

1. It is possible that the proposed hypotheses were not correct, and that factors not analyzed in this study (such as local gap dynamics) are more correlated with canopy complexity in the study sites.

2. The metric rumple index may not represent the elements of canopy complexity associated with differing disturbance histories and moisture limitation.

3. It is possible that using only one response variable, regardless of what the response variable is, did not represent canopy complexity well enough to test the proposed hypotheses.

4. The range of data across each variable was limited in some areas. This could have influenced the results of analysis.

Influence of gap dynamics

My findings do not provide evidence that canopy complexity in the studied sites is detectably affected by the severity of the most recent fire, time since most recent fire, or PRR. Reilly and Spies (2015) found that Douglas-fir/western hemlock stands' structural and canopy complexity varied widely, particularly depending on whether the stands were in SR or NSR environments. The lack of correlation between a stand's rumple index and its PRR value and time since fire, and lack of interaction with most recent fire severity, in Douglas-fir/Western hemlock forests theoretically adheres with Reilly and Spies' finding that Douglas-fir/Western hemlock forests in this region contain stands with a wide variety of degrees of structural and canopy complexity. As seen in Figure 5 above, the rumple indices varied more within age-structure types than across them—the variability of rumple index is not correlated with the chosen explanatory variables.

One possible reason for the lack of evidence for these hypotheses could be that the studied stands may be more affected by local stand dynamics than by their disturbance past or topography. As Pacific Northwest Douglas-fir forests develop, structural and canopy development transitions from being catalyzed by stand-scale process, such as high severity fire, to being catalyzed by gap-scale processes and local stand dynamics, such as a single tree or small clump of trees dying and creating a canopy gap (Franklin et al. 2002, Franklin et al. 1987). Local stand dynamics may include heterospecific and conspecific competition for sunlight or growing space, damage from high winds or heavy snowfall, mortality from insects or disease, low-intensity fires, and soil moisture and characteristics (Franklin et al. 2002, North et al. 2004). Time since fire in this study's transects ranged from 100 to 850 years since fire, and moist PNW Douglas-fir/Western hemlock forests may be considered old growth once they reach 200-250 years old (Spies et al. 2018). It is very possible that after a long enough time, the impact of gap dynamics as described above overshadows the impact that a past fire had on canopy complexity. However, it is also worth noting that the rate at which canopy complexity develops through time varies widely between sites, supporting the idea that age is not always a reliable indicator of successional state and complexity (Spies and Franklin 1988). This is a potential downside for relying on time since fire as an indicator of successional conditions. Additionally, the data for this study lacked a subset of ages: stands that last burned approximately 220-370 years ago were not represented in this study.

Rumple Index as Metric

Rumple index, which was the single response variable in this study, was likely a problematic measure in this study system. Rumple index is determined based on the canopy height model, which measures only the exposed top of the canopy (Kane et al. 2010a). As such, rumple index is not meant to characterize a potential secondary canopy, which is an important aspect of the ecology in this study site—NSR transects, and most transects in this study, generally have at least two cohorts of trees. In the transects used in this study, canopies in transects that experienced at least one NSR fire in between SR fires often have multiple distinct canopies or a continuous range of tree heights starting from the upper canopy. 73% of the stands in this study had at least two postfire age cohorts and thus very likely two height cohorts (Tepley et al. 2013).

In another study in the Blue River watershed, Van Pelt and Franklin (2000) also found that shade-tolerant trees had formed a distinct secondary canopy under a much taller shade-intolerant canopy 200 years post-fire. The 2018 Northwest Forest Plan Science Synthesis notes that old, moist PNW forests typically have multiple canopy layers (Spies et al. 2018). Additionally, Franklin et al. (2002) note that many LSOG Douglas-fir/western hemlock forests have continuous canopy distribution.

Only 15 of the 124 stands (12%) studied saw a SR fire between 1780 and 1940, while 95 of the 124 stands (77%) show evidence of an NSR fire in this same time frame. Tepley et al.'s 2013 study using the same stands, found that NSR fires, whether they occur infrequently between SR fires or relatively chronically, lead to environments conducive to multiple age cohorts with distinct cohorts of shade tolerant and intolerant species. These authors concluded that NSR fires in this study system send stands into alternate successional pathways; however, these pathways mainly differed in the age, size and canopy distributions of shade tolerant trees (Tepley et al. 2013).

Rumple index is a useful tool for measuring the upper canopy of a forest, but can only capture certain measures of forest heterogeneity. This study was conducted on recovery after fires ranging from 100 to 850 years ago; therefore, shade-tolerant trees in these study sites have had at least a century to regenerate secondary or continuous canopies. Thus, even sites that experienced only infrequent SR fire and followed a classical progression of shade intolerant species have had hundreds of years for shade tolerant species to establish, either continuously post-fire or in pulses, and become part of the canopy (Tepley et al. 2013). Continuing this example, by the time these sites reach old growth, canopies have multiple layers or a continuous vertical distribution in which shade tolerant species are integrated with shade intolerant species (Spies et al. 2018, Franklin et al. 2002, Tepley et al. 2013, Van Pelt and Franklin 2000). Rumple index's vertical heterogeneity measurement is limited to the upper canopy, and in the productive LSOG forests in this study, being able to characterize the entire vertical distribution of canopy foliage is important. Due to the presence of shade tolerant species in every age-structure type, a metric that explicitly examines secondary and sub-canopies, and can discern between shade tolerant and intolerant species, could have provided more information for this study and should be considered by researchers interested in similar studies. Adding more response variables using metrics that include the whole canopy would be better. Since canopy complexity is a multifaceted concept, more response variables may allow for more accurate mathematical representation of complexity (see Single Response Variable section below). Leaf area index (LAI) may be a good choice: it examines the full canopy, whether in a continuous canopy or discrete layers, and can be estimated with aerial lidar (Wang and Fang 2020, Zheng and Moskal 2009). Another option is combining high density aerial lidar data with logistic regression modeling to detect and differentiate between multiple layers of forest canopy (Mund et al. 2015). An index describing structural complexity by synthesizing multiple variables into one value is another option; see section Structural Complexity as an Ecological Concept later in this paper for more information.

Kane et al. (2010a)'s finding that a suite of lidar data (95^{th} percentile height, rumple index, and canopy density) can be used to measure successional stage in Pacific Northwest conifer forests was based on correlation with field metrics. Their suite included rumple index to measure variability of height, which these authors equated to canopy structural complexity. Rumple index in their study was correlated with field-measured mean DBH, SD of DBH, and SD of height. However, the same study notes that, because they only used first return lidar data, their measurements largely represent the upper canopy and should not be used to characterize secondary or subcanopies (Kane et al. 2010a). In my study, differences in the distribution of shade tolerant species within secondary, continuous or sub-canopies seem to be where the largest differences between age-structure types lie (Tepley et al. 2013). Because rumple index measures heterogeneity of the upper canopy by design, potential effects of topography and past fires on secondary canopies and understory in shade tolerant species may not be well represented. The lack of penetration into the canopy is an issue with rumple index, not with lidar. Aerial lidar can be used to measure forest subcanopy and understory, but its accuracy is dependent on the lidar density, the canopy orientation, and most relevantly, the lidar metrics used (LaRue et al. 2020).

PRR as Metric

Although PRR was expected to represent water availability, which considered the limiting factor in tree growth in this ecosystem (Chen et al. 2010, Littell et al. 2008), it is possible that it did not—using PRR as a proxy for water availability may be improved by instead using a more direct measure of water availability. Or perhaps water was not a limiting factor for growth in the studied transects. One challenge of using PRR at this scale is that water availability may only vary slightly at the small spatial scale of the 7200 m^2 transects that made up this study's sampling. The estimated PRR approach used in this study provides a level of detail "appropriate for landscape-scale vegetation analysis" (Pierce et al. 2005). This metric is calculated using a DEM. Therefore, depending on the footprint of the DEM, PRR can be calculated for a small footprint, but may not be an appropriate metric for the scale of this study—the sampling units used in this study, transects, are on a stand-level scale rather than a landscape-level scale. Finally, it would be better overall to use a metric that is a more directly related to the hypothesis being tested—for example, using a metric explicitly measuring moisture availability if that's the variable in question. One other metric that could have been used is topographic position index (TPI). TPI is calculated by comparing the elevation of a certain point or area to the elevation of its neighbors to determine if the area is a peak, ridge, valley, or is flat. TPI can be calculated using any pixel size, so its scale can be tailored to the needs of the study. A benefit to TPI is that it describes a given area's topography in relation to its surroundings, which can help predict the microclimate of that area. TPI is also often correlated with moisture availability, since water can accumulate in relatively lower-elevation areas (Maidment 1992). However, TPI and PRR do represent different aspects of topography: moisture drainage and incoming radiation, respectively. Another potential metric is topographic relative moisture index (TRMI), which is calculated based on topographic position, aspect, slope steepness, and slope configuration, and was developed for use in mountainous terrain (Parker 1982). This would have the benefit of including both topographic position and moisture data, and has been shown to be effective in associating forest patterns with environment in Yosemite National Park (Parker 1982). Water balance (actual evapotranspiration and climatic water deficit) would be another good choice and has been associated with forest structure (Kane et al. 2015), provided fine resolution water balance data were available. Another possibility is that the problem was not with PRR as a metric, and that biotic factors were more strongly associated with canopy dynamics than abiotic factors, including topography and/or moisture availability.

Single Response Variable

Using a single metric, rumple index, as the only measure of canopy complexity was likely an oversimplification of a complex concept. Comparison with the following studies, largely in similar study sites, shows that these other studies used more response variables in their analyses. Kane et al. (2010b) calculated individual regression analyses using six response variables (rumple index, canopy density, 95th percentile height, mean DBH, standard deviation of DBH, and canopy closure). A study relating global structural complexity patterns to climate used four response variables: a structural complexity index, canopy height, canopy openness, and basal area (Ehbrecht et al. 2021). Another study on rates of productivity in structurally complex forests across the eastern US used nine canopy metrics and three species diversity metrics for a total of twelve response variables (Gough et al. 2019). However, see also Kane et al. (2013), in which part of the analysis included using linear regressions with only one structural or canopy metric as the response variable to test for changes in vertical structure across forest types. Finally, Kane et al. (2010a) note explicitly that “no single field or lidar measurement captures the state of a stand’s structural development”. As noted in the Rumple Index as Metric section above, potentially better options for metrics include LAI, high density aerial lidar data with binary logistic regression modeling (Mund et al. 2015), and/or a structural complexity index.

Data and Data Distribution

Lack of variation in some explanatory variables relative to RI and to each other may also have affected results. It’s also possible that, data distribution within the range of minimum and maximum values seen in this study notwithstanding, the minimum-maximum range itself of explanatory and response variable values was insufficiently large to observe the hypothesized relationships.

Hypothesis 1 predicted differences in canopy complexity between transects that most recently experienced SR vs. NSR fire, and predicted that differences were at their maximum at year 0 post-fire and decline over time. The shortest times since fire in this study were 100 years post-fire. Therefore, the aspect of hypothesis 1 regarding differences immediately post-fire was not testable with this study’s data. However, including this aspect of the hypothesis in the study had the benefit of having a conceptual, combined hypothesis of canopy complexity’s relationship with time since fire, fire severity and topography across a length of time ranging from immediately post-fire to well into LSOG ages (Franklin and Spies 1988, Spies 1998, Spies et al. 2018).

The pairs plot in Figure 3 shows that time since fire in NSR transects ranges from approximately 100 to 340 years since fire, while in SR transects it ranges from approximately 120 to 850 years since fire. However, the transect with 850 years since fire is an outlier—the second-oldest SR transect is 550 years old. There is also a gap in data between 270-400 years since fire in SR transects. Douglas-fir forests in the PNW usually take from between 150 and 350+ years to reach LSOG decadence (Franklin et al. 2002, Spies and Franklin 1988), though moist PNW Douglas-fir forests typically exhibit LSOG characteristics at 200 to 250+ years (Spies et al. 2018). Additionally, as PNW Douglas-fir forests age, they can transition from a foliage distribution that is heavy in the upper canopy to one that is more evenly distributed throughout the canopy (Franklin et al. 2002, Lindenmayer et al. 2000), which would not be detectable using this study's metrics (RI). These data are also skewed towards forests with shorter times since fire, as is evident in Figure 3.

Figure 3 also shows that the dataset includes more NSR transects than SR transects: 97 NSR transects and 27 SR transects were sampled. Because transects were chosen randomly for sampling, this should be a representative estimate of the proportion of NSR to SR fires in this study area. RI values were distributed across RI's entire range of values (approximately 2.5 to 8.5) across TSF's entire range (between 100 and 600 years, plus one outlier at a value of approximately 850). RI values were distributed across RI's entire range of values across PRR's entire range of values (approximately 6000 to 21000). In NSR transects, RI values were distributed across RI's entire range. In SR transects, RI has a slightly smaller range (approximately 3.25 to 8). PRR values were distributed across PRR's entire range across TSF's entire range. PRR values were distributed across PRR's entire range of values in NSR transects, and across almost all of PRR's range of values in SR transects (approximately 8250 to 20000).

Subsequent research in a similar vein to this study may benefit from a larger number of samples from areas that most recently experienced SR fire than were used in this study, as well as data with a more even distribution of times since fire. Simply having a larger dataset with a higher number of transects sampled should help with this issue.

Forest Complexity as an Ecological Concept

Many aspects of structure and function in forest ecology are often interrelated (Bormann and Likens 1979, Franklin et al. 1981, Spies 1998, Franklin et al. 2002, Franklin and Van Pelt 2004, Ishii et al. 2004, Kane et al. 2010a). Theoretically, structural complexity is a measure of different structural attributes, the diversity of these attributes, and their relative abundance. In practice, structural complexity can be nebulous and does not have a standardized definition (McElhinny et al. 2005). According to a review of structural complexity literature, structural complexity can include foliage arrangement, canopy cover, tree diameter, tree height, tree spacing, stand biomass, understory vegetation, and dead wood, and that any attempt to calculate structural complexity should include many of these variables (McElhinny 2005). The same review found that numerous indices have been created in an attempt to synthesize multiple variables into a single value describing structural complexity, but no one index is agreed upon in the literature (McElhinny 2005).

However, this review also found that studies done on LSOG Douglas-fir and its structural and canopy patterns (e.g. Franklin et al. 1981, Franklin et al. 1987, Spies and Franklin 1991, Spies 1998, Franklin et al. 2002) were more consistent in their definitions of structural complexity, metrics used to identify complexity, and defining associated benefits of that complexity on animal habitat, than the general literature (McElhinny et al. 2005). These papers were also successful in using structural and canopy complexity metrics (SD of DBH, number of Douglas-fir trees >100 cm DBH, mean DBH, >5 m tall snag density, >50 cm DBH snag density, >60 cm DBH downed log density, snag volume (Spies and Franklin 1991)) to identify successional stages in Douglas-fir forests.

Further literature on structural and canopy complexity could benefit from attempting to create accepted and specific definitions of them, in order to shift them from concepts to solid metrics. However, a one-size-fits-all approach may prove problematic as well. For example, the metrics that accurately describe the structural and canopy complexity of a PNW LSOG forest low in species diversity versus that of a tropical forest high in species diversity may differ. Further research is needed to define structural and canopy complexity in a way that is useful in multiple forest ecosystems.

Next Steps
Further research building on this study should consider including more variables for both explanatory and response terms, as is common in published ecological literature using similar analysis methodologies. Specifically, further research should consider using a metric like LAI to measure the full canopy when considering long-term effects of fire and topography on forest structure and canopy, or a structural complexity index. Another option for using lidar to detect multiple canopy layers is high density lidar data combined with binary logistic regressions. Further research may also consider choosing a topographic metric, or combination of metrics, more directly related to the phenomenon being studied. Additionally, although 85% of the samples in Tepley et al. (2013) were cross dated, cross dating all samples and employing cohort analysis *sensu* Merschel 2021 would provide a more accurate fire history.

Conclusions

I found **a lack of evidence** to support these hypotheses:

1. There are differences in canopy complexity between transects that most recently experienced SR vs. NSR fire and these differences are at their maximum at year 0 post-fire and decline over time.

2. Given enough time, transects will converge on the same asymptote of canopy complexity, with transects that experienced SR fire take longer to reach this asymptote than transects that experienced NSR fire.

3. At drier sites, forest development is slower, and the convergence between NSR and SR transects takes longer than at wetter sites.

These findings conflicted with much of the literature on canopy complexity in late successional and old growth Douglas-fir forests in the Pacific Northwest. This study was limited by the exclusion of stands that experienced stand replacing fires between 220-400 years ago, and by a low sample size of stands that had experienced stand replacing fire most recently, as a result of data availability. More importantly, this study was limited by the use of a single variable (rumple index) as the response variable, and would have benefitted from including a response variable that measures the complete canopy.

Acknowledgements

I would like to first thank my two advisors, Drs. Lisa Ganio and David M. Bell, for their time, support, guidance and patience throughout the research process. Thanks also to my committee member Dr. Meg Krawchuk for committing her time, expertise and encouragement in helping me throughout this process. This research was partially supported by Nancy Fischer and the Achievement Rewards for College Scientists, to whom I am deeply appreciative, as well as the USDA Forest Service Pacific Northwest Research Station. Thanks to Dr. Alan Tepley for his generosity in letting me use data from his dissertation research. Thanks to Dr. Brian Harvey for helpful conversations about fire and seral states in the Pacific Northwest. I am grateful to the College of Forestry and to the Forest Ecosystems and Society program for funding. Data [and/or facilities] were provided by the HJ Andrews Experimental Forest and Long Term Ecological Research (LTER) program, administered cooperatively by Oregon State University, the USDA Forest Service Pacific Northwest Research Station, and the Willamette National Forest. This material is based upon work supported by the National Science Foundation under the grant LTER8 DEB-2025755.

Literature Cited

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C. 493 p.

Agee, J.K. 2005. The complex nature of mixed severity fire regimes. pp. 1–10 *in* L. Taylor, J. Zelnik, and B. Hughes (eds.). Mixed Severity Fire Regimes: Ecology and Management. Symposium Proceedings. The Association for Fire Ecology. November 17–19, 2004. Spokane, WA.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In Second Intl. Symposium on Information Theory, pages 267–281. Akademinai Kiado.

Allen, C.D, M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M. Hoffman, and J.R. Klingel. 2002. Ecological restoration of southwestern Ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418-1433.

Beland, M., G. Parker, B. Sparrow, D. Harding, L. Chasmer, S. Phinn, A. Antonarakis, and A. Strahler. 2019. On promoting the use of lidar systems in forest ecosystem research. Forest Ecology and Management 450:117484.

Bond, B.J., M.Z. Czarnomski, C. Cooper, M.E. Day, and M.S. Greenwood. 2006. Developmental decline in height growth in Douglas-fir. Tree Physiology 27:441-453.

Bormann, F.H., and G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer, New York, 253 pp.

Chen, P.Y, C. Welsh, and A. Hamann. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biology 16:3374–3385.

Davis, R.J., J.L. Ohmann, R.E. Kennedy, W.B. Cohen, M.J. Gregory, Z. Yang, H.M. Roberts, A.N. Gray, and T.A. Spies. 2015. Northwest Forest Plan–the first 20 years (1994-2013): status and trends of late-successional and old-growth forests. Gen. Tech. Rep. PNW-GTR-911. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 112 p.

Donato, D.C., J.L. Campbell, and J.F. Franklin. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? Journal of Vegetation Science 23:576-584.

Dyer, J.M. 2009. Assessing topographic patterns in moisture use and stress using a water balance approach. Landscape Ecology 24:391-403.

Ehbrecht, M., D. Seidel, P. Annighöfer, H. Kreft, M. Köhler, D.C. Zemp, K. Puettmann, R. Nilus, F. Babweteera, K. Willim, M. Stiers, D. Soto, H.J. Boehmer, N. Fisichelli, M. Burnett, G. Juday, S.L. Stephens, and C. Ammer. 2021. Global patterns and climatic controls of forest structural complexity. Nature Communications 12:519.

Franklin, J.F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedeii, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen.Tech. Rep. PNW-118, 48 p. Pac. Northwest Forest and Range Experimental Station, Portland, Oreg.

Franklin, J.F., and M.A. Hemstrom. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, Darrell C.; Shugart, Herman H.; Botkin, Daniel B., eds. Forest succession: concepts and application. New York: Springer-Verlag; 1981: chapter 14.

Franklin, J.F., H.H. Shugart, and M.E. Harmon. 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. BioScience 37:550-556.

Franklin, J.F., and T.A. Spies. 1983. Characteristics of old-growth Douglas-fir forests. New Forests for a Changing World: Proceedings of the 1983 SAF National Convention, Portland, Oregon.

Franklin, J.F., T.A. Spies, R. Van Pelt, A. B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

Franklin, J.F. and R. Van Pelt. 2004. Spatial aspects of structural complexity in old-growth forests. Journal of Forestry 102:22-28.

Franklin, J. F. and R.H. Waring. 1980. Distinctive features of the northwestern coniferous forest:

development, structure, and function. Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon, USA, 59-86.

Frey, S.J.K., A.S. Hadley, S.L. Johnson, M. Schulze, J.A. Jones, and M.G. Betts. 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests. Science Advances 2:e1501392.

Gough, C.M., J.W. Atkins, R.T. Fahey, and B.S. Hardiman. 2019. High rates of primary production in structurally complex forests. Ecology 100:e02864. 10.1002/ecy.2864

Gray, A.H. and T.A. Spies. 1996. Gap Size, Within-Gap Position and Canopy Structure Effects on Conifer Seedling Establishment. Journal of Ecology 84:635-645.

Harvey, B.J., and B.A. Holzman. 2014. Divergent successional pathways of stand development following fire in a California closed-cone pine forest. Journal of Vegetation Science 25:88-99.

Hessberg, P.F., T.A. Spies, D.A. Perry, C.N. Skinner, A.H. Taylor, P.M. Brown, S.L. Stephens, A.J. Larson, D.J. Churchill, N.A. Povak, P.H. Singleton, B. McComb, W.J. Zielinksi, B.M. Collins, R.B. Saler, J.J. Kean, J.F. Franklin, and G. Riegel. 2016. Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. Forest Ecology and Management 366:221-250.

Hood, S.M., D.R. Cluck, S.L. Smith, and K.C. Ryan. 2008. Using bark char codes to predict post-fire cambium mortality. Fire Ecology 4:57-73.

Ishii, H.T., S. Tanabe, and T. Hiura. 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. Forest Science 50:342-355.

Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. Wildlife Society Bulletin 32:829–839.

Johnston, J.D., C.J. Dunn, and M.J. Vernon. 2018. Tree traits influence response to fire severity in the western Oregon Cascades, USA. Forest Ecology and Management 433:690-698.

Kane, V.R., Gillespie, A.R., McGaughey, R., Lutz, J.A., Ceder, K., and Franklin, J.F. 2008. Interpretation and topographic compensation of conifer canopy self-shadowing. Remote Sensing of Environment 112: 3820–3832.

Kane, V.R., R.J. McGaughey, J.D. Bakker, R.F. Gersonde, J.A. Lutz, and J.F. Franklin. 2010a. Comparisons between field- and LiDAR-based measures of stand structural complexity. Canadian Journal of Forest Research 40:761–773.

Kane, V.R., J.D. Bakker, R.J. McGaughey, J.A. Lutz, R.F. Gersonde, and J.F. Franklin. 2010b. Examining conifer canopy structural complexity across forest ages and elevations with LiDAR data. Canadian Journal of Forest Research 40:774–787.

Kane, V.R., J.A. Lutz, S.L. Roberts, D.F. Smith, R.J. McGaughey, N.A. Povak, and M.L. Brooks. 2013. Landscape-scale effects of fire severity on mixed-conifer and red fir forest structure in Yosemite National Park. Forest Ecology and Management 287:17-31.

Kane, V.R., M.P. North, J.A. Lutz, D.J. Churchill, S.L. Roberts, D.F. Smith, R.J. McGaughey, J.T. Kane, and M.L. Brooks. 2014. Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne lidar data in Yosemite National Park. Remote Sensing of Environment 141:89-101.

Kane, V.R., J.A. Lutz, C.A. Cansler, N.A. Povak, D.J. Churchill, D.F. Smith, J.T. Kane, and M.P. North. 2015. Water balance and topography predict fire and forest structure patterns. Forest Ecology and Management 338:1-13.

Krawchuk, M. A., S. L. Haire, J. Coop, M.-A. Parisien, E. Whitman, G. Chong, and C. Miller. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7:e01632.10.1002/ecs2.1632.

LaRue, E.A., F.W. Wagner, S. Fei, J.W. Atkins, R.Y. Fahey, C.M. Gough, and B.S. Hardiman. 2020. Compatibility of aerial and terrestrial lidar for quantifying forest structural diversity. Remote Sensing 12:1-14.

Lindenmayer, D.B., C.R. Margules, and D.B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. Conservation Biology 14:941-950.

Lefsky, M.A., Hudak, A.T., Cohen, W.B., and Acker, S.A. 2005. Patterns of covariance between forest stand and canopy structure in the Pacific Northwest. Remote Sensing of Environment 95: 517–531.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Littell, J.S., D.L. Peterson, and M. Tjoelker. 2008. Douglas-fir growth in mountain ecosystems: Water limits tree growth from stand to region. Ecological Monographs 78:349–368.

Lorenz, T.J., M.G. Raphael, R.D. Young, D. Lynch, S.K. Nelson, and W.R. McIver. 2021. Status and trend of nesting habitat for the marbled murrelet under the Northwest Forest Plan, 1993 to 2017. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 64 p.

Lutz, J.A., J.W. van Wagtendonk and J.F. Franklin. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37:936-950.

Maidment, D.R. 1992. Handbook of hydrology. McGraw-Hill, New York, NY, USA.

McElhinny, C., P. Gibbons, C. Brack, and J. Bauhus. 2005. Forest and woodland stand structural complexity: Its definition and measurement. Forest Ecology and Management 218:1–24.

Meddens, A.J.H., C.A. Kolden, J.A. Lutz, A.M. S. Smith, C.A. Cansler, J.T. Abatzoglou, G.W. Meigs, W.M. Downing, and M.A. Krawchuk. 2018. Fire refugia: what are they, and why do they matter for global change? Bioscience 68:944-954.

Merschel, A. 2021. Historical forest succession and disturbance dynamics in Coastal Douglas-fir forests in the southern western Cascades of Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Moeur, M., T.A. Spies, M. Hemstrom, J.R. Martin, J. Alegria, J. Browning, J. Cissel, W.B. Cohen, T.E. Demeo, S. Healey, and R. Warbington. 2005. Northwest Forest Plan–The first 10 years (1994-2003): status and trend of late-successional and old-growth forest. Gen. Tech. Rep. PNW-GTR-646. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 142 p.

Mund, J.P., R. Wilke, M. Körner and A. Schultz. 2015. Detecting multi-layered forest stands using high density airborne lidar data. Journal for Geographic Information Science 3:178-188.

Muscarella, R., S. Kolyaie, D.C. Norton, J.K. Zimmerman, and M. Uriarte. 2019. Effects of topography on tropical forest structure depend on climate context. Journal of Ecology 108:145-159.

North, M., J. Chen, B. Oakley, B. Song, M. Rudnicki, A. Gray, and J. Innes. 2004. Forest Stand Structure and Pattern of Old-Growth Western Hemlock/Douglas-Fir and Mixed-Conifer Forests. Forest Science 50:299-311.

Ogunjemiyo, S., Parker, G., and Roberts, D. 2005. Reflections in bumpy terrain: Implications of canopy surface variations for the radiation balance of vegetation. IEEE Geoscience Remote Sensing Letters 2:90–93.

Parker, A.J. 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Physical Geography 3:160-168.

Parker, G.G., and M.E. Russ. 2004. The canopy surface and stand development: assessing forest canopy structure and complexity with near-surface altimetry. Forest Ecology and Management 189:307-315.

Perry, D.A., P.F. Hessburg, C.N. Skinner, T.A. Spies, S.L. Stephens, A.H. Taylor, J.F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management 262:703–717.

Pierce, K.B., T. Lookingbill, and D. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. Landscape Ecology 20:137–147.

Poage, N.J., P.J. Weisberg, P.C. Impara, J.C. Tappeiner, and T.S. Sensenig. 2009. Influences of climate, fire, and topography on contemporary age structure patterns of Douglas fir at 205 old forest sites in western Oregon. Canadian Journal of Forest Research 39:1518–1530.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reilly, M.J., and T.A. Spies. 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California. Ecosphere 6:192.

Roussel, J.R., D. Auty, N.C. Coops, P. Tompalski, T.R.H. Goodbody, A. Sãnchez Meador, J.F. Bourdon, F. De Boissieu, and A. Achim. 2020. lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. Remote Sensing of Environment 251:112061.

Seidl, R., T.A. Spies, W. Rammer, E.A. Steel, R.J. Pabst, and K. Olsen. 2012. Multi-scale drivers of spatial variation in old-growth forest carbon density disentangled with lidar and an individual-based landscape model. Ecosystems 15:1321-1335.

Spies, T.A. 1998. Forest Structure: A Key to the Ecosystem. Pages 34-39 in J.A. Trofymow and A. MacKinnon, editors. Proceedings of a workshop on Structure, Process, and Diversity in Successional Forests of Coastal British Columbia, February 17-19, 1998, Victoria, British Columbia. Northwest Science 72:34-39.

Spies, T.A. 2004. Ecological concepts and diversity of old-growth forests. Journal of Forestry 102:14-20.

Spies, T.A. and J.F. Franklin. 1988. Old Growth and Forest Dynamics in the Douglas-Fir Region of Western Oregon and Washington. Natural Areas Journal 8:190-201.

Spies, T.A. and J.F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H., tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-285. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 91-109.

Spies, T. A., P. A. Stine, R. A. Gravenmier, J. W. Long, and M. J. Reilly. 2018. Synthesis of science to inform land management within the Northwest Forest Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 1020 p. 3 vol. 966.

Sugihara, N.G., J.W. Van Wagtendonk, and J. Fites-Kaufman. 2006. Fire as an ecological process. In: Sugihara, N.G.; J.W. Van Wagtendonk; K.E. Shaffer; J. Fites-Kaufman; A.E. Thode, eds. Fire in California’s ecosystems. University of California Press 2006.

Tepley, A.J. 2010. Age Structure, Developmental Pathways, and Fire Regime Characterization of Douglas-fir/Western Hemlock Forests in the Central Western Cascades of Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Tepley, A.J., F.J. Swanson and T.A. Spies. 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. Ecology 94:1729-1743.

Turner, M.G., W.H. Romme, and D.B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and Environment 7:351-358.

Van Pelt, R., and J.F. Franklin. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Canadian Journal of Forest Research 30:1231-1245.

Wang, Y., and H. Fang. 2020. Estimation of LAI with the lidar technology: a review. Remote Sensing 12:34-57.

Weisberg, P.J. 2004. Importance of Non-Stand-Replacing Fire for Development of Forest Structure in the Pacific Northwest, USA. Forest Science 50:245-258.

Weisberg, P.J. and F.J. Swanson. 2003. Reginal synchroneity in fire regimes of western Oregon and Washington, USA. Forest Ecology and Management 172:17-28.

Wickham, H. 2009. Ggplot2: Elegant Graphics for Data Analysis. Springer New York 2009.

Zald, H.J.S., T.A. Spies, R. Seidl, R.J. Pabst, K.A. Olsen, and E.A. Steel. 2016. Complex mountain terrain and disturbance history drive variation in forest aboveground live carbon density in the western Oregon Cascades, USA. Forest Ecology and Management 366:193-207.

Zheng, G., and L.M. Moskal. 2009. Retrieving leaf area index (LAI) using remote sensing: theories, methods and sensors. Sensors 9:2719-2745.