Riparian Vegetation Structure and Composition in the Fire–Prone Ecosystem of Eastern Washington

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Abstract

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The objectives of this study were to compare riparian and upland areas, summarize the range of vegetation conditions present in the second half of the 20th century, and correlate vegetation with processes on the landscape. Matching research to management, the spatial extent of the study was the area managed by the Tapash Sustainable Forest Collaborative. To meet study objectives, this research used Interior Columbia Basin Ecosystem Management Project photo-interpreted 1949 and 1992 resource aerial photos, GIS, Permutational Multivariate Analysis of Variance (PERMANOVA), and Nonmetric Multidimensional Scaling (NMDS). Measures of vegetation structure included total crown cover, overstory crown cover, number of canopy layers, and structural stage. Measures of vegetation composition included dominant overstory species, dominant understory species, and riparian-wetland designation. Riparian areas, as defined by the Northwest Forest Plan, were not found to be significantly different than their upland counterparts for any measure of vegetation structure or composition in either time period. Composed of more Douglas-fir and less ponderosa pine, the Tapash was structurally similar, but was compositionally unique from the rest of eastern Washington. Elevation was the most important predictor of vegetation with higher elevations tending to be denser and composed of true firs, hemlocks, spruce, and redcedar. Conservation status did not have clear effects on vegetation. Logging promoted early structural stages. Indicating a mixed-severity fire history in the second half of the 20th century, greater fire prevalence was associated with zero and one canopy layer and bare understory. Fire prevalence was also positively correlated with riparian-wetland areas, suggesting fire reduced coniferous encroachment or directly promoted fire-adapted riparian vegetation. In outlining both the legacy of the landscape and the relative importance of variables influencing vegetation, this research offers agencies working in the Tapash the local science needed for effective management.

EXECUTIVE SUMMARY

The objectives of this study were to compare riparian and upland areas, summarize the range of vegetation conditions present in the second half of the 20th century, and correlate vegetation with processes on the landscape. Matching research to management, the spatial extent of the study was the area managed by the Tapash Sustainable Forest Collaborative. To meet study objectives, this research used Interior Columbia Basin Ecosystem Management Project (ICBEMP) photo-interpreted 1949 and 1992 resource aerial photos, GIS, Permutational Multivariate Analysis of Variance (PERMANOVA), and Nonmetric Multidimensional Scaling (NMDS). Measures of vegetation structure included total crown cover, overstory crown cover, number of canopy layers, and structural stage. Measures of vegetation composition included dominant overstory species, dominant understory species, and riparian-wetland designation.

Riparian areas, as defined by the Northwest Forest Plan, were not significantly different than their upland counterparts. The guidelines for the Northwest Forest Plan were based on the ecology of western Washington riparian areas, but applied throughout spotted owl habitat, including eastern Washington. The similarity between riparian and upland areas within this study indicates that fire may be able to move through riparian areas. Though narrower, ecologically unique riparian conditions likely exist on the landscape, policy-defined riparian areas are not protecting fundamentally distinctive vegetation structures or compositions. While careful management in riparian areas may be beneficial in some cases, policy-defined riparian areas may be serving as corridors of connectivity in an otherwise fragmented landscape.

The Tapash was structurally consistent, but compositionally unique from the Northern Cascades region of the ICBEMP. Both spatial extents had predominately (45-58% in the Tapash) 70-90% total crown cover, roughly evenly distributed overstory crown cover, two canopy layers (over 50% in the Tapash), and more than half the area consisting of understory re-initiation and young forest multi-story. Old forest structures cumulatively composed less than 10% of the Tapash. Compositionally, the Tapash was characterized by an overstory of predominately (>30%) Douglas-fir, 10-12% ponderosa pine and Pacific silver fir, and 5-10% of subalpine fir – Engelmann spruce and western hemlock – western redcedar. Douglas-fir was more common in the Tapash than in the Northern Cascades (23-26% in ICBEMP), whereas ponderosa pine was less common (17-21% of the Northern Cascades). Pacific silver fir was nearly twice as abundant in the Tapash. Douglas-fir – grand fir – Pacific silver fir covered greater than 40% of the understory in the Tapash, compared to 20% in the Northern Cascades. At both spatial extents, area designated as riparian-wetland was between 3% and 10% depending on the location and time period. These differences confirm the importance of management decisions based on local information rather than regional characterizations.

Changes in both structure and composition were limited, though the rate of change from 1949 to 1992 offers unique insight for managers. Across the Tapash, average total crown cover decreased, overstory crown cover increased, the number of canopy layer decreased, and young forest structures increased at the expense of old forest structures. Douglas-fir became more dominant and ponderosa pine more limited. Riparian-wetland areas nearly

doubled. These changes were generally small (<5%) and indicate a slow rate of change in the second half of the 20th century. Relative to the decades immediately following the beginning of fire exclusion, the rate of change has likely decreased. A slower rate of change suggests we may be approaching a new semi-stable forest state. Rather than attempt to recreate conditions prior to Euro-American settlement, management may be more effective at implementing strategies grounded in local needs and objectives.

Elevation, conservation status, logging history, and fire prevalence helped to explain patterns of vegetation in the Tapash. For structure and composition, elevation played a fundamental role in shaping vegetation; high elevation sites tended to be denser, contain older forest structures, and host true firs, hemlock, and redcedar. These areas appeared to be sheltered from disturbance, including logging and fire. Logging tended to be important in upland vegetation structure and composition, reducing midranges of crown closures, but not adversely affecting Douglas-fir or ponderosa pine abundance. Indicating a mixed-severity fire history from 1949-1992, fire prevalence was associated with zero and one canopy layer and bare understory. Fire prevalence was also associated with greater upland areas designated as riparian-wetland. This tentatively indicates that fire reduced conifer encroachment and or promoted fire-adapted mesic vegetation. Processes affect patterns of vegetation and patterns of vegetation influence future processes.

Results indicate that large fires are possible across the Tapash. The Tapash became more homogenous from 1949 to 1992 in all measures of structure and composition except for understory species. Whereas heterogeneity offers natural fuel breaks to wildfire, continuity in structure and composition allows fire to move across the landscape uninterrupted. During the 2012 fire season in eastern Washington numerous fires covered spatial extents greater than historically existed. These fires also burned continuously through riparian areas. These recent fires confirm the findings of this work as well as support the need for further research exploring the role of fire in the Tapash.

With special consideration given to riparian areas, future research should use higher resolution aerial images to analyze more recent vegetation. Higher resolution increases the ability to identify unique riparian vegetation and decreasing minimum polygon size would allow smaller patches of riparian vegetation to be recognized and included in analysis. These changes would help to distinguish and manage for unique riparian conditions across the Tapash. Analysis of an additional, more current time step would further our understanding of the effect of fire exclusion, divergent management objectives, and climate change. This study found a slow rate of change and increased homogeneity from 1949 to 1992; an additional, more current time period would confirm the likelihood of a new semi-stable forest state and the potential for large fire events. As a result of the 1994 Northwest Forest Plan, the USFS has shifted from logging to restoration work. Other agencies have not paralleled this shift; the additional period would help to illustrate the effects of divergent management objectives. After accounting for fire prevalence and management practices, exploration of an additional 20 years of change might suggest the effects of climate change. Though the existing research stands alone in value, additional work would help to illuminate the unique characteristics of riparian areas as well as the effects of continued fire exclusion, ownership, and climate change.

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INTRODUCTION

Ecological Foundations

Effective ecological research addresses issues of process and pattern at the appropriate scale. Process and pattern are two inextricably linked components of landscape ecology and exploring them in tandem enhances our understanding of the existing landscape as well as how to manage it. Natural disturbances create and maintain landscape patterns while patterns of vegetation affect future processes, wildfire in particular (Camp et al. 1997, Everett et al. 2000). Scale, including resolution and spatial and temporal extent, dictates the patterns and processes observed. This study explores the patterns and processes within the area managed by the Tapash Sustainable Forest Collaborative (Tapash); it does so at the spatial scale of management goals and at a temporal scale that offers an empirical historical context.

Patterns and Process

In eastern Washington, fire has been the predominant process driving landscape patterns. Historically, low-severity, frequent fires promoted and maintained open stands of fire tolerant species (Camp 1999, Everett et al. 2000, Hessburg 2005), while less frequent, higher-severity fires created patches for early seral species (Wright and Agee 2004, Franklin and Johnson 2012). Collectively, low- and mixed-severity fires created heterogeneity in stand structure, fuel loads, and habitats across the landscape (Agee 1993, Harrod et al. 1999, Hessburg et al. 2005). The extreme temperatures and high wind exposure at high elevation support subalpine fir, Engelmann spruce, and grand fir; lower and drier areas host lower densities, and primarily ponderosa pine (Turner et al. 2001, Halofsky and Hibbs 2009). Logging and conservation practices also affect patterns of vegetation (Oliver et al. 1994). Selective logging targets specific species – locally, western larch and ponderosa pine; regeneration harvesting tends to create large openings; thinning changes stand density and structure (Wissmar et al. 1994, Camp 1999, Hessburg et al. 2005). These and other processes affect vegetation structure and composition, but their relative influence depends on location and spatial and temporal extents. Furthermore, these processes do not work in isolation but together to create vegetation patterns. This research assesses multiple processes simultaneously to determine the relative influence of each process.

In the fire-prone area of eastern Washington, patterns of vegetation have a dramatic effect on the severity and size of disturbances. Areas with high-density and vertically continuous canopies sustain higher-severity fires, whereas open areas support lower-severity ground fires (Hessburg et al. 2005, Falk et al. 2007, Keeley et al. 2009, Van de Water and North 2011). For example, during the 2012 fire season, as the Wild Rose Fire entered the area of the 2009 Kaboom prescribed fire, it transitioned from a high-severity to a low-severity fire (Jim Bailey, personal communication). Vegetation patterns also affect insect and disease outbreak and animal migration, nesting, and foraging (Turner et al. 2001). Knowing and contextualizing vegetation conditions allows ecologists and managers to predict and prepare for corresponding processes.

Scale

The scale of a study affects the processes and patterns observed. As resolution, the level of detail, decreases, homogeneity increases (Turner et al. 2001). Management plans targeting the common management goal of increasing landscape heterogeneity must first consider the scale of heterogeneity desired. Extent is a measurement of scale and is the area or time period under consideration. As extent increases, the number of species (or unique habitats) also increases (Weins 1989). Patterns evident at smaller scales may be reduced under larger extents. For example, Hessburg et al. (1999) found no significant changes in vegetation from 1949 to 1992 at the scale of the North Cascades region, but did find individual watersheds had changed substantially.

Research at the scale of local management will be most accurate and effective. Ecological and policy emphasis has shifted from stand to landscape-scale management. The United States Department of Agriculture Forest Service (USFS) federally funds the Collaborative Forest Landscape Restoration Program (CFLRP), whose purpose is to "encourage the collaborative, science-based ecosystem restoration of priority forest landscapes" (USDA 2013). These efforts strive to manage a single landscape holistically and across ownerships. Despite these landscape-level objectives, the best science is commonly conducted at the scale of an entire region rather than the scale of a specific management area.

Within landscape assessments, riparian areas are particularly important. Ecologically, riparian areas are immediately adjacent to waterways support vegetation adapted to elevated water tables, high soil moisture, or periodic flooding (Naiman and Décamps 1997). These areas protect aquatic integrity by reducing erosion, providing large woody debris, and, in smaller streams, providing allochthonous nutrients and energy. Relative to their upland counterparts, riparian areas are consistently more diverse, functioning as corridors for dispersal and migration (Naiman and Décamps 1997). These areas tend to have cooler and moister microclimates, as well as greater vegetation complexity and density (Olson and Agee 2005, Van de Water and North 2011, Messier et al. 2012). Despite the critical role of these areas, relatively little research directly addresses their vegetation patterns.

Forest ecosystems can reasonably be described by their composition, function, and structure (Franklin et al. 2002). In the context of a fire-dependent ecosystem, structure and composition reflect historic fire activity and suggest future fire behavior. As discussed, denser stands with vertical continuity and fire intolerant species will likely experience greater fire severity than open stands with single canopies and fire tolerant species (Van de Water and North 2011). This study focused on structure and composition in order to give a more complete understanding of the study area.

Similar to spatial scaling, temporal scale affects research outcomes and subsequent management. An extensive body of work has used pre-Euro American settlement conditions (~1850) to explicitly or implicitly inform our understanding of "natural" and, therefore, the priorities of management (Howell 2001, Dwire and Kaufman 2003, Hessburg et al. 2004, Gärtner et al. 2008). However, understanding of the range of historical and potential conditions offers greater context for current conditions. For example, climate changes on varying temporal scales: ice ages come and go with the 200,000 year

Milankovitch cycle; the Pacific Decadal Oscillation affects temperature and precipitation on 20-30 year cycles; La Niña and El Niño affect weather on the scale of five years; and solar exposure dictates weather seasonally (Turner et al. 2001). In lieu of complete data, the historical range of variability (Quigley et al. 2001) and the future range of variability (Thompson et al. 2009, Duncan et al. 2010) have offered a broader context for current vegetation by using modeled and reconstructed vegetation. At the grain and extent desired by landscape-level assessments, resource aerial photos provide the highest resolution data available. Photographs span the second half of the twentieth century and form the basis of an empirical set of vegetation conditions. This range of observations is a powerful tool for assessing vegetation over the last 70 years and contextualizing current conditions.

Objectives

Focused on the spatial extent of the area of the Tapash Sustainable Forest Collaborative and the temporal extent of the second half of the 20th century, the objectives of this study are: first, to describe the range of vegetation conditions and processes in 1949 and 1992 and second, to explore vegetation changes and their causes. Science has a distinct role in informing policy and carrying out management (Mills and Clark 2001). This study directly meets the goals of the Tapash Sustainable Forest Collaborative at a scale that is appropriate for both the ecology and management of the area.

Specifically, this study will:

I. Explore the range of vegetation conditions, and the processes affecting them, that are present in the second half of the 20th century
    i. Determine if riparian areas, as defined by the Northwest Forest Plan, are ecologically distinct from upland areas
    ii. Describe 1949 and 1992 vegetation structure and composition as defined by total crown cover, overstory crown cover, number of canopy layers, structural stage, dominant overstory species, dominant understory species, and riparian-wetland designation
    iii. Correlate patterns of vegetation to ongoing processes; including spatial location, elevation, fire prevalence, logging history, conservation status, and ownership

II. Examine changes in vegetation conditions in the second half of the 20th century and suggest processes responsible for change
    i. Determine whether 1949 and 1992 vegetation conditions are different
    ii. Detect whether riparian and upland areas changed differently
    iii. Describe how vegetation structure changed from 1949 to 1992
    iv. Correlate processes on the landscape to changing vegetation patterns

METHODS

Study Site

Interior Columbia Basin Ecosystem Management Project

At the broadest level, this study site was situated within the bounds of the Interior Columbia Basin Ecosystem Management Project (ICBEMP). The ICBEMP study included all of eastern Washington and eastern Oregon, the majority of Idaho, substantial sections of Montana and Wyoming, and small areas of Nevada, California and Utah (Figure 1). The project, which sought to quantify changes in vegetation composition and structure between the mid-twentieth century (1949) and the late twentieth century (1992), photo-interpreted resource aerial photographs to examine change across the interior basin. At a minimum patch size of 4ha, polygons were delineated and assigned a set of attributes representing various measures of vegetation (Hessburg et al. 1999).

Eastern Washington

This study focused on the ecosystem of eastern Washington, though implications may extend to other dry forests with similar disturbance histories. The Cascade Mountain Range delineates the western edge of the eastern ecosystem and greatly contributes to precipitation, temperature, and elevation gradients. As a result of the rain-shadow effect, precipitation, which mostly falls as snow, is 1380cm at the crest of the cascades and 51cm in the far eastern foothills. In addition to the dramatic elevation decrease from the crest eastward (1700-500m), the northern Cascades are at a higher elevation than the southern Cascades (Hessburg et al. 1999). The Southwest, Rocky Mountains, and Great Plains exhibit similar aridity and climate to that found in eastern Washington, allowing results to be tentatively applied to these areas as well (Wissmar 2004).

Vegetation in eastern Washington changes along the elevation gradient. Subalpine fir and Engelmann spruce, with occasional whitebark pine and alpine larch, generally occupy the subalpine environment. Grand fir, Douglas-fir, western larch, and ponderosa pine distinguish the montane zone. Ponderosa pine and sagebrush steppe characterize the lowlands (Hessburg et al. 1999); historically, these low-density stands were patchy, open, and predominately single canopy (Wright and Agee 2004, Hessburg et al. 2005).

Though fire was historically the dominant disturbance in eastern Washington, the more recent relationship between fire and vegetation remains unclear. Dendrochronological studies from Nile Creek in eastern Washington estimated that the pre-settlement (1750-1860) mean fire-free interval was 7 years across aspects, 10.2 years during the period of settlement (1960-1910), and 43.0 years post-suppression (1910-1996; Everett et al. 2000). Frequent, low-severity fires historically promoted fire tolerant ponderosa pine, open stand structure, and a heterogeneous landscape (Camp 1999, Everett et al. 2000, Harrod et al. 1999, Hessburg 2005). The effect of less frequent but higher-severity fires on landscape-level patterns of vegetation has not been thoroughly explored.

The Tapash Sustainable Forest Collaborative

The study was further restricted to the bounds of the Tapash Sustainable Forest Collaborative ("Tapash"), which is situated in the Yakima River Basin between Wenatchee and Yakima on the eastside of the Washington Cascades. Of the sixth-level hydrologic unit code (HUC) watersheds ("subwatershed") photo-interpreted during the ICBEMP, 15 were within the bounds of the Tapash. These 15 subwatersheds (9916ha average, 297,493ha total), nested within three larger subbasins (4th level HUC, 536,127ha average size), formed the basis of this study. The Tapash is a federally funded Collaborative Forest Landscape Restoration Project (CFLRP) consisting of the Okanogan Wenatchee National Forest, The Yakama Nation, The Nature Conservancy (TNC), the Washington Department of Fish and Wildlife, and the Washington State Department of Natural Resources (DNR). The objective of the partnership is to "improve ecosystem health and natural functions of the landscape through active restoration projects backed by best science, community input and adaptive management" (Tapash.org). Matching the scale of management, this study provides best science on vegetation structure and composition.

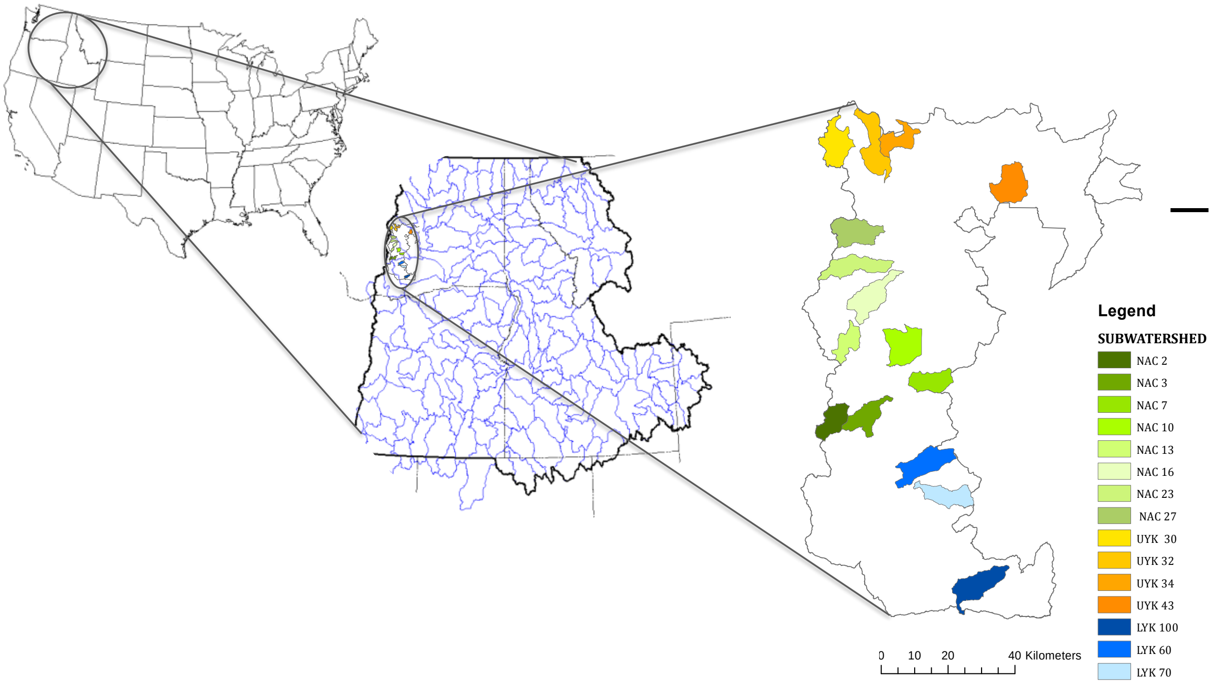

Figure 1: Spatial extent of the Interior Columbia Basin Ecosystem Management Project and The Tapash Sustainable Forest Collaborative. Base image is from the ICBEMP.

Riparian Areas

Though studies have extensively looked at vegetation shifts between 1949 and 1992 in the ICBEMP (Hessburg et al. 1999), few studies have explicitly studied riparian corridors separate from their upland counterparts. Recent dendrochronological work has shown that, historically, riparian areas experienced frequent, and often high-severity, fire events (Olson and Agee 2005, Everett et al. 2003, Van de Water and North 2010). Evolutionary mechanisms employed by common riparian vegetation – epicormic and basal sprouting or fire-enhanced flowering and fruit production further suggest that fire historically played a role in shaping riparian vegetation (Dwire and Kauffman 2003). Similar to the upland, fire exclusion has likely caused changes in riparian vegetation.

The riparian area was delineated for use in analysis within each of the 15 subwatersheds. Ecologically, riparian areas range from the low to high water marks where vegetation is influenced by flooding, high water tables, or mesic soils (Naiman and Décamps 1997). Yet in practice this area can be hard to identify on the ground and harder still to recognize in aerial photos. To avoid haphazard designations and to provide relevant information to managers in the Tapash, this study based riparian areas on guidelines from the Pacific Northwest Forest Plan. Using policy guidelines for riparian areas directly addresses whether the riparian reserves in the Northwest Forest Plan protect unique habitats, which is especially pertinent as new forest plans are currently under development. Using DNR stream data, which included spatial location and fish-bearing status, fish-bearing streams were given a buffer on each side of 91.44m (300ft) and non-fish-bearing streams a buffer of 45.72m (150ft) (DNR, USDA 1994). The end result was a riparian area buffering known streams, which accounted for 10.7-29% of the subbasins.

Data Collection

Response Matrices

Vegetation structure and composition attributes interpreted and derived during the ICBEMP formed the response matrices analyzed in this study. These attributes included total crown cover, overstory crown cover, number of canopy layers, structural stage overstory species composition, understory species composition, and riparian-wetland designation. Total crown cover and overstory crown cover, of trees only, were evaluated for each polygon and estimated to the nearest 10% by the photo-interpreter (11 categories)[1]. Crown cover is the "proportion of the forest floor covered by the vertical projection of the tree crowns" (Jennings et al. 1999); total crown cover included the trees in all canopy layers and overstory crown cover included just overstory trees. The number of canopy layers was recorded by the photo-interpreter and was grouped into four categories: no canopy layers, one canopy layer, two canopy layers, or more than two canopy layers. Structural stage was derived based on photo-interpreted attributes and an algorithm developed by Latham et al. (1998). Consolidating 19 original categories into 11, structural stage included non-forest[2], herbland, shrubland, woodland and seven forest stages (stand initiation, stem exclusion open canopy, stem exclusion closed canopy, understory re-

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[1] In a few cases, photo-interpreters attributed polygons with values not on a 10% interval. These values were subsequently attributed to the next nearest category (e.g.: values categorized as 98% re-assigned to 100% category). In the case of a value ending in five, the value was split evenly between surrounding categories (e.g.: values of 25% split evenly between 20 and 30%).

[2] Non-forest includes rock, water, wet meadow/marsh, alpine meadow, dry meadow/grassland, shrubland, post logging bare ground – burned, post logging bare ground – slumps and erosion, post logging – grass/forb stage, cropland, urban/rural, pasture, grassland, and woodland.

initiation, young forest multi-story, old forest multi-story, and old forest single story)[3]. Dominant overstory or understory species categories that did not cover at least one percent of three separate subwatersheds were removed from analysis[4]. The remaining 11 overstory categories included no classification (0), Douglas-fir, ponderosa pine, ponderosa pine – Douglas-fir, lodgepole pine, western larch, grand fir, Pacific silver fir, subalpine fir – Engelmann spruce, western hemlock – western redcedar, and mountain hemlock. The remaining 11 understory categories were no classification, ponderosa pine, western larch – lodgepole pine, Douglas-fir – grand fir – Pacific silver fir, subalpine fir – Engelmann spruce, western hemlock –western redcedar, mountain hemlock, hardwood, shrub, grass-forb, and bare. The photo-interpreter also recorded whether the polygon was a riparian or wetland area (yes or no). (See Appendix A for spatial distribution of response variables). These four measures of vegetation structure and three measures of vegetation composition were the basis of analysis in this study.

Vector analysis in GIS transformed the spatial data from ICBEMP into response matrices. Vector analysis was completed on each discrete area (subwatershed and riparian, n=30) in each time period (n=2, N=60). After removing rare and redundant categories as described, this yielded 60x11 matrices for overstory crown cover, understory crown cover, structural stage, dominant overstory species, and dominant understory species, a 60x4 matrix for number of canopy layers and a 60x1 vector for riparian-wetland designation. Riparian-wetland designation was a single vector because the original two columns of riparian-wetland designation were complementary to each other. Each response matrix was a set of areas corresponding to categories within an experimental unit for a single time period. For example, the response matrix for number of canopy layers included, for each time and unit, the area with no canopy layer, area with one canopy layer, area with two canopy layers, and area with more than two canopy layers. This multivariate approach was preferable to a univariate approach (a single value for a given area) because it allowed a more nuanced and complete understanding of the experimental units. Each matrix was then prepared for analysis and analyzed separately.

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[3] Original categories included non-forest, two herb stages (open herbland, closed herbland), four shrub stages (open low-medium shrub, closed low-medium shrub, open tall shrub, and closed tall shrub), five woodland categories (woodland stand initiation, woodland stem exclusion, woodland, understory re-initiation, woodland old multi-story, and woodland old single story), and the seven forest stages.

[4] The original 14 overstory categories were 0 (No classification), Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), Douglas-fir -ponderosa pine, lodgepole pine (*P. contorta*), western larch (*Larix occidentalis*), grand fir – white fir (*Abies grandis – A. concolor*)*, Pacific silver fir (*A. amabilis*), subalpine fir – Engelmann spruce (*A. lasiocarpa – Picea engelmannii*), western hemlock – western redcedar (*Tsuga heterophylla – Thuja plicata*), mountain hemlock (*T. mertensiana*), whitebark pine - subalpine fir (*P. albicaulis – A. lasiocarpa*), western white pine – sugar pine (*P. monticola – P. lambertiana*), or hardwood. The original 17 understory species categories were 0, ponderosa pine, ponderosa pine – Douglas-fir, ponderosa pine – lodgepole pine, lodgepole pine, western larch – lodgepole pine, Douglas-fir – grand fir – white fir – Pacific silver fir*, subalpine fir – Engelmann spruce, lodgepole pine – Engelmann spruce, western hemlock – western redcedar, mountain hemlock, mountain hemlock – white fir – sugar pine, whitebark pine – subalpine larch (*L. lyallii*), hardwood, shrub, grass-forb, or bare ground.

Explanatory Variables

Primary explanatory variables originated from the ICBEMP, TNC, and the USFS; they included measures of elevation, fire prevalence, logging history, conservation status, and ownership. Each explanatory variable was included to capture a distinct set of conditions or processes predicted to affect vegetation.

Elevation, taken from ICBEMP photo-interpretation, included six elevation classes but was condensed into two variables. ICBEMP elevation determination was based on 90m digital elevation models; a polygon was attributed to the 305m (1000ft) elevation band it overlapped the most. These six elevation groups were condensed into a weighted average elevation and a highest elevation. The value of the center of the ICBEMP elevation band was used for these calculations. Average elevation ranged from 668m to 1578m, with an average of 1209m. Thirty-four sites had a high elevation of 1676m and 26 had a high elevation of 1981m. Elevation, measured by weighted average and highest elevation, was included to capture coarse-scale changes in climate and plant associations (Hessburg et al. 1999, Halofsky and Hibbs 2009).

Point data from the USFS, which has recorded all wildland fires since 1970, was used to determine the number of fires, number of years with fire events, and area burned. Over the period of record each subwatershed had 8-91 fire events across 6-20 fire years (Figure 3). The majority of fires were 0.04ha (0.1 acre) or less, the minimal reporting unit. The average subwatershed had a total of 51.9ha burned during the 22 years of reporting.

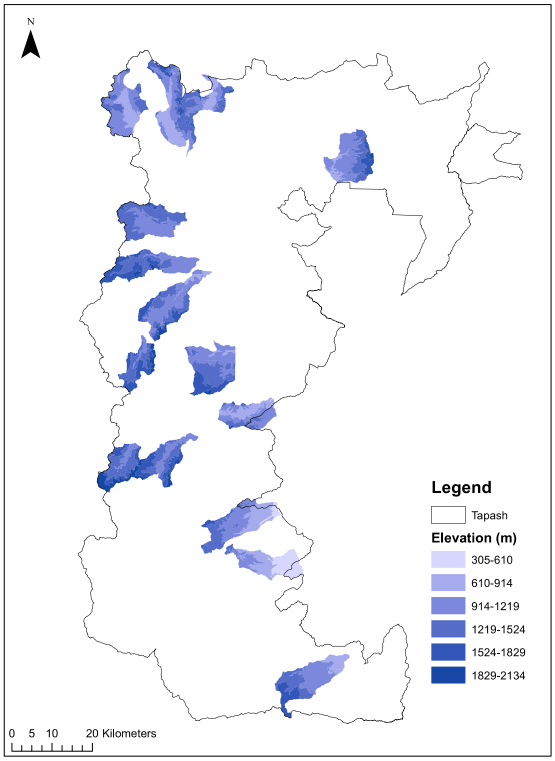

Figure 2: Spatial distribution of elevation in the 15 subwatersheds used in analysis.

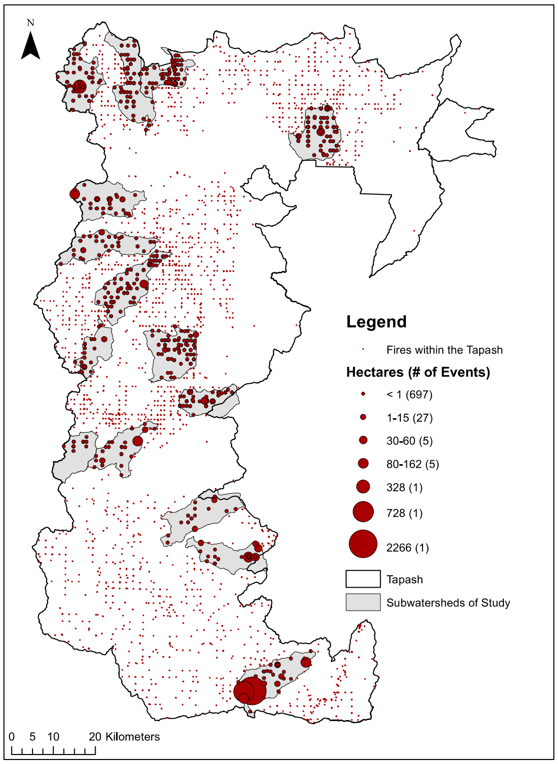

Figure 3: Location and size of fires in the Tapash. Fires used in analysis are coded by size.

Logging history included five categories, but was consolidated into three for analysis. Logging data originated from ICBEMP photo interpretation; original categories included no logging apparent, regeneration (clearcut, shelterwood, seedtree harvest), selective harvest (selective harvest, overstory removal, final removal), thinning (commercial, precommercial), and patch clearcut logging (clearcut patches < 4ha). In 1949, 93.6% of the landscape had no apparent logging; by 1992, 76% of the study site had no apparent logging. Selective harvest was the most common form of logging, covering 5.6% of the study area in 1949 and 12.2% of the area in 1992. Regeneration logging covered less than 1% of the 1949 landscape, but rose to 10.4% by 1992. The areas of patch clearcuts and thinning were removed from further analysis because they covered a small portion of the study area <1%), had low variance (<0.001), and changed little between the two time periods (<1%; Figure 4). As a result, three logging history variables were used in analyses.

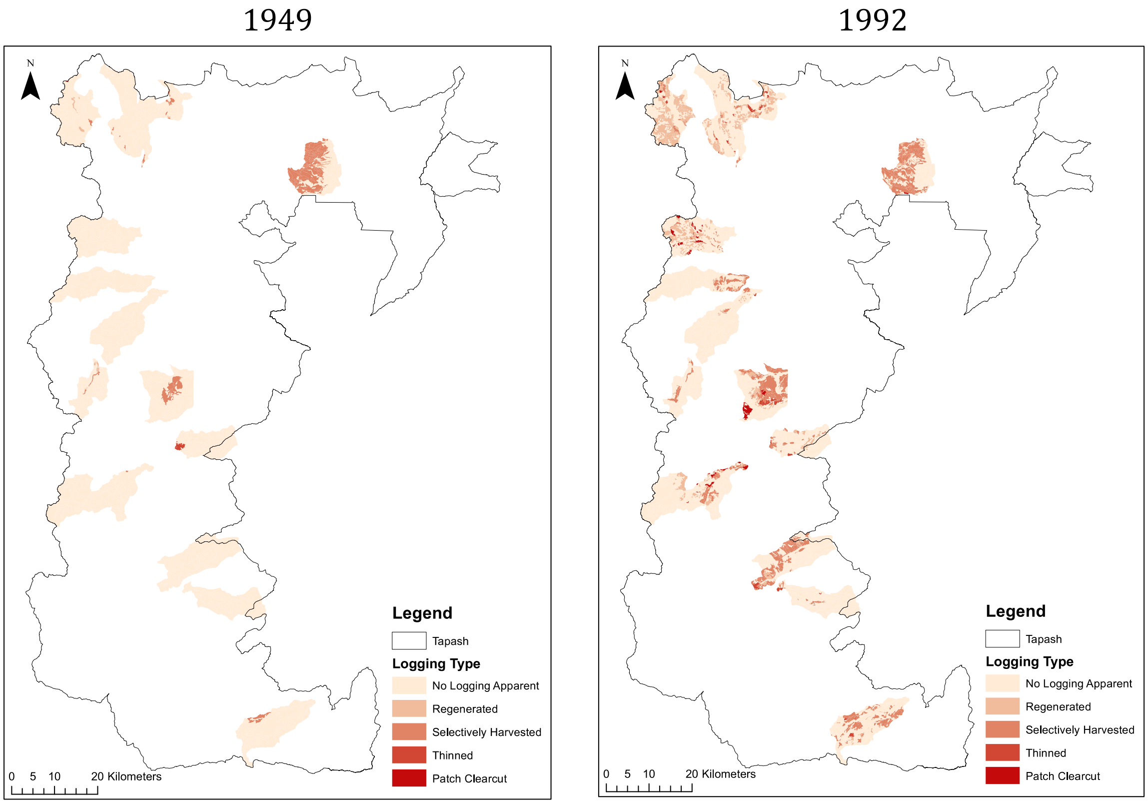

Figure 4: Spatial distribution of logging practices, 1949 and 1992.

Of five categories of conservation status provided by TNC, four were used in analyses. TNC provided raster data of conservation status for the Tapash area; data have not been published and were obtained through personal communication. The original categories representing conservation status were: 1) legally protected (encompassed areas that are legally dedicated to protection and preservation of characteristic of natural landscapes), 2) managed for conservation (retention of forested areas or native vegetation for a variety of reasons such as the conservation of endangered species or for maintaining forested corridors along areas of visual or biological importance), 3) partially retained (partial-retention with the potential for longer rotations or more experimental management strategies), 4) modified (major modification of the landscape including general forested, developed recreation, mining, and grazing), and 5) private modification (privately owned land which may be less restrictive than public lands). Nine of 15 subwatersheds had greater than 1% of their area under legal protection; the mean was 21.57%. Area managed for conservation was similarly common (23.1% average), present in greater than 1% on 10 sites. Area of partial retention was the most common (42.7% average). Area modified, though generally of small area (11.6% average), was present on 12 sites. Area of private modification was removed from further analysis because it covered more than 1% of the area in only two subwatersheds (Figure 5). Four variables were subsequently used to represent different conservation statuses.

Ownership data was consolidated into a single explanatory variable. Ownership data also came from TNC. Ownerships included Bureau of Land Management (BLM), USFS, Tribal, Private, and State ownership. BLM and the State owned only small portions of land and were therefore removed from further analysis (BLM: 0.006 max, 0.0002 average; State: 0.045 max, 0.0076 average). The USFS was the dominant landholder, owning the majority of 12 subbasins (0.692 average). The three subwatersheds in the Lower Yakima subbasin were all tribally owned. In the Upper Yakima and Naches subbasins, ownership was divided between federal and private (Figure 6). As a result of the nature of these relationships, only the area under federal ownership was used as an explanatory variable.

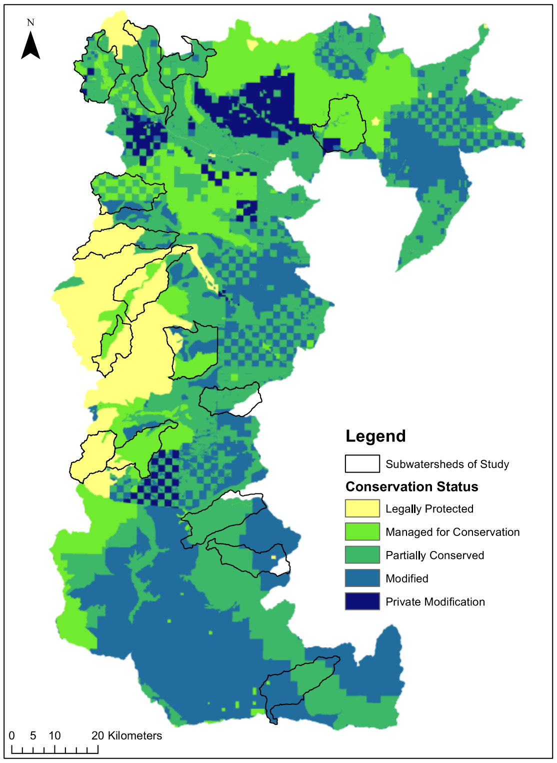

Figure 5: Spatial distribution of conservation status in the Tapash. Subwaterheds used in this study are outlined.

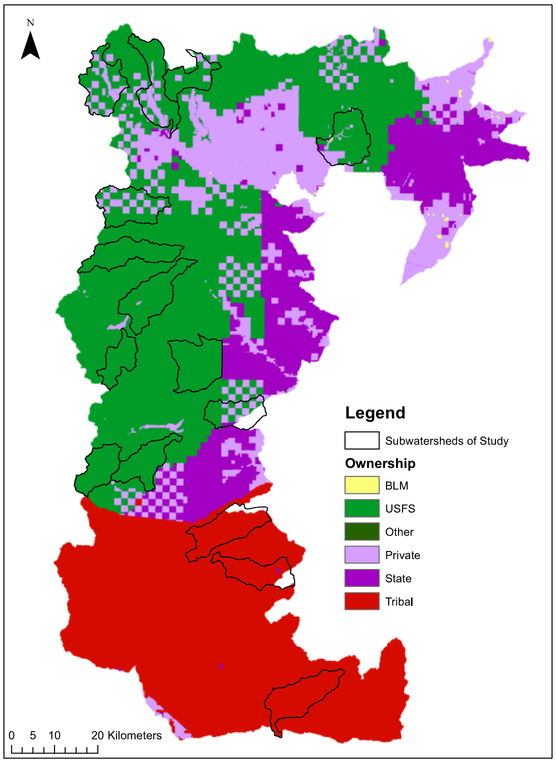

Figure 6: Spatial distribution of ownership in the Tapash. Subwatersheds used in this study are outlined.

Identifiers and coordinates were given to each experimental unit. Each experimental unit had a unique ID in order to track the same unit across time. The location (riparian or upland) was also designated. The 15 subwatersheds were nested within the Upper Yakima, Lower Yakima, and Naches subbasins; an identifier was given to these subbasins. Finally, the geographic centroid of each experimental unit was calculated in GIS to give latitude and longitude coordinates to each unit.

Data Preparation

Relativizations/Transformations

Data were further formatted and prepared for analysis. Vector and raster analysis converted the spatial explanatory variables into data frames. Upland area was calculated as the difference between the data for the entire subwatershed and data for the riparian corridor. All subsequent analyses used the upland and riparian areas as experimental units. In order to allow for comparisons between experimental units of different size, area values were converted to proportions. Fire prevalence data were adjusted by unit size to allow for comparison between experimental units. This yielded proportion of area burned, number of fire events per hectare, and number of fire years per hectare. There were no further transformations.

Data Subsets

In order to conduct whole-plot and split-plot Permutational Multivariate Analysis of Variance (PERMANOVA) tests, a series of data frames were created with the previously explained data. For use in the whole-plot PERMANOVA, the data was initially subset in averaged 1949 and 1992 data, just 1949 data, and just 1992 data. These data subsets were further subset to break apart riparian and upland areas for each time period. Split-plot PERMANOVA was completed with three datasets, each of which included both time periods: the entire data set, just riparian data, and just upland data.

Data Reduction

Principal Component Analyses (PCA)[5] was used to evaluate whether variables could be combined. The objective of PCA was to reduce the overall dimensionality of the dataset and to increase the strength of correlation between response and explanatory variables. For example, if three measures of fire prevalence can be reduced to a single principal component, that single fire principal component may explain more variation in a response matrix than any single fire variable alone (Haugo et al. 2011). If PCA was unable to reduce dimensions, it indicated that variables were unique from one another.

Only in the case of fire prevalence was PCA able to reduce the dimensions of the data. Variables in PCA were scaled to allow for equal contribution regardless of variation. Scree plots and a cutoff value of 75% total variation were used to determine how many principal components warranted further investigation (McCune and Grace 2002). Loadings with an absolute value of at least 0.4 were evaluated (Summerville et al. 2006). PCAs were completed on all explanatory data together (fire prevalence, logging, conservation status, and ownership variables) to evaluate overall disturbance and on subsets of explanatory data alone (elevation, logging history, conservation status, and ownership) to assess redundancy. None of these analyses yielded meaningful reductions in dimensionality, indicating that the variables were unique from one another and warranted independent inclusion in subsequent analyses. PCA of fire prevalence did reduce three fire variables to a single principal component. This principal component explained 81% of the cumulative variation in which all fire variables were positively correlated.

The final product of data collection and reduction was seven response matrices and 19 explanatory variables. The response matrices included total crown cover (60x11), overstory crown cover (60x11), canopy layers (60x4), structural stage (60x11), dominant overstory species (60x11), dominant understory species (60x11), and riparian-wetland

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[5] Prcomp function in standard R package, version 0.97.332

designation (60x1). Explanatory variables included two elevation descriptors, four fire categories (three original plus one principal component), three logging categories, four conservation status groups, one ownership measure, latitude, longitude, and three identifiers (experimental unit, time, and subbasin).

Data Analysis

Range of Patterns and Processes in 1949 and 1992

Riparian Compared to Upland Vegetation Conditions

Permutational Multivariate Analysis of Variance (PERMANOVA) is a particularly strong statistical test well suited to multivariate community ecology data. The multivariate nature of PERMANOVA allowed each experimental unit to be summarized not by a single measure, but by a series of values. In ecological research, this type of multivariate analysis contributes to a more nuanced understanding of vegetation structure and composition. The second main advantage of PERMANOVA is that it uses permutations of the data to inform the pseudo-F statistic. Ecological data rarely meet conditions of normality of homogeneity of variance; using permutations avoids having to meet theses assumptions (Anderson 2001, Davies et al. 2012).

Whole-plot PERMANOVAs[6] were used to determine whether riparian and upland areas were different (Davies et al. 2012). Tested as the first term, the significance (alpha=0.10, 99,999 permutations) of the area (riparian or upland) term indicated the difference between the two areas. This test was completed with averaged 1949 and 1992 data, 1949 data, and 1992 data. This determined whether riparian and upland areas were different on whole, different in 1949, and different in 1992. The Bray-Curtis distance measure was used to focus on shared abundance (Faith et al. 1987, McCune and Grace 2002, Reiss et al. 2010). If significant, associated R^2 values indicated how much variation could be attributed to riparian or upland location.

Bar charts and Non-metric Multidimensional Scaling (NMDS) ordination (metaMDS, monoMDS engine) were used to explore the data and visualize PERMANOVA results. Bar charts were used to compare riparian and upland areas in each category of each response matrix. NMDS was used to visualize the statistical difference between riparian and upland areas. NMDS makes no assumptions about linear relationships and is appropriate for non-normal community data (Kruskal 1964, Minchin 1987, McCune and Grace 2002). Each analysis was completed with the Bray-Curtis distance measure to focus on relative shared abundance, two dimensions to maximize interpretation, 100 iterations of random starting configurations, 200 iterations for configuration adjustments, a Monte Carlo test with 100 randomizations, and a stability criterion of 0.00001 (McCune and Grace 2002, Laughlin et al. 2004). Experimental units with identical dissimilarities were positioned at identical distances apart. Stress plots evaluated how well the ordination displayed the dissimilarity matrix. Overlays enhanced the visualization of PERMANOVA results.

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[6] Adonis function, Vegan package 2.0-2, R version 0.97.332

Processes Affecting Patterns of Vegetation Conditions

Spatial Autocorrelation

Mantel tests were used to assess the spatial autocorrelation between each response matrix and its spatial coordinates (Laughlin et al. 2004, Parra et al. 2006, Davies et al. 2012). Testing spatial autocorrelation with a Mantel test allowed two matrices to be compared; the first was the two-column matrix of latitude and longitude and the second was the multivariate response matrix. The greatest advantage of a Mantel test is the permutation-based p-value, avoiding assumptions of normality.

The specifications of the Mantel test included the distance measures, correlation method, and number of permutations used. For the geographic coordinates, Euclidean distances were used to create the dissimilarity matrix as suggested for physically located data (McCune and Grace 2002). Bray-Curtis is widely accepted for community ecology data (Faith et al. 1987, McCune and Grace 2002, Clarke et al. 2006, Reiss et al. 2010) and was used for all response matrices. The Pearson method of correlation, preferred for non-ranked data, compared the two matrices (McCune and Grace 2002). Alpha was 0.1. Published values are based on 99,999 permutations (Anderson 2001, McCune and Grace 2002).

In addition to Mantel tests, latitude and longitude were tested to determine the presence of north-south and east-west gradients. The variation explained by latitude and longitude is distinct from the Mantel test because latitude and longitude capture gradients rather than neighborhood similarities. After testing latitude and longitude as first terms in PERMANOVA, they were removed from subsequent analyses because they may account for variation that would otherwise be explained by a more detailed variable. For example, elevation decreases from west to east. Including longitude in the model before elevation may weaken or eliminate the significance of elevation. Latitude and longitude were retested as final terms to determine remaining significance. Testing coordinates as first and final terms in the model provided a more detailed understanding of the relationship between vegetation conditions and spatial gradients.

Elevation, Fire Prevalence, Logging History, Conservation Status, and Ownership

Whole-plot PERMANOVAs were used to explore relationships between explanatory variables and 1949 and 1992 vegetation conditions; NMDS was used to visualize results. Using a forward selection model approach, the explanatory variable that significantly explained the greatest amount of variation was selected as the next term to include. Non-significant first-terms were continually evaluated in the subsequent model selection process. No interaction terms were included in whole-plot model building. Because of the small sample size used in these analyses, a maximum of three explanatory variables were included in the final model. To gain a more detailed understanding of what contributed to vegetation conditions, ownership and subbasin identity were excluded from initial steps in the model building process. Similar to latitude and longitude, the breadth of these variables makes it difficult to understand how these factors affect vegetation conditions. After three terms were included in the model, ownership and then subbasin identity were tested for significance. These analyses were completed independently for riparian and upland areas in each time period; a total of four models were created to explain each measure of vegetation structure and composition following methods previously outlined for whole-plot PERMANOVAs. NMDS and ordination overlays were used, as previously outlined, to visualize results.

Vegetation Changes (1949-1992) and Their Causes

Differences in 1949 and 1992 Vegetation Conditions

Split-plot PERMANOVAs, a type of repeated measures analysis, were used to determine if the two time steps were significantly different. Split-plot PERMANOVA evaluates the effect of time on experimental units without issues of pseudo-replication. For split-plot analyses, the experimental unit identifier and time were included as the first and second terms. Split-plot PERMANOVA followed all steps previously outlined for whole-plot PERMANOVA. This analysis was completed with all data, with riparian data, and with upland data – in order to test whether time periods were different regardless of area, whether riparian areas changed, and whether upland areas changed. The significance of the time identifier indicated whether the two time periods were different.

NMDS with NMDS overlays as well as bar plots were used to interpret the results. Ordihull was used to encompass each time period in order to look for ordination differences in location and dispersion. Bar plots provided summaries of data within each time period to allow for comparison.

Riparian Compared to Upland Changes in Vegetation Conditions

Bar charts were used to explore the data while split-plot PERMANOVAs determined whether riparian and upland changed differently. All protocols previously outlined for split-plot PERMANOVA were followed. Only the analysis with all data addressed whether riparian and upland areas changed differently. The interaction term between time and area (upland and riparian) was tested as the third order term after experimental unit identifier and time. This interaction term of time and area signified whether riparian and upland areas changed differently.

Processes Attributed To Changes in Vegetation Conditions

The final use of split-plot PERMANOVA was to determine which explanatory variables were correlated with the change in vegetation structure or composition; results were visualized in NMDS. Split-plot PERMANOVA followed the protocols and forward selection model building process outlined for whole-plot PERMANOVA. All terms after experimental unit identifier and time were interaction terms between time and a given explanatory variable. The significance of the interaction term indicated whether the explanatory variable affected the way vegetation structure or composition changed between the two time steps.

RESULTS

Range of Patterns and Processes in 1949 and 1992

Riparian Compared to Upland Vegetation Structure

Riparian and upland areas were not significantly different in either time period for any measure of vegetation structure or composition. This remained true whether looking at averaged 1949 and 1992 data, 1949 data, or 1992 data. The overlap in the location of hulls encompassing riparian and upland areas visualizes the similarity between these two areas (Figure 7, Figure 8). In the case of 1992 total crown cover (Figure 7b), 1992 overstory crown cover (Figure 7d), and 1949 and 1992 number of canopy layers (Figure 7e, f), upland areas were more dispersed. Though these differences were not statistically significant, the broader range of conditions and consequent greater diversity in the upland areas is ecologically significant. In contrast, riparian-wetland designation had a greater range of variability within the study riparian areas. While PERMANOVA found riparian and upland areas to be statistically similar, NMDS ordination helped to identify ecological differences.

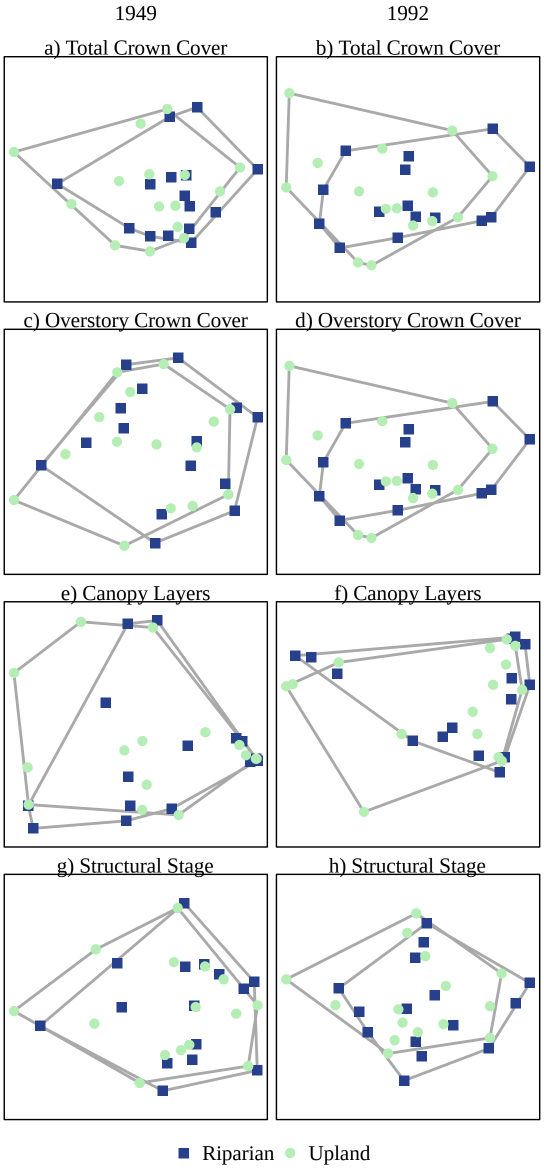


Figure 7: Ordinations of vegetation structure with riparian and upland overlay. Riparian and upland areas were not significantly different for any measure of vegetation structure. Averaged 1949 and 1992 were used for ordination.

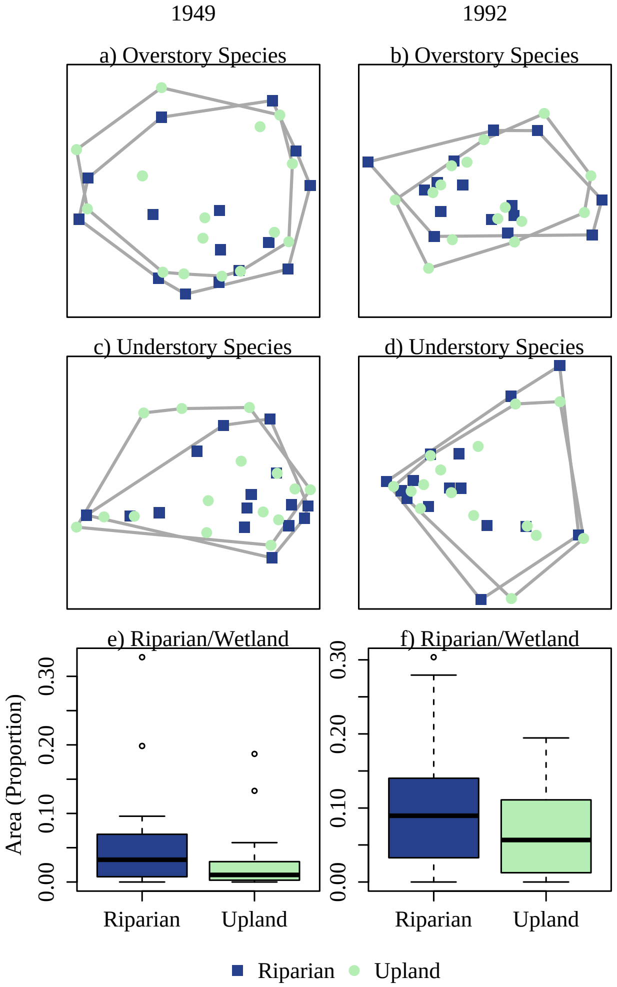


Figure 8: Ordinations of vegetation composition with riparian and upland overlay. Riparian and upland areas were not significantly different for any measure of vegetation composition. Averaged 1949 and 1992 were used for ordination.

Patterns of 1949 and 1992 Vegetation Structure

Differences between riparian and upland areas were more pronounced with total crown cover than overstory crown cover. In both areas and time periods the greatest amount of area (45-58%) fell between 70-90% total crown cover. In 1949 and 1992, riparian areas had 8-9% more area in this category than upland areas (Figure 9). With overstory crown cover, 73% of riparian areas and 76% of upland areas had 0-50% cover. In upland areas, overstory crown cover was more skewed towards lower cover; for the two time periods, the area-weighted average of overstory crown cover was 39% and 41% in riparian areas and 36% and 37% in upland areas (Figure 10). Regardless of area or time period, total crown cover was strongly skewed towards greater cover and overstory crown cover slightly skewed towards lower cover.

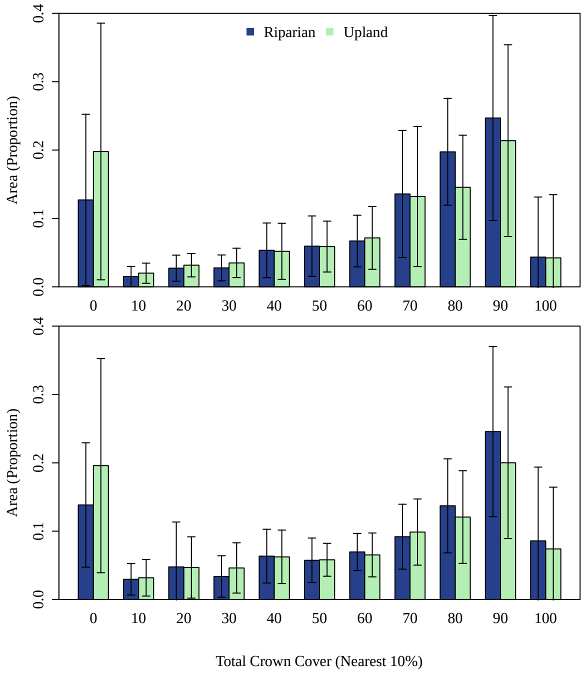


Figure 9: Total crown cover of riparian and upland areas in 1949 (top) and 1992 (bottom). Error bars represent one standard deviation.

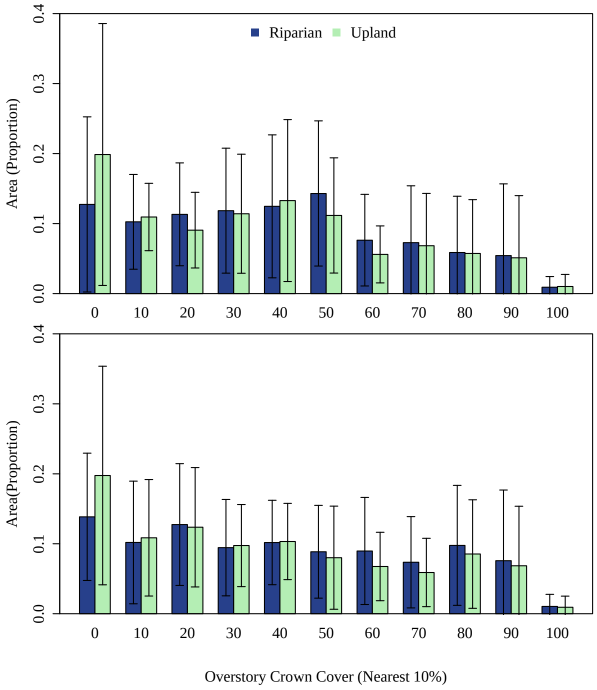


Figure 10: Overstory crown cover in 1949 (top) and 1992 (bottom). Error bars represent one standard deviation.

Riparian areas and upland areas were more similar in the number of canopy layers than in structural stage. In 1949, an average of 57% of a riparian unit and 54% of an upland unit had two canopy layers. In 1992, these numbers were slightly lower; 55% of a riparian unit and 53% of a riparian unit had two canopy layers (Figure 11). Understory re-initiation and young forest multi-story were the dominant structural stages in both areas, though understory re-initiation was more common in riparian areas. Riparian areas had 4.7% and 4.1% greater area categorized as understory re-initiation in 1949 and 1992 respectively. On average, old forest structures cumulatively composed less than 10% of the area. Riparian areas also had greater area under stem exclusion and old forest. Upland areas had notably more stand initiation and herb and shrub area (Figure 12).

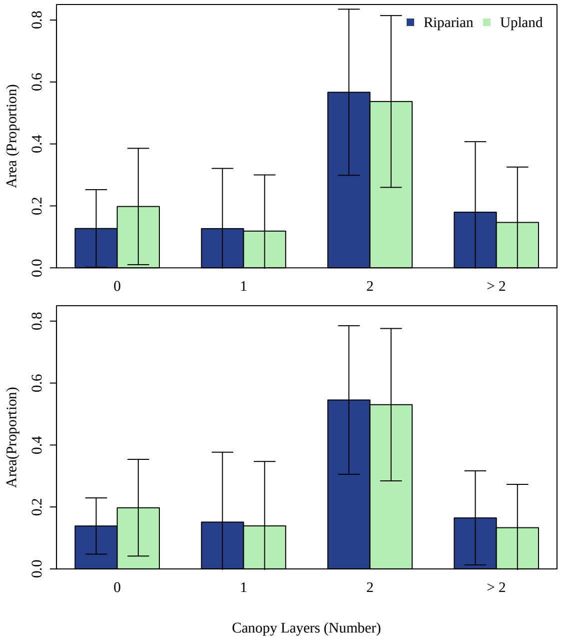


Figure 11: Number of canopy layers of riparian and upland areas in 1949 (top) and 1992 (bottom). Error bars represent one standard deviation.

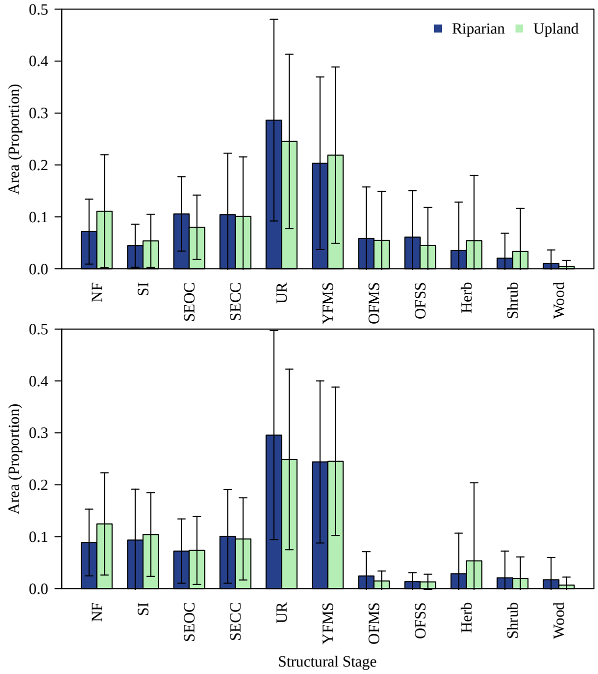


Figure 12: Structural stage of riparian and upland areas in 1949 (top) and 1992 (bottom). NF=non-forest, SI=stand initiation, SECC=stem exclusion open canopy, SECC=stem exclusion closed canopy, UR=understory re-initiation, YFMS=young forest multi-story, OFMS=old forest multi-story, OFSS=old forest single story. Error bars represent one standard deviation.

Overstory and understory species composition was similar between time periods and across areas. Douglas-fir was the dominant overstory species, covering 29.5% of the study area in 1949 and 33% of the area in 1992. On average, riparian areas had roughly 4.5% more of their area comprised of Douglas-fir than upland areas (Figure 13). Across subwatersheds, coverage by Douglas-fir ranged from less than one percent to 72.5% in 1949 and 0 to 58.2% in 1992. Slightly more common in riparian areas, ponderosa pine covered, on average, 11.2% of the study area. Ponderosa had the greatest range across subwatersheds, covering up to 69.8% of subwatersheds in 1949 and 71.1% in 1992 (Figure 13). Understory species composition was predominately Douglas-fir – grand fir – Pacific silver fir with small areas of subalpine fir – Engelmann spruce and less than 5% of other species. Douglas-fir – grand fir – Pacific silver fir covered an average of 48.9% of the study area in 1949 – 53% in riparian areas and 44.7% in upland areas - and 46% of the area in 1992 – 47.6% of riparian areas and 44.4% of upland areas (Figure 14). This category ranged from 8.7% to 80% of an experimental unit in 1949 and from 1.5% to 88% of a unit in 1949. With the exception of subalpine fir – Engelmann spruce, other species generally covered less than 5% of a unit (Figure 14).

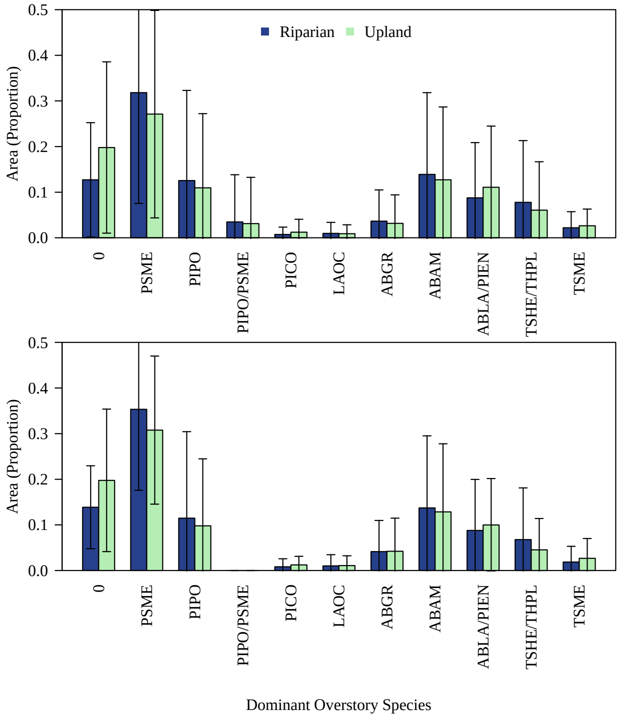


Figure 13: Overstory species in riparian and upland Areas in 1949 (top) and 1992 (bottom). 0=no classification, PSME=Douglas-fir, PIPO=ponderosa pine, PICO=lodgepole pine, LAOC=western larch, ABGR=grand fir, ABAM=Pacific silver fir, ABLA=subalpine fir, PIEN=Engelmann spruce, TSHE=western hemlock, THPL=western redcedar, TSME=mountain hemlock. Error bars represent one standard deviation.

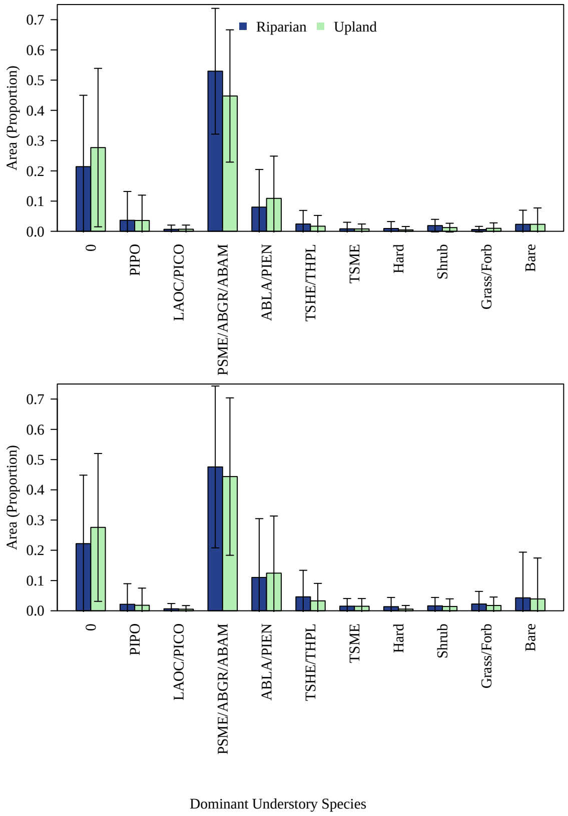


Figure 14: Understory species of riparian and upland areas in 1949 (top) and 1992 (bottom). Error bars represent one standard deviation.

Of all measures of structure and composition, riparian and upland areas were the most different in terms of riparian-wetland designation. In 1949, riparian-wetland designated areas covered 6.2% of riparian areas and 3.3% of upland areas. Riparian and upland areas were similarly different in 1992 – 10.3% of riparian areas were designated riparian-wetland, compared to 6.7% of upland areas (Figure 15). In 1949, the proportion of the study riparian unit designated as riparian-wetland ranged from 0 to 0.328; in the upland, the range of area designated as riparian-wetland was from 0 to 0.187. In 1992, the range in riparian-wetland areas was 0-30.4% in riparian areas and 0-19.4% in upland areas. Though riparian-wetland areas compose a small proportion of the study area, the differences between riparian and upland area are relatively large.

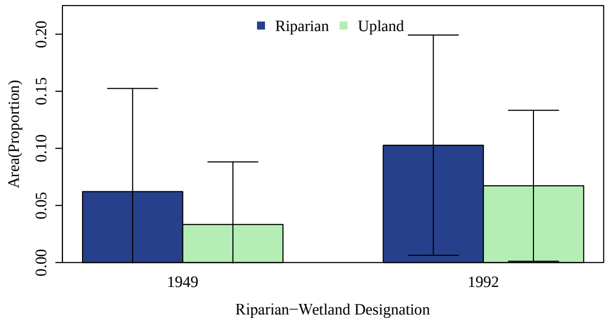


Figure 15: Area of riparian-wetland designation in riparian and upland areas in 1949 and 1992. Error bars represent one standard deviation.

Processes Affecting Patterns of Vegetation Structure

Spatial Autocorrelation

Mantel tests revealed significant spatial autocorrelation in most response matrices. With the exception of riparian-wetland designation, all measures of vegetation structure and composition exhibited significant spatial autocorrelation in 1949. In 1992, only total and overstory crown cover displayed spatial autocorrelation. Riparian and upland areas had similar levels of spatial autocorrelation. Though temporally varied, spatial autocorrelation was significant in most cases.

Table 1: Mantel Results for Spatial Autocorrelation for Different Data Subsets. Reported R2 are based on Pearson's Correlation Coefficient. Averages do not include non-significant results. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, "*" at 0.05, and "." at 0.1.

	Riparian 1949	Riparian 1992	Upland 1949	Upland 1992
Total Crown Cover	0.084 *	NS	0.110 *	NS
Overstory Crown Cover	0.079 *	NS	0.095 **	NS
Canopy Layers	0.152 **	0.090 *	0.156 **	0.069 *
Structural Stage	0.137 **	0.204 ***	0.170 **	0.152 **
Overstory Species	0.051 *	NS	0.128 **	NS
Understory Species	0.052 .	NS	0.040 .	NS
Riparian/Wetland	NS	NS	NS	NS

Evaluated as first terms in PERMANOVA models, longitude was more important to vegetation structure and longitude more important to vegetation composition. Consistent with Mantel results, spatial gradients were stronger with the 1949 than the 1992 data (Table 2). Though no neighborhood associations were detected with Mantel tests, latitude explained significant variation in 1949 riparian wetland designation. Latitude and longitude identify gradients that may be caused or compounded by elevation, logging history, conservation status, or fire prevalence.

Table 2: Summary of latitude and longitude as first terms in PERMANOVA models. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, "*" at 0.05, and "." at 0.1.

		Riparian 1949	Riparian 1992	Upland 1949	Upland 1992
Total Crown Cover	Lat.	0.137 .	0.162 .	NS	NS
	Long.	0.190 **	NS	0.212 **	NS
Overstory Crown Cover	Lat.	NS	NS	NS	NS
	Long.	0.197 **	NS	0.214 **	0.134 .
Canopy Layers	Lat.	NS	NS	NS	NS
	Long.	0.234 *	0.186 .	0.214 *	0.157 .
Structural Stage	Lat.	NS	NS	NS	NS
	Long.	NS	0.232 **	0.151 .	0.230 **
Overstory Species	Lat.	0.248 **	0.310 **	0.209 **	0.275 **
	Long.	0.168 *	NS	0.222 **	NS
Understory Species	Lat.	NS	0.142 .	NS	NS
	Long.	NS	NS	NS	NS
Riparian/Wetland	Lat.	0.301 *	NS	0.320 *	NS
	Long.	NS	NS	NS	NS

Elevation, Fire Prevalence, Logging History, Conservation Status, and Ownership

PERMANOVA results helped to reveal the relative important of each explanatory variable. Elevation explained the greatest amount of variation in the greatest number of measures of vegetation. Conservation status was particularly important in 1949 and logging history in 1992. Whereas fire helped to explain fewer measures of structure and composition, it had especially strong relationships with the number of canopy layers, understory species, and riparian-wetland areas. After including these detailed factors, ownership, subbasin identity, latitude, and longitude explained limited amounts of variation, especially in measures of composition.

In 1949, higher elevation was associated with greater density and vertical complexity. For total crown cover, average elevation explained 18.3% of variation (p=0.0037) in riparian areas and 24% of variation in upland areas (p=0.0019). Average elevation was also important for overstory crown cover, explaining 15.1% of variation in riparian areas (p=0.0308) and 16.3% of variation in upland areas (p=0.0147; Table 4). Higher average elevation generally corresponded to greater area with low and high levels (20-40, 70-100%) of total crown cover and mid to high (30-90%) levels of overstory crown cover. For upland areas only, highest elevation and average elevation cumulatively explained 42.9% of variation in the number of canopy layers (p=0.0013, p=0.0327; Table 4). The area with greater than two canopy layers was greatest from 1,000-2,000m and more common above 1250m than below 1000m; more than two canopy layers was also positively correlated with high elevation. Highest elevation further explained 24.4% of variation in structural stage (p=0.0001; Table 4) and was associated with greater area of understory re-initiation and young forest multi-story (most common from 1100-1400m).

Relationships between elevation and vegetation structure were similar in 1992 to the 1949 relationships. In riparian areas, the presence of high elevation explained 38.2% of variation in total crown cover (p=0.0002), 19.9% of variation in overstory crown cover (p=0.0163), 24.7% of variation in number of canopy layers (p=0.0006), and 19.7% of variation in structural stage (p=0.0009). In the upland, average elevation explained 30.2% of variation in total crown cover (p=0.0001), 20.9% of variation in overstory crown cover (p=0.0013), and 22.2% of variation in structural stage (p=0.0007). High elevation explained 33.7% of variation in number of canopy layers (p=0.0014; Table 5). Units with high elevation tended to have more 80-100% total crown cover, more 50-90% overstory crown cover, and more than two canopy layers. In addition, higher elevation tended to have more understory re-initiation and old forest structures and less area of non-forest, stand initiation, and stem exclusion.

Elevation was a critical variable in explaining variation in vegetation composition in both 1949 and 1992. In riparian areas, average elevation explained 19.9-25.8% of variation in overstory species (p=0.0010, p=0.0013),) and 14.7-17% of variation in understory species (p=0.0906, p=0.0074). In the upland, average elevation explained 19.5-26.5% of variation in overstory species composition (p=0.0008, p=0.0002). High elevation in 1949 and average elevation in 1992 explained, on average, 25.4% of variation in understory species (p=0.0148, p=0.0012). Average elevation explained also 21.8% of variation in riparian-wetland designation in 1949 riparian areas (p=0.0455; Table 4, Table 5). Relative to other species, ponderosa pine occurred at relatively low elevations, from 9-1200m. Douglas-fir was most common on mid elevations, from 1,100-1,300m, while Pacific silver fir covered mid to high elevations above 1,100m. Subalpine fir – Engelmann spruce, western hemlock – western redcedar, and mountain hemlock were found almost exclusively above 1200m (Figure 16). In the understory, similar associations existed – ponderosa pine tended to be at lower elevations (< 1,150m), subalpine fir – Engelmann spruce at high elevations (> 1,300m). Douglas-fir – grand fir – Pacific silver fir ranged across all elevations, but was most abundant between 1,100 and 1,300m (Figure 17). The positive relationship between elevation and riparian-wetland designated area was particularly strong with the riparian corridors of this study (Figure 18).

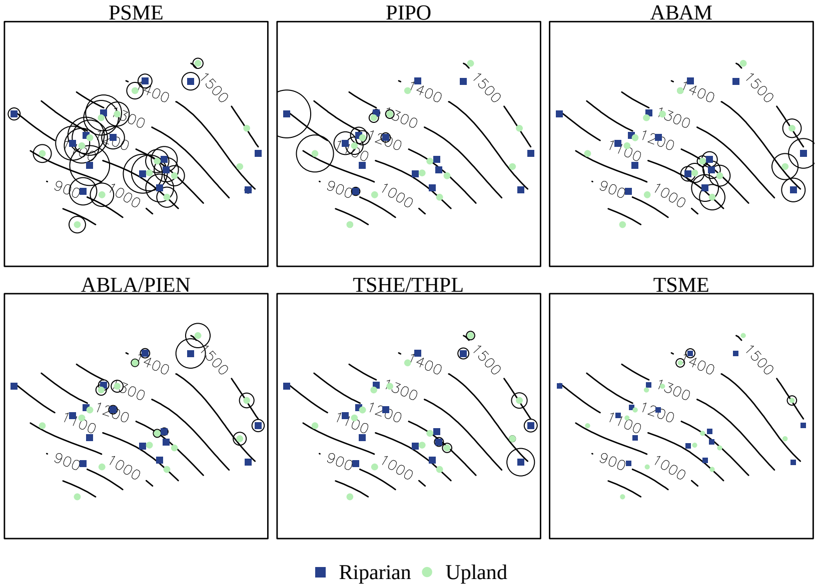


Figure 16: Overstory species and average elevation, 1992. Surfaces are elevation in meters. Circles are proportional to given species abundance.

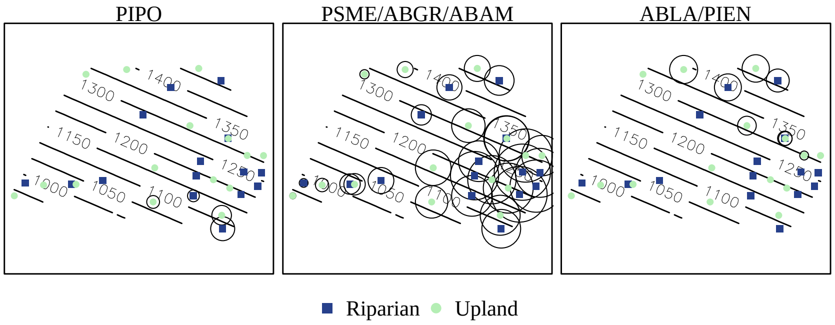


Figure 17: Understory species and average elevation, 1949. Surfaces are average elevation in meters. Circles are proportional to given species abundance.

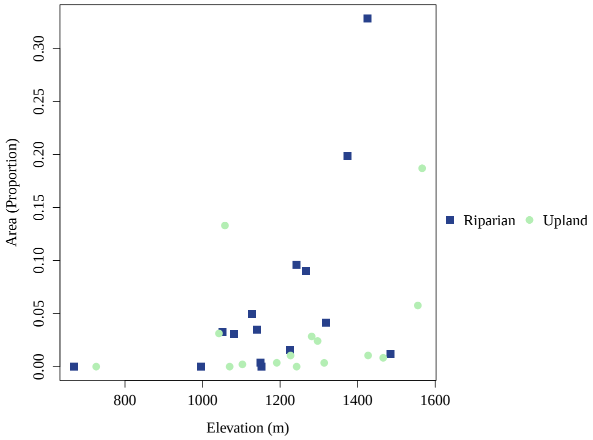


Figure 18: Riparian-wetland designation and elevation 1949.

Greater conservation was associated with low overstory crown cover and high total crown cover, whereas less stringent conservation was associated with extremes of canopy layers and structural stages. In the upland, the area legally protected explained 13.6% of variation in overstory crown cover (p=0.0338; Table 4) in 1949 and 17% of variation in overstory crown cover in 1992 (p=0.0154; Table 5). Legal protection was positively correlated with low cover (10-50%). The area managed for conservation explained 13.7% of variation in upland 1992 total crown cover (p=0.0186; Table 5) and was positively correlated with higher total crown cover (70, 90-100%, Figure 19). In 1949 riparian areas, area of partial retention explained 31.6% of variation in the number of canopy layers (p=0.0005) and 28.6% of variation in structural stage (p=0.00001; Table 4). Area of partial retention was negatively correlated with 2 canopy layers and positively correlated with late structural stages (stem exclusion open canopy, stem exclusion closed canopy, old forest multi-story, old forest single-story, and shrub, herb, and woodland). The area modified explained significant variation in the number of canopy layers, 13.1% in 1949 (p=0.0274; Table 4) and 14.1% in 1992 (p=0.0327; Table 5). The area modified also explained significant variation in structural stage, 16% in 1949 (p=0.0029; Table 4) and 11% in 1992 (p=0.0354; Table 5). The area modified was positively correlated with zero or more than two canopy layers and stem exclusion open canopy and old forest multi-story (as well as herb, shrub, woodland). Conservation status did not illuminate clear divides in vegetation structure.

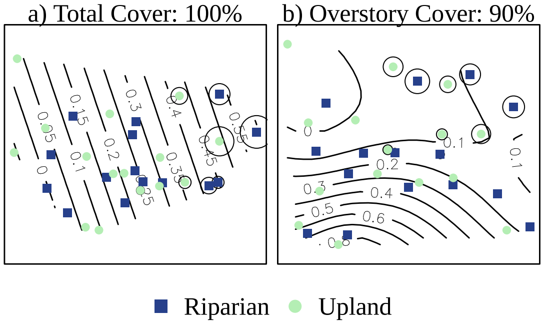


Figure 19: Conservation status and vegetation structure 1992. A) Ordination surface is proportion of area managed for conservation. Circles are proportional to area with 100% total crown cover. B) Ordination surface is proportion of area legally protected. Circles are proportion to area with 90% total crown cover.

For composition, greater conservation was associated with riparian-wetland designation and ponderosa pine. In 1992 riparian areas only, the area legally protected was strongly positively correlated with greater riparian-wetland areas (p=0.0006, R^2=0.610; Table 5). The area of partial retention explained significant variation in overstory composition in both riparian areas - 15.1% in 1949 (p=0.0162) and 17% in 1992 (p=0.0165) – and upland areas, 12% in 1949 (p=0.0318) and 10.9% in 1992 (p=0.0449; Table 4, Table 5). In 1949, the area modified explained an additional 10.8% of variation (p=0.0599) in riparian areas and 14.3% of variation in upland areas (p=0.0087) in overstory species composition. Area modified also explained 13.6% of variation in understory species composition (p=0.0148; Table 4). Ponderosa pine was most abundant with less area of partial retention while the inverse was true of Pacific silver fir. Douglas-fir ranged across all levels of partial retention (Figure 20). Douglas-fir was most abundant in areas with low levels of modification and ponderosa pine was most abundant with low to mid levels of modification (5-25% of experimental unit). Ponderosa pine – Douglas-fir was most abundant with greater levels of modification, but few sites contained this overstory class, making interpretation difficult.

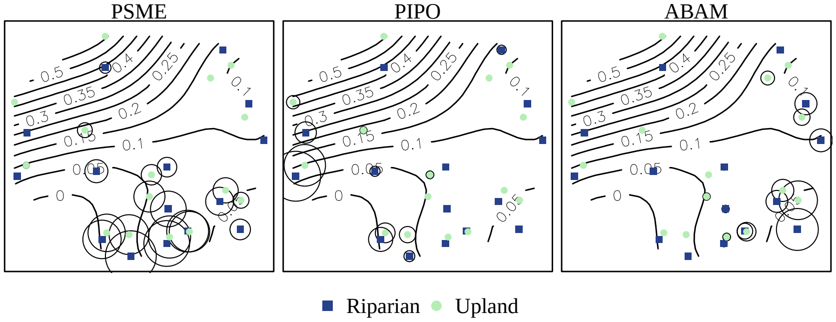


Figure 20: Relationships between area modified and overstory species composition, 1949. Ordination surfaces are proportion of the experimental unit that has been modified. Circles are proportional to area of structural component indicated in title.

Logging history was important in explaining only vegetation structure in the later time period and was particularly important in upland areas. Selective harvesting explained 10.3% of variation in total crown cover (p=0.0537) within upland areas. The amount of regeneration logging explained 26.5% of variation in structural stage (p=0.0001) in riparian areas. In the upland, regeneration logging explained 15.2% and 24.3% of variation in the number of canopy layers and structural stage, respectively (p=0.0347, p=0.0009; Table 5). Selective harvesting was positively correlated with 30-80% crown cover. Regeneration logging was positively correlated with two or more canopy layers and an array of structural stages including both early and old structures.

Logging history was the least important variable in explaining vegetation composition, only predicting significant variation in upland overstory and understory species composition in 1992. The area selectively harvested explained 17.2% of variation in overstory species (p=0.0063)), whereas the area regeneration logged explained 13.7% of variation in understory species (p=0.0425; Table 5). Of all overstory species, Douglas-fir and ponderosa pine had relatively greater abundances with greater areas of selective harvesting. Conversely, Pacific silver fir and subalpine fir – Engelmann spruce were strongly associated with lower levels of selective harvesting (Figure 21). In the understory, Douglas-fir – grand fir – Pacific silver fir ranged across most levels of regeneration logging. Subalpine fir – Engelmann spruce was associated primarily with low levels of regeneration logging (Figure 22). Logging appears to target true firs and spruce, while leaving Douglas-fir and ponderosa pine.

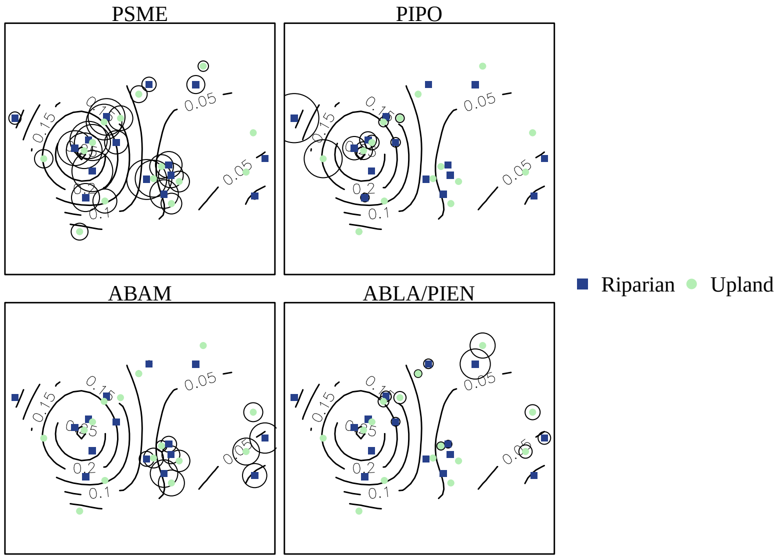


Figure 21: Overstory species composition and selective harvesting. Surfaces are proportion of the experimental unit with selective harvesting. Circles are proportional to the abundance of the species indicated.

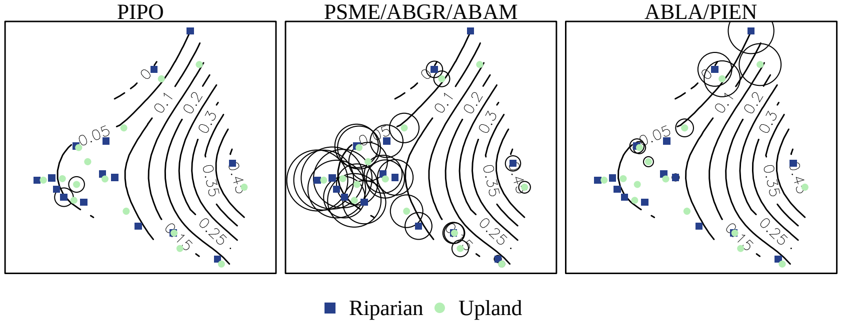


Figure 22: Understory species composition and regeneration logging. Surfaces are proportion of the experimental unit with regeneration logging. Circles are proportional to the abundance of the species indicated

Fire prevalence explained a significant amount of variation in the number of canopy layers, but not other structural measures. As fire data did not precede 1949, fire could only be used to understand 1992 vegetation. In riparian areas, the number of fire events explained 35.9% of variation in the number of canopy layers (0.0007; Table 5). The number of fires was positively correlated with zero and one canopy layer and negatively correlated with two and more than two canopy layers (Figure 23). Fire prevalence did not explain significant variation in riparian total crown cover, overstory crown cover, structural stage, or any measure of upland vegetation structure.

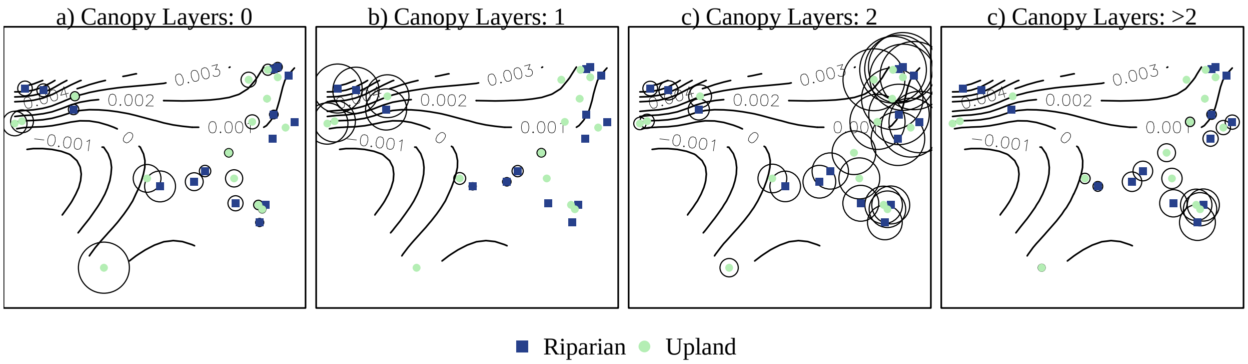


Figure 23: Number of fires and canopy layers. Ordination surface is the number of fire events per hectare. Circles are proportional to area with number of canopy layers indicated.

Fire prevalence explained substantial variation in both riparian and upland 1992 vegetation composition. Fire prevalence did not help to explain overstory species composition. In riparian areas, the number of fires explained 19.5% of variation (p=0.0139) and the area burned explained an additional 12.4% (p=0.0509) in understory species (Table 5). The number of fires was positively correlated with understory categories not classified (0), bare, and subalpine fir – Engelmann spruce; the area burned was positively correlated with only bare understory. Overall fire prevalence (the principal component) explained 24.6% of variation in upland riparian-wetland designation (p=0.0600). Area designated as riparian-wetland was positively correlated with fire prevalence (Figure 24). As a whole, increased fire was associated with increased bare and subalpine fir – Engelmann spruce in the riparian understory and increased riparian-wetland designation in the upland.

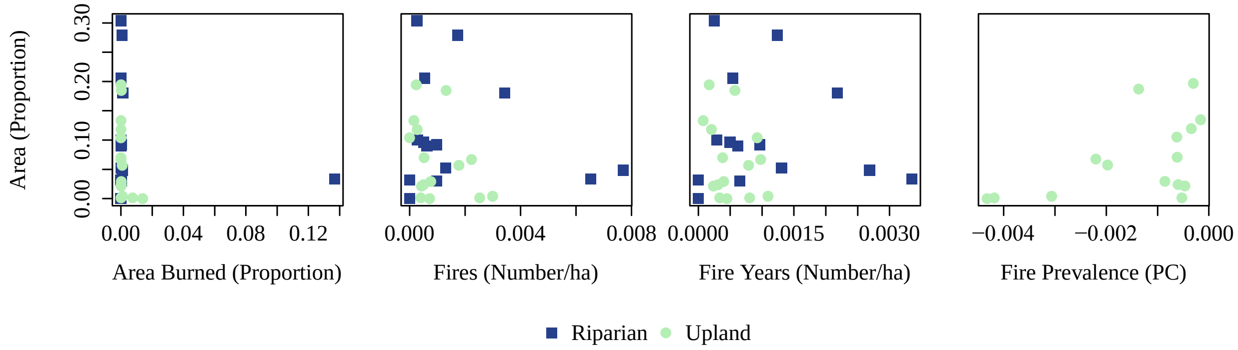


Figure 24: Upland riparian-wetland designation and fire variables.

Following testing of more detailed explanatory variables, federal ownership explained significant variation in total crown cover, overstory crown cover, structural stage, and overstory species. In 1949, the area of federal ownership explained 11.7% of variation in total crown cover (p=0.0400) and 15.3% of variation in structural stage (p=0.0030) in riparian areas. In the upland, federal ownership explained significant variation in overstory crown cover (p=0.0392, R^2=0.134), structural stage (p=0.0005, R^2=0.216), and 9.8% of variation in overstory composition (p=0.0608; Table 4). In 1992, ownership explained 10.1% of variation in total crown cover (p=0.0860) in riparian areas and 14.2% of variation in overstory crown cover (p=0.0154; Table 5). Greater federal ownership was correlated with both extremes of total crown cover, greater overstory crown cover (70-100%), and with earlier structural stages (non-forest, stand initiation, stem exclusion closed canopy, understory re-initiation, and young forest multi-story). Federal ownership was also associated with greater abundances of Pacific silver fir, subalpine fir – Engelmann spruce, western hemlock – western redcedar. Ponderosa pine had the greatest abundance at mid levels of federal ownership and grand fir was most abundant in areas with little to no federal ownership (and nearly complete tribal ownership). Ownership was more important in upland than riparian areas, in 1949 than 1992, and with structural than compositional measures.

The broadest explanatory variable tested, subbasin identity, explained significant variation in few measures of vegetation structure. For 1949 conditions, subbasin identity explained significant variation in riparian ($p=0.0244$, $R^2=0.210$) and upland ($p=0.422$, $R^2=0.213$) total crown cover as well as 18.3% of variation in riparian number of canopy layers ($p=0.0433$; Table 4). For 1992 riparian conditions, subbasin identity explained 14.5% of variation in number of canopy layers ($p=0.0453$) and 14.7% of variation in structural stage ($p=0.075$; Table 5). The Lower Yakima had the greatest area in zero and 60-70% total crown cover and with zero and more than two canopy layers; this subbasin also had the only herb, shrub, woodland component. The Upper Yakima had the most areas with one canopy layer and 90% total crown cover, and tended to be composed of early structural stages (non-forest, stand initiation, stem exclusion open canopy, stem exclusion closed canopy). The Naches subbasin had the greatest area with understory re-initiation and young-forest multi-story as well as the greatest area with at least two canopy layers and high total crown cover. A variety of reasons may account for these subbasin differences – climate, cultural history, and natural disturbance – thus the significance of subbasin identity is a starting point in understanding the forces shaping vegetation structure.

Tested as final terms, latitude and longitude accounted for little additional variation. In riparian areas in 1949, latitude explained 12.1% of variation in total crown cover ($p=0.0150$), 7.5% of variation in structural stage ($p=0.0313$), and 11.5% of variation in overstory species ($p=0.0258$). In the upland, latitude explained 12.2% of variation in total crown cover ($p=0.0238$) and 32% of variation in riparian-wetland designation ($p=0.0348$). In 1992, latitude explained 6.4% of variation in the number of canopy layers ($p=0.0636$) and 11.7% of variation in structural stage ($p=0.0058$). In 1949, longitude explained 5.6% of variation in riparian structure stage ($p=0.0880$) and, in the upland, 10% of variation in the number of canopy layers ($p=0.0655$) and 9.1% in overstory species ($p=0.0591$; Table 3). More northern sites had low to mid total crown cover (0, 20, 40-70%), complex structural stages (young forest multi-story and old forest multi-story as well herb, shrub, and woodland), and greater area of Douglas-fir, ponderosa pine, lodgepole pine, grand fir in both the understory and overstory. There was greater area of riparian-wetland designation to the south. More western sites had greater area of 1-2 canopy layers as well as early (non-forest, stand initiation, stem exclusion closed canopy, understory re-initiation) and late structural stages. More western sites had greater area of Douglas-fir, subalpine fir, and hemlock. Once more detailed variables are included in the model, latitude and longitude explain minimal variation in measures of structure and composition.

Table 3: Significance of latitude and longitude as final terms in structure and composition models. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

		Riparian 1949	Riparian 1992	Upland 1949	Upland 1992
Total Crown Cover	Lat.	0.121 *	NS	0.122 *	NS
	Long.	NS	NS	NS	NS
Overstory Crown Cover	Lat.	NS	NS	NS	NS
	Long.	NS	NS	NS	NS
Canopy Layers	Lat.	NS	0.064 .	NS	NS
	Long.	NS	NS	0.100 .	NS
Structural Stage	Lat.	0.075 *	0.117 **	NS	NS
	Long.	0.056 .	NS	NS	NS
Overstory Species	Lat.	0.115 *	NS	NS	NS
	Long.	NS	NS	0.091 .	NS
Understory Species	Lat.	NS	NS	NS	NS
	Long.	NS	NS	NS	NS
Riparian/Wetland	Lat.	NS	NS	0.320 *	NS
	Long.	NS	NS	NS	NS

Elevation, conservation status, fire prevalence, and logging history all helped to explain variation in vegetation structure and composition. Higher elevation sites were associated with higher total crown cover, mid to high overstory crown cover, two or more canopy layers, and greater abundance of true firs, hemlock, and redcedar, whereas low elevation had greater abundance of ponderosa pine. Greater conservation was associated with low overstory crown cover, high total crown cover, ponderosa pine, and riparian-wetland areas; less stringent conservation was associated with extremes of canopy layers and structural stages. Logging and fire prevalence were important in explaining only 1992 vegetation conditions. Selective logging was positively correlated with ponderosa pine and Douglas-fir overstory; regeneration logging was negatively associated with two or more canopy layers and subalpine fir – Engelmann spruce understory. Regeneration logging was positively correlated with two or more canopy layers and an array of structural stages including both early and old structures. Increased fire prevalence was associated with less than two canopy layers, increased bare and subalpine fir – Engelmann spruce in the understory, and increased riparian-wetland designation.

Beyond the specific associations between process and pattern, the relative significance of each process is important. Elevation was consistently more important than conservation status, logging history, or fire prevalence. Whereas conservation status was the second greatest predictor of vegetation conditions in 1949, logging history was important to 1992 vegetation. Fire prevalence helped to explain fewer measures of structure and composition, but had particularly strong relationships with the number of canopy layers, understory species, and riparian-wetland designation. The relative roles of these factors shapes our understanding of the landscape.

Table 4: Explanatory variables included in final models for 1949 vegetation structure and composition. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1. Dark blue variables are related to elevation, green variables are related to conservation status, federal ownership is in light purple, and subbasin identity is in light blue.

	Riparian 1949			Upland 1949		
Total Crown Cover	Average Elevation	0.183	**	Average Elevation	0.240	**
	Federal Ownership	0.117	*	Subbasin	0.213	*
	Subbasin	0.210	.			
	Variation Explained	0.511		Variation Explained	0.453	
Overstory Crown Cover	Average Elevation	0.151	*	Average Elevation	0.163	*
				Legally Protected	0.136	*
				Federal Ownership	0.134	*
	Variation Explained	0.151		Variation Explained	0.433	
Canopy Layers	Partial Retention	0.316	***	Highest Elevation	0.300	**
	Modified	0.131	**	Modified	0.141	*
	Subbasin	0.183	*	Average Elevation	0.129	*
	Variation Explained	0.630		Variation Explained	0.569	
Structural Stage	Partial Retention	0.286	***	Highest Elevation	0.244	***
	Modified	0.160	**	Modified	0.110	*
	Federal Ownership	0.152	**	Federal Ownership	0.216	***
	Variation Explained	0.598		Variation Explained	0.571	
Overstory Species	Average Elevation	0.199	***	Average Elevation	0.195	***
	Partial Retention	0.151	*	Modified	0.143	**
	Modified	0.108	.	Partial Retention	0.120	*
				Federal Own.	0.098	.
	Variation Explained	0.458		Variation Explained	0.458	
Understory Species	Average Elevation	0.147	.	High Elevation	0.255	*
				Modified	0.136	.
	Variation Explained	0.147		Variation Explained	0.391	
Riparian/ Wetland	Average Elevation	0.273	.	*Latitude*	*0.320*	*
	Variation Explained	0.273				

Table 5: Explanatory variables included in final models for 1992 vegetation structure. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1. Dark blue variables are related to elevation, green variables are related to conservation status, orange variables are related to logging, red variables are related to fire, federal ownership is in light purple, and subbasin identity is in light blue.

	Riparian 1992			Upland 1992		
Total Crown Cover	Highest Elevation	0.382	***	Average Elevation	0.302	***
	Federal Ownership	0.101	.	Selective Harvest	0.103	.
				Mng for Conservation	0.137	*
	Variation Explained	0.414		Variation Explained	0.471	
Overstory Crown Cover	Highest Elevation	0.199	*	Average Elevation	0.209	***
				Legally Protected	0.170	**
				Federal Ownership	0.142	*
	Variation Explained	0.199		Variation Explained	0.506	
Canopy Layers	Number of Fires	0.359	***	Highest Elevation	0.337	**
	Highest Elevation	0.247	***	Regeneration Logging	0.152	*
	Subbasin	0.145	*			
	Variation Explained	0.751		Variation Explained	0.489	
Structural Stage	Regeneration Logging	0.265	***	Regeneration Logging	0.243	***
	Highest Elevation	0.197	***	Average Elevation	0.222	***
	Subbasin	0.147	.			
	Variation Explained	0.610		Variation Explained	0.465	
Overstory Species	Average Elevation	0.258	**	Average Elevation	0.265	***
	Partial Retention	0.170	*	Selective Harvest Log	0.172	**
				Partial Retention	0.109	*
	Variation Explained	0.429		Variation Explained	0.545	
Understory Species	Number of Fires	0.196	*	Average Elevation	0.253	**
	Average Elevation	0.170	**	Regeneration Log	0.137	*
	Fire Acres	0.124	.			
	Variation Explained	0.489		Variation Explained	0.390	
Riparian/ Wetland	Legally Protected	0.610	**	Fire PC	0.246	.
	Variation Explained	0.610		Variation Explained	0.246	

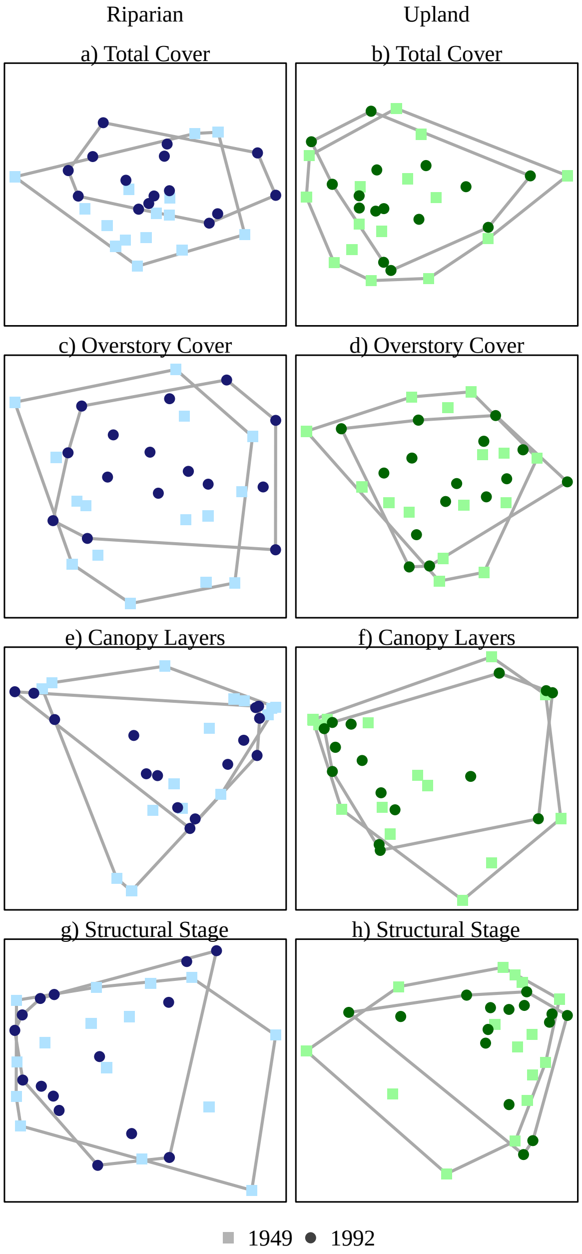
Vegetation Changes (1949-1992) and Their Causes

Differences in 1949 and 1992 Vegetation Structure and Composition

Conditions were significantly different in 1949 and 1992 in terms of total crown cover, overstory crown cover, and structural stage. There was no significant difference in the number of canopy layers or in any measure of composition between time periods. This remained true regardless of the data subset used. Across the three measures of vegetation structure for which the two time periods were different, time period explained an average of 3.4% of the variation in riparian areas, 2.1% of the variation in upland areas, and 2.6% of variation across the entire data set (Table 6). For total crown cover, overstory crown cover, and structural stage, the differences are primarily in dispersion rather than location. Characterized by more dispersed ordinations, 1949 conditions were more diverse than those in 1992 (Figure 25). Though not statistically different, there were ecologically significant differences in other measures of structure and composition. The number of canopy layers and overstory species were more diverse in 1949 (Figure 25), while understory species and riparian-wetland designation were more heterogeneous in 1992 (Figure 26). As a whole, the change in dispersion was more pronounced in riparian than in upland areas.

Table 6: Variation explained by time for each measure of vegetation structure in whole-plot PERMANOVA. Averages are of significant results. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

	All Data R^2	Riparian R^2	Upland R^2
Total Crown Cover	0.032 **	0.048 **	0.021 *
Overstory Crown Cover	0.025 *	0.029 *	0.023 .
Number of Canopy Layers	NS	NS	NS
Structural Stage	0.021 **	0.026 *	0.019 *
Overstory Species	NS	NS	NS
Understory Species	NS	NS	NS
Riparian-Wetland Designation	NS	NS	NS



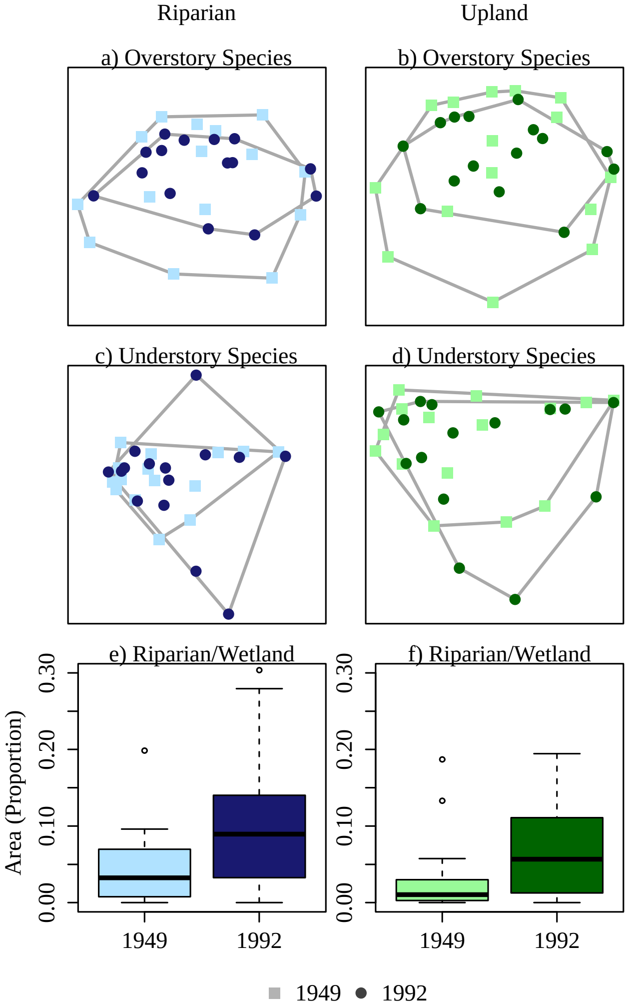


Figure 26: Difference between historical and current time periods for each areas and each measure of vegetation composition.

Figure 25: Difference between historical and current time periods for riparian and upland areas for each measure of vegetation composition.

Riparian Compared to Upland Changes in Vegetation Structure

Riparian and upland areas did not change significantly differently from 1949 to 1992. This is, in part, because conditions were similar between the two time periods. Visual comparison of riparian and upland conditions confirms that these areas changed similarly.

Changes in location and dispersion were similar between riparian and upland units (Figure 25, Figure 26). Statistically and ecologically, riparian and upland areas did not appear to change differently from one another.

Changes in Vegetation Structure from 1949 to 1992

The greatest changes in total crown cover were in the upper categories of cover. Change in 0-60% cover was limited, at most 2.1%. In both riparian and upland areas, the proportion of an experimental unit with 10-40% total crown cover increased, but only slightly. Upper cover classes from 70-100% saw more drastic changes. Area with 70 and 80% total crown cover had the greatest decreases. In riparian areas, the amount of 70% cover decreased from 13.6% to 9.1% cover; the amount of 80% cover decreased from 19.7% to 13.7%. Complete crown cover (100%) had the greatest increase, 4.3%, from 4.3% in 1949 to 8.6% in 1992. In the majority of cover categories, riparian areas changed more than their upland counterparts. Though change was still relatively small (≤6%), 70-100% total crown cover had the greatest changes from 1949-1992 (Figure 27).

Changes in overstory crown cover were smaller and less consistent than those in total crown cover. In riparian areas, the area-weighted average increased slightly from 39% to 41%; in upland areas, the averaged increased from 35.6% to 36.8%. In both riparian and upland areas, the area with 0%, 20%, 60%, 80% and 90% crown cover increased. In riparian areas, the greatest increase was in 80-90% crown cover, which changed 3.9% and 2.2% respectively. In upland areas, the greatest increase in area, from 9.4% to 12.4%, was in 20% cover. The greatest decreases in areas were in 30-50% crown cover. Riparian areas with 50% cover decreased, on average, from 14.3% of an experimental unit to 8.9%. As with total crown cover, the majority of shifts are more extreme in riparian areas than in upland areas (Figure 28).

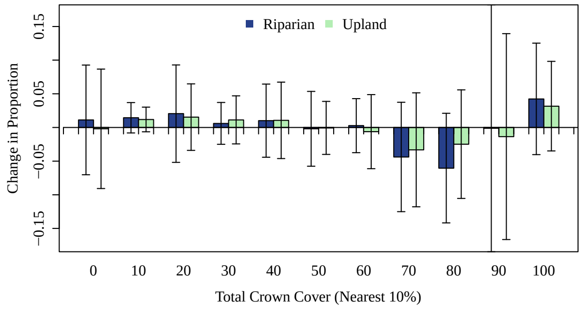


Figure 27: Riparian and upland changes in total crown cover from 1949 to 1992. Error bars represent one standard deviation.

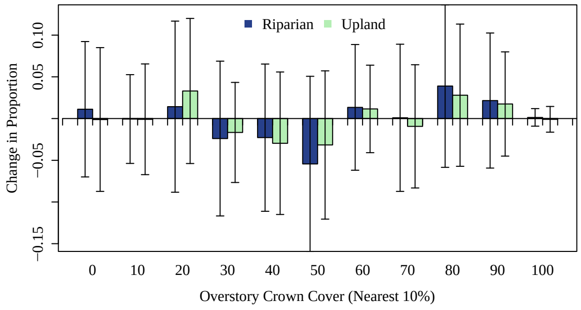


Figure 28: Riparian and upland changes in overstory crown cover from 1949 to 1992. Error bars represent one standard deviation.

Between 1949 and 1992, the area with 0-1 canopy layers increased while the area with ≥ 2 decreased. The composition of canopy layers of experimental units did not change significantly. The area with no canopy layers increased in riparian areas slightly, from 12.7% to 13.9%. The increase in area with one canopy layer was larger, though still relatively minor, between 2% and 2.5%. The area with two or more canopy layers decreased. The greatest decrease, in riparian areas with two canopy layers, from 56.7% to

54.6%, is likely not ecologically meaningful (Figure 29). In all canopy categories, riparian areas changed more than their upland counterparts. Though the distribution of canopy layers changed over the 43 year time period, the changes are neither statistically nor ecologically significant.

Across structural stages, the area of young or developing stages generally increased while the area of old structural stages decreased. The greatest increases were in non-forest, stand initiation, and young forest multi-story. Averaging across areas, area of non-forest increased 1.6% and stand initiation increased 5%. Young-forest multi-story increased 4.1% in riparian and 2.7% in upland areas. The greatest decreases were in stem exclusion open canopy and both old forest structures. In riparian areas, the area with stem exclusion open canopy decreased from 10.6% to 7.2%; in the upland, the change was far less drastic, from 8% to 7.4%. Old forest multi-story decreased, on average, 3.7%. Old forest single-story decreased, on average, 3.9%. These old forest structures made up a small component of the landscape in 1949; a loss of 3.7-3.9% means that more than half of the old forest structure that existed in 1949 was no longer present in 1992. As with other measures of vegetation structure, riparian areas generally changed more than their upland counterparts (Figure 30).

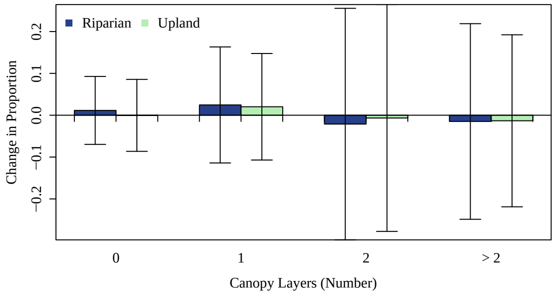


Figure 29: Riparian and upland changes in number of canopy layers from 1949 to 1992. Error bars represent one standard deviation.

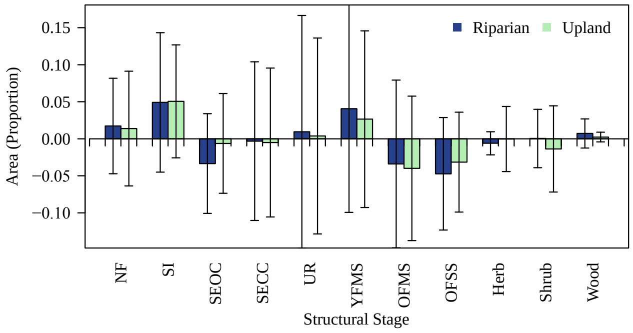


Figure 30: Riparian and upland changes in structural stages from 1949 to 1992. Error bars represent one standard deviation.

The greatest changes in overstory species composition, while still relatively small, were in Douglas-fir and ponderosa pine abundance. Both ponderosa pine and ponderosa pine – Douglas-fir decreased from 1949 to 1993; ponderosa pine decreased from 11.7% of the study area to 10.6% of the study area. Ponderosa pine – Douglas-fir did not cover any area in 1992 and subsequently decreased 3.5% in riparian areas and 3.1% in upland areas. There were, however, corresponding increases in Douglas-fir area, from 29.5% to 33%. This averaged change, approximately 3.5%, is relatively small given the area covered by Douglas-fir. Across grand fir – Pacific silver fir, subalpine fir – Engelmann spruce, and western hemlock – western redcedar, riparian areas changed slightly less than their upland counterparts (Figure 31). These changes were relatively small, around 1%; larger changes in Douglas-fir and ponderosa pine remained less than 5%.

More categories of understory composition changed from 1949 to 1992, though the changes remained relatively small. Four categories of understory composition increased moderately, between 1.1% and 2.3% (Subalpine fir – Engelmann spruce, western hemlock

– western redcedar, grass – forb, and bare ground). The only substantial decreases were in ponderosa pine (1.6%) and Douglas-fir – grand fir – Pacific silver fir (2.9%). In all of these species, riparian areas changed more than their upland counterparts (Figure 32). Yet the changes are all relatively small; the represented shifts in understory species composition are neither statistically significant nor ecologically meaningful.

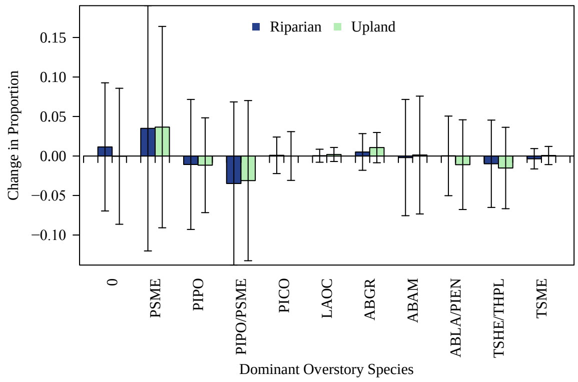


Figure 31: Riparian and upland changes in overstory species from 1949 to 1992. Error bars represent one standard deviation.

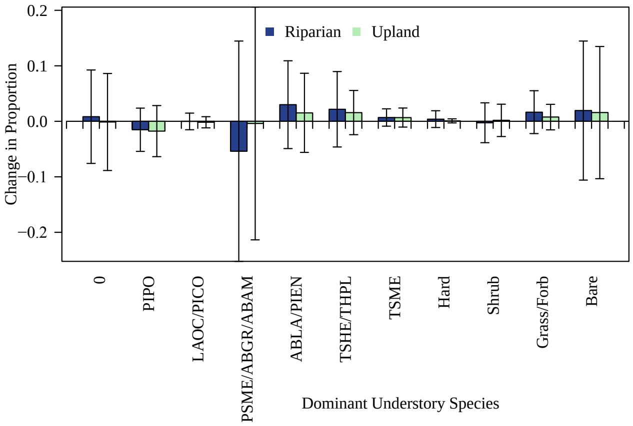


Figure 32: Riparian and upland changes in understory species from 1949 to 1992. Error bars represent one standard deviation.

Relative to shifts in overstory and understory composition, changes in riparian-wetland designation were larger. In riparian areas, riparian-wetland designation increased from 6.2% of the study area to 10.3%. Area designated as riparian-wetland more than doubled in the upland, from 3.3% to 6.7% (Figure 33). Though not statistically significant, increases in riparian-wetland designation were relatively large, representing an ecologically meaningful change.

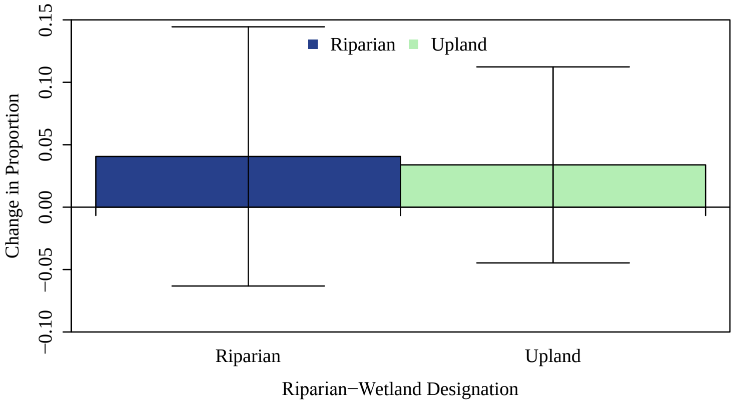


Figure 33: Riparian and upland changes in riparian-wetland designation, 1949-1992. Error bars represent one standard deviation.

Processes Attributed To Significant Changes in Vegetation Conditions

Models built to explain changes in overstory crown cover, total crown cover, and structural stage between 1949 and 1992 included fire prevalence, logging history, conservation status, and elevation. Models were not built for non-significant changes (canopy layers, overstory species, understory species, riparian-wetland designation). Fire prevalence – area burned in riparian areas and number of fire years in upland areas – was included in nearly every model and cumulatively explained the greatest amount of change. Logging was similarly important in explaining change; the area with no apparent logging and area modified were the only logging variables included in any model. Conservation status and elevation were important explanatory variables, but were less consistently included in models. The models suggest areas for further exploration in understanding vegetation changes.

In riparian areas, fire prevalence emerged as the most important predictor of change in vegetation. The proportion of the area burned explained significant amounts of variation in the change in total crown cover ($p=0.0002$, $R^2=0.097$), in overstory crown cover ($p=0.00001$, $R^2=0.091$), and in structural stage ($p=0.0693$, $R^2=0.027$; Table 7). Area burned was negatively correlated with high total crown cover (50-80, 100%). Correlations with overstory crown cover were inconsistent. Area burned was positively correlated with non-forest, stand initiation, stem-exclusion open canopy, old-forest multi- story and old-forest single-story and negatively correlated with stem-exclusion closed canopy, understory re-initiation, young forest multi-story, shrub, herb, and woodland. In riparian areas, fire prevalence decreased total crown cover and promoted early and old forest structures.

In the upland, fire remained an important predictor, though the number of fire years was more important than the area burned. The number of fire years was significantly correlated to total crown cover ($p=0.0086$, $R^2=0.047$) and overstory crown cover ($p=0.0313$, $R^2=0.044$); no measure of fire prevalence was included in the model for structural stage. The number of fire years was negatively correlated to the amount of area with 10%, 30%, 50% and 80-90% total crown cover and to area with low overstory crown cover (0-50%).

Following fire prevalence, logging history explained the greatest amount of variation from 1949 to 1992 in all measures of riparian vegetation structure. The area with no apparent logging explained a significant amount of change in the total crown cover ($p=0.0014$, $R^2=0.078$) and overstory crown cover ($p=0.0107$, $R^2=0.046$), while the area with regeneration logging explained significant amount of change in structural stage ($p=0.0001$, $R^2=0.069$; Table 7). No logging was negatively correlated with the area with 10-70% total crown cover and the area with mid to high (20-40, 60-80, and 100%) overstory crown cover. Regeneration logging was positively correlated to non-forest, stand initiation, stem-exclusion open canopy, and stem-exclusion closed canopy, and negatively correlated to all other structural stages.

Regeneration logging and no apparent logging were also important in predicting upland changes in vegetation structure. The amount of regeneration logging was correlated to change in total and overstory crown cover ($p=0.0002$, $R^2=0.080$; $p=0.0108$, $R^2=0.053$), while the area of no apparent logging was correlated to the change in structural stage ($p=0.0142$, $R^2=0.037$; Table 7). Regeneration logging was positively correlated to 0-20%, 40% and 100% total crown cover, and negatively correlated to mid-range overstory crown cover (30-70%). The amount of no logging was negatively correlated to non-forest, stand initiation, and young-forest multi-story.

Conservation status, though less important than fire prevalence and logging history, was a significant predictor of riparian and upland vegetation structure change in overstory crown cover and structural stage. In riparian areas, the area managed for conservation was a significant predictor of change in overstory crown cover ($p=0.0854$, $R^2=0.018$), and the area legally protected was a significant predictor in the change in structural stage ($p=0.0102$, $R^2=0.026$; Table 7). The area managed for conservation was positively correlated with 40-50% and 70-90% overstory crown cover. In the upland, conservation status was significantly correlated with only the change in structural stage ($p=0.0034$, $R^2=0.032$; Table 7). In both riparian and upland areas, the area legally protected was positively correlated to non-forest, stand, initiation, understory re-initiation, and young-forest multi-story.

Elevation, the least important variable included in the models, was a significant predictor of change in riparian and upland total crown cover. The highest elevation of the experimental unit explained a significant amount of variation in riparian total crown cover ($p=0.0724$, $R^2=0.023$). High elevation sites had, on average, a decrease in 70% and 80% and an increase in 90% and 100% total crown cover. The highest elevation also predicted change in upland total crown cover ($p=0.0214$, $R^2=0.025$; Table 7). Similarly, high elevation sites saw a decrease in 70-80% and increase in 90-100% total crown cover.

While riparian and upland areas did not change between 1949 and 1992 in significantly different ways, separate models built for each suggest small differences do exist. The area burned explained the change in riparian vegetation structure (total crown cover, overstory crown cover, structural stage), while the number of fire years more commonly explained the change in upland vegetation structure (total and overstory crown cover). Fire prevalence overall was positively correlated with lower total crown cover. Logging history was important in explaining the variation in riparian and upland areas, but no apparent logging was included in more riparian models (total and overstory crown cover) while regeneration logging was included in more upland models (total crown cover, structural stage). Logging was associated with high total crown cover and early structural stages. Two measures of conservation status – legally protected and managed for conservation – explained the change between the two time steps for riparian overstory crown cover and riparian and upland structural stage. This greater level of conservation was associated with mid and high overstory crown cover and early structural stages. Finally, high elevation sites saw increases in higher total crown cover categories in both riparian and areas. Ownership, subbasin identity, latitude, and longitude were not significant predictors of any measure of vegetation structure change in riparian or upland areas. These models offer a starting point from which to explore the relationships between processes and patterns of change on the landscape.

Table 7: Final split-plot PERMANOVA models explaining change in riparian and upland vegetation structure, 1949-1992. Blue variables are related to elevation, green variables are related to conservation status, orange variables are related to logging, and red variables are related to fire.

	Riparian			Upland		
Total Crown Cover	ID	0.665	***	ID	0.759	***
	Time	0.048	**	Time	0.021	*
	Fire Area	0.097	***	Regeneration Logging	0.080	***
	No Logging	0.078	**	Number of Fire Years	0.047	**
	Highest Elevation	0.023	.	Highest Elevation	0.025	*
	Variation Explained	0.910		Variation Explained	0.932	
Overstory Crown Cover	ID	0.736	***	ID	0.784	***
	Time	0.029	*	Time	0.023	.
	Fire Area	0.091	***	Number of Fire Years	0.044	*
	No Logging	0.046	*	Regeneration Logging	0.053	*
	Mng for Conservation	0.018	.			
	Variation Explained	0.921		Variation Explained	0.905	
Structural Stage	ID	0.791	***	ID	0.836	***
	Time	0.026	*	Time	0.019	*
	Regeneration Logging	0.069	***	No Logging	0.037	*
	Legally Protected	0.026	*	Legally Protected	0.032	**
	Fire Area	0.027	.			
	Variation Explained	0.938		Variation Explained	0.925	

DISCUSSION

Range of Patterns and Processes in 1949 and 1992

Riparian Compared to Upland Vegetation Structure

The similarity between riparian and upland vegetation is consistent with recent fire ecology research. Recent research from the Oregon Cascades found similar fire return intervals in riparian and upland areas (Olson and Agee 2005). In the Washington Cascades, Everett et al. (2003) found fire events to be less frequent, but more severe in riparian areas. Similar fire regimes suggest similar vegetation existed in these areas. In reconstructed historical stands of the Northern Sierra, riparian and upland areas did not differ in vegetation structure or modeled fire behavior (Van de Water and North 2011). Despite these similarities, it is unlikely that no ecological differences exist between vegetation at stream edge and in the upland.

A univariate approach or larger sample size may have changed the statistics but not the ecological findings, of this work. Compared to the upland, riparian areas in both time periods had greater area between 70% and 90% total crown cover (8-9%) and greater area of understory re-initiation (4.4%). Riparian areas had greater cover of Douglas-fir (4.6%), ponderosa pine (1.7%), Pacific silver (1%), and western hemlock – western redcedar (2%), and less cover of subalpine fir – Engelmann spruce (2%) and mountain hemlock (1%). Riparian areas also had relatively greater areas designated as riparian-wetland (3%). A univariate approach may have found significant differences within a single category, but would not have captured the more important community-level differences. Though the statistical significance may have changed, a larger sample size would not have increased the ecological similarities of riparian and upland areas at the resolution and extent of this study.

The similarity between riparian and upland areas may be the result of the specific measures of structure and composition used in this study, measures which may have been too broad to capture differences. For example, the number of canopy layers alone does not capture the characteristics of those layers. Two canopy layers in the upland may be dominant ponderosa pine and sparse shrub understory, whereas two layers in the riparian area may be midsized Douglas-fir and grand fir undergrowth. Similarly, a dominant overstory of Douglas-fir does not reflect the size of spacing of trees. Regardless of these potentially unmeasured differences, the differences between riparian and upland areas were not great enough to be captured by broader measures of structure and composition.

Finally, the scale of riparian areas used in this study may not capture ecological differences between riparian and upland areas. Too wide a riparian area would dilute distinct riparian vegetation that might naturally exist in a narrower corridor. Similarly, the four-hectare minimum polygon used in photo-interpretation may be too large to capture differences. Existing finer resolution field data suggest that, ecologically, riparian areas are narrower than those in the Northwest Forest Plan. In a field study in the northern Sierras, only the 20m immediately adjacent to the stream edge were significantly different from the upland. The greater density in riparian areas found in that study echo differences in the Tapash (Van de Water and North 2011). At an even finer resolution, higher moisture levels in eastern Washington and Oregon riparian areas were found to extend only 10m beyond the stream edge (Danehy and Kirpes 2000). In a study of western Washington riparian areas and environmental gradients, Naiman et al. (2000) found that soil moisture extended to only 0.25-.5 tree heights from the stream; soil temperature extended 1 tree height; and air temperature extended 1.75 tree heights. Though a finer resolution and extent might reveal differences, the similarity of riparian and upland areas at this coarse scale suggests that ecological and policy-driven boundaries for riparian areas are not aligned.

The similarity between riparian and upland conditions has three primary management implications. First, similarity between riparian and upland vegetation conditions may suggest similar susceptibility to fire (Dwire and Kauffman 2003). Results from this study are complementary with those that have found similar historical fire regimes between riparian and upland areas (Everett et al. 2003, Olson and Agee 2005, Van de Water and North 2010). Depending on the consistency of moisture levels and fuel loads, managers and fire crews should be aware of the potential for fire to move through riparian areas as riparian areas do consistently act as natural barriers to fire (Camp et al 1997). Second, riparian reserves, as defined by the Northwest Forest Plan, are not providing fundamentally unique habitat. In order to protect habitat diversity and aquatic integrity, management in policy-defined riparian areas should protect ecologically distinct riparian conditions and soil stability. Third, even if riparian corridors as they exist in policy do not represent an ecologically unique habitat, they may be providing corridors of connectivity in an otherwise fragmented landscape. Depending on surrounding levels of fragmentation, management within the policy-defined riparian areas may be beneficial. Further research would benefit from gradient analysis and a finer resolution to determine the width of the ecological riparian area, from a more current time period to confirm that trends have continued, and from spatial analysis to assess fragmentation.

Patterns of 1949 and 1992 Vegetation Structure and Composition

Vegetation structures in 1949 and 1992 were consistent with ICBEMP results for the Northern Cascades. At the broadest level, vegetation structure was similar in both 1949 and 1992 to those in the ICBEMP (Hessburg et al. 1999). Total crown cover was predominately 0% or 70-90%, overstory crown cover was about evenly distributed between classes, over 50% of the area had two canopy layers, and the understory re-initiation and young forest multi-story covered more than half the experimental units. While these consistencies suggest coarse-scale homogeneity, the even distribution of overstory between many classes indicates greater variety. Understanding the range of vegetation structures across the second half of the 20th century offers context for current vegetation in the Tapash. Consistencies in structure between the Tapash and the Northern Cascades region of the ICBEMP suggest that other patterns of structure in the Northern Cascades may be applicable to the Tapash.

Conversely, the Tapash was compositionally unique from the rest of the Northern Cascades. Primarily, overstory Douglas-fir cover was more abundant and ponderosa pine cover less abundant in the Tapash. Douglas-fir cover ranged from 27-35% in the Tapash, but was found to be 23-26% in the Northern Cascades region. The Tapash also had a greater proportion of Pacific silver fir – 13.3%, in contrast to 7.2% for the Northern Cascades as a whole. The Tapash had relatively greater cover of grand fir (3.8% compared to 1.6%) and western hemlock – western redcedar (6.3% compared to 2.2%). On the other hand, Ponderosa pine composed 11% percent of the Tapash, but 17-21% of the North Cascades region. Sites just north of the Tapash have found ponderosa pine coverage closer to 40% (Agee and Lehmkuhl 2009). Subalpine fir – Engelmann spruce was also less common in the Tapash than in the Northern Cascades region as a whole (9.6% compared to 14.8%). In the understory, The Tapash had an additional 20% classified as Douglas-fir – grand fir – Pacific silver fir, similar area classified as subalpine fir – Engelmann spruce, and less area categorized as ponderosa pine or western larch – lodgepole pine. Riparian-wetland designation was comparable between the Tapash and the Northern Cascades region (Hessburg et al. 1999). In comparison to the greater Northern Cascades region, the Tapash has greater area of typically mid-elevation vegetation (Douglas-fir and most true firs) and less vegetation typically associated with high and low elevations (subalpine fir – Engelmann spruce, ponderosa pine).

Though the majority of literature from Eastern Washington characterizes the area as open stands of fire tolerant species, primarily ponderosa pine (Camp 1999, Hessburg et al. 2005), the Tapash does not fit this description. The Tapash is a complex landscape that contains not only contains elements of ponderosa pine dry forest but also substantial components of Douglas-fir and true firs. Management objectives in the Tapash should be based on local information rather than regional characterizations.

Processes Affecting Patterns of Vegetation Structure and Composition

Spatial Autocorrelation

Spatial autocorrelation was indirectly accounted for in other explanatory variables. With the exception of the number of canopy layers and structural stage, Mantel tests indicated weak spatial autocorrelation for all measures of structure and composition. Latitude and longitude, tested as first terms, echoed these findings. However, tested as final terms in the model after the inclusion of elevation, fire prevalence, logging history, conservation status, ownership, and subbasin identity, latitude and longitude were significant in less than a third of models. Low levels of spatial autocorrelation were consistent with findings from other ponderosa pine forests, especially when samples were greater than 300m apart (Laughlin et al. 2004). The diminished significance of latitude and longitude indicate that much of the spatial autocorrelation found in the Mantel tests were accounted for in other explanatory variables. This allows for relative confidence that spatial autocorrelation has been appropriately accounted for.

Elevation, Fire Prevalence, Logging History, Conservation Status, and Ownership

Processes on the landscape determine patterns of vegetation; patterns, in turn, influence processes (Turner et al. 2001). Insights into the relationships between process and pattern are fundamental to understanding past and future vegetation structure and composition. The consistent effect of elevation will continue regardless of conservation, logging, or fire. Though the effect of fire on vegetation has changed, vegetation will continue to influence future fire events. Whereas the effect of conservation status was ambiguous, the reduction in canopy layers and specific species caused by logging will remain a legacy in the landscape. These relationships offer insight into current and future patterns and processes.

In both 1949 and 1992, structure and composition existed along predictable elevation gradients (Agee 1993, Halofsky and Hibbs 2009), which will continue regardless of future conservation, logging, or fire. Lower elevations were less dense, whereas higher elevation corresponded with higher total crown cover, mid overstory crown cover, and areas of understory re-initiation and young forest multi-story. Ponderosa pine existed most prominently at low elevation (<1,200m) where, in the east-west gradient of the Cascades, conditions are drier and hotter. Subalpine fir – Engelmann spruce, western hemlock – western redcedar and mountain hemlock, tolerant of shade and excessive moisture, occupied high elevations (>1,400m). Riparian-wetland designation was greater at high elevation. Douglas-fir and Pacific silver fir, tolerant of a broader range of conditions, occupied most elevations but were most abundant at mid elevations. Elevation creates gradients of solar radiation, temperature, and moisture. Different species, each with varying evolutionary adaptations, will continue to occupy different niches along this gradient. This gradient also creates the conditions that foster or suppress growth, thereby affecting density. The range of elevations and corresponding vegetation communities in the Tapash require that management be equally diverse.

The correlations between fire and vegetation structure suggest that the effect of fire on the landscape is changing. Dendrochronological work indicated that fire historically worked to maintain low-density, single canopy stands of mature fire-resistant trees (Everett et al. 2000, Hessburg et al. 2005). In the Tapash, greater fire prevalence was correlated with no or one canopy layer and bare understory. This suggests a range of fire severities occurred; stand-replacing fires would have resulted in no canopy layers and low-severity fires would have resulted in one canopy layer with a bare understory. Site-specific analysis of burned areas and current vegetation would help to clarify the post fire-suppression-policy relationship between fire and vegetation. Even with a small sample size, it is surprising that fire was not correlated with more components of structure and composition. This tentatively indicates that, while fire was historically the primary driver of vegetation structure, it may no longer be the dominant process affecting landscape patterns. Despite the limited influence of fire on 1992 vegetation, wildfires will continue to be affected by existing vegetation.

Relationships between fire and riparian-wetland designation in the Tapash improve our understanding of these vital areas. Hessburg et al. (1999) hypothesized that fire exclusion has allowed mesic areas to develop, explaining the increase in riparian-wetland areas from 1949 to 1992. Results from the Tapash, however, indicate the opposite. Indirect or direct causes may be responsible for the positive relationship between fire and riparian-wetland areas. Indirectly, increased fire may be preventing encroachment of forests into riparian-wetland areas (Hessburg et al. 2005). Fire may be directly promoting riparian vegetation with basal or epicormic sprouting or other fire-adapted evolutionary mechanisms. Repeating the analysis with a larger sample size or more recent time period would further strengthen these results. Relationships from the Tapash suggest that, especially in the upland, fire promotes rather than discourages riparian-wetland areas to develop.

Two implications stem from the data when exploring the relationship between logging and vegetation conditions. First, the impact of logging drastically increased in the second half of the twentieth century; second, logging activities – as a human controlled disturbance – have the ability to alter vegetation in a myriad of ways. No logging variables explained significant variation in riparian or upland 1949 vegetation measures. Ninety-four percent of the area used in this analysis had no apparent logging in 1949; it follows that the logging that did exist would have had little impact on vegetation. Historical records indicate that the majority of logging pre-1950 was tree specific and that products were used primarily in Naches and Yakima. Logging after 1950, however, included commercial thinning, clearcuts, and partial cuts (Wissmar et al. 1994). These logging activities had profound impacts on vegetation. Regeneration logging decreased the area with 2 or more canopy layers and, surprisingly, was positively correlated not only to early structural stages but also to old forest structures. Selective harvest was related to the decrease in area of 0-20% and 90-100% total crown cover. Selective logging was positively correlated with ponderosa pine and Douglas-fir indicates, indicating that selective logging did not reduce Douglas-fir and ponderosa pine, but may have actually created the conditions needed for them to increase. The legacy of logging will continue, but policy and mangers can influence future logging activities.

Though greater conservation has protected riparian-wetland areas, the overall effect of conservation on vegetation conditions was ambiguous. The positive association between legal protection and riparian-wetland areas suggests that National Parks are protecting the processes that allow riparian-wetland conditions to develop. On-site evaluation might further reveal the nature of this relationship. For other measures of structure and composition, areas of greater conservation (legally protected and managed for conservation) were associated with greater total crown cover, lower overstory crown cover, and ponderosa pine. This structural dynamic is characteristic of multistory canopy structure, indicating that greater conservation preserved complex and multi-layers stands rather than open stands. Lower conservation status (modified) supported greater area of old forest multi-story, but not old forest single story. Conservation status did not distinguish clear communities in structure or composition, thereby limiting the ability to use conservation status to predict future relationships.

Ownership, while a coarse scale variable, informed vegetation structure, and can also aid in future management. As the area of federal ownership in an experimental unit increased, so did the area with 80-100% total crown cover, mid to high levels of overstory crown cover, and young forest structure (non-forest, stand initiation, understory re-initiation, stem exclusion, young forest multi-story). Together, these results suggest that historical USFS logging resulted in reduced old forest structure with open, low-density stands. Even as the USFS moves towards restoration, the record of extraction will likely continue to affect federal lands and should be considered in future management decisions.

In all cases, the legacy of the landscape will influence future processes and patterns of vegetation. Elevation will continue to create gradients of density and composition. Although fire may continue to be of mixed-severity, the positive association with riparian-wetland areas may continue. Greater conservation may continue to protect ponderosa pine and riparian-wetland areas. The location, extent, and type of logging can promote desired structure or composition. Similarly, in recognizing the history of public lands at a landscape level, federal managers can counteract historical management practices by promoting older forest structures less prone to wildfire. Existing patterns of vegetation, whether affected by elevation or logging, will impact future processes, including insect and disease outbreak as well as fire severity and extent. This study does not seek to determine management objectives, but rather to offer historical context that can inform future management.

Vegetation Changes (1949-1992) and Their Causes

Differences in 1949 and 1992 Vegetation Structure and Composition

Regardless of statistical significance, changes from 1949 to 1992 in the Tapash may indicate larger trends. With the exception of understory species and riparian-wetland designation, the range of vegetation conditions narrowed from 1949 to 1992. Increased homogeneity in structure and overstory composition has the potential to increase fire extent by removing natural breaks created by diverse conditions (Hessburg et al. 2005). Conversely, increased heterogeneity in the understory might counteract this effect. Furthermore, as the understory grows into the overstory, greater heterogeneity may serve to decrease wildlife extent. Other studies have found evidence of fundamental shifts in vegetation as a result of fire exclusion (Wissmar et al. 1994, Camp et al. 1999, Hessburg et al. 1999, Hessburg 2000, Howell 2001, Hessburg et al. 2005). Though results from the Tapash do not indicate such a drastic shift, changes do suggest increasing homogeneity.

Though changes may be part of a larger shift in vegetation, the differences found in this study - 2-5% across 43 years - are relatively small compared to shifts suggested by longer-term studies (Wissmar et al. 1994, Camp et al. 1999, Hessburg et al. 1999, Hessburg 2000, Howell 2001, Hessburg et al. 2005). Fire exclusion began with the disruption and removal of indigenous tribes during the mid-1800s and intensified with the Weeks Act of 1911, supporting complete fire suppression (Keeley et al. 2009). The first resource aerial photo over the Tapash is from 1949, nearly a century after Euro-American settlement, and 38 years after fire suppression was implemented. It is possible that the rate of change in the initial 40-100 years following the beginning of fire exclusion, which were not included in this study, was greater than the change expressed from 1949 to 1992. Dendrochronological-based studies infer vegetation based on fire frequency and severity, but operate at a different scale than the present study (Heyerdahl et al. 2007). The relatively low rate of change between 1949 and 1992 may suggest that forests have reached a new post-fire exclusion state.

Riparian Compared to Upland Changes in Vegetation Structure and Composition

Riparian and upland areas did not change differently between the two time periods, suggesting literature on departure from historical conditions in the upland may be applicable to riparian areas. While the ICBEMP is the most extensive and relevant research examining changes in vegetation across time, many others have also explored departure from historical conditions (Camp 1999, Hessburg et al. 1999, Wright and Agee 2004, Gärtner et al. 2008). The wealth of research on changing conditions can now tentatively be applied to riparian corridors, broadening our understanding of these areas and informing appropriate management.

Changes in Vegetation Structure and Composition from 1949 to 1992

Many specific changes in the Tapash from 1949 to 1992 echo those found within the Northern Cascades region of the ICBEMP. The Northern Cascades region covers eastern Washington from the crest of the Cascades to the ecotone with shrub-steppe. An additional 3.7% of the Tapash landscape was designated as riparian or wetland, a similar magnitude reported by the ICBEMP. Both spatial extents experienced increases in high total crown cover (60-90%). Increases to 100% cover were greater in the Tapash. The area with 80-90% overstory crown cover increased, suggesting that trees are expanding their canopies or, more likely, that more trees now make up the overstory. Furthermore, changes in structural stage at both extents signify a conversion from single-story and old forests to young multi-canopy forests and, in the Northern Cascades, to stem exclusion and understory re-initiation. The loss of old forest structures was unique to the Tapash.

The degree of change in composition differed between the Tapash and the Northern Cascades. Understory composition in particular changed more dramatically in the Tapash riparian areas than elsewhere in the region. Where no changes were found regionally, Douglas-fir – grand fir – Pacific silver fir decreased over 5%, subalpine fir – Engelmann spruce increased 3%, and western hemlock – western redcedar increased 2% in the Tapash. In the overstory, changes in Douglas-fir (increased 3.6%) and western hemlock – western redcedar (decreased 1.3%) were greater in the Tapash than in the Northern Cascades (where Douglas-fir increased 2% and western hemlock – western redcedar decreased 0.4%; Hessburg et al. 1999). Conversely, changes in ponderosa pine (decreased 1.1%), grand fir (increased 0.8%), and subalpine fir – Engelmann spruce (decreased 0.5%) were smaller than those in the Northern Cascades (where ponderosa pine decreased 4%, grand fir increased 1.2%, and subalpine fir – Engelmann spruce decreased 3%; Hessburg et al. 1999). The difference in results between the Tapash and the North Cascades highlights the importance of matching the scale of analysis to that of management.

These changes, though small, have implications for fire risk, habitat, and ecosystem function. Fire risk changes with the transition, however minor, from old forest structures and ponderosa pine to young forest multi-story and Douglas-fir or grand fir. As a result of vertical continuity, increased density, less fire-tolerant trees, and greater overstory homogeneity, fires may be larger in extent and of higher severity (Hessburg et al. 2005, Falk et al. 2007, Keeley et al. 2009, Van de Water and North 2011). Conversely, heterogeneity in understory and increased riparian-wetland areas may offer natural fuel breaks. Changes in structure and composition affect also habitat. Species dependent on old forest structures or the open canopy associated with ponderosa pine overstory may decline, while early seral species may benefit from the increased area of non-forest and stand initiation (Franklin and Johnson 2012). In other areas, species that require more cover may benefit from increased density of Douglas-fir – grand fir – Pacific silver fir in the understory. The changes during the second half of the 19th century were relatively small but not inconsequential, especially if they are continuations of longer, more dramatic shifts.

Processes Attributed To Changes in Vegetation Structure

Fire prevalence, logging history, conservation status, and elevation were each correlated to different changes in vegetation structure, offering insight into how specific management can be used to meet local objectives.

Increased fire prevalence reduced crown cover and maintained open canopies and old forests in both riparian and upland areas. The association between fire and riparian vegetation is consistent with research that low-severity, relatively frequent fires were historically an important disturbance in riparian areas (Everett et al. 2003, Olson and Agee 2005, Van de Water and North 2011). The association between fire prevalence and reduced overstory crown cover suggests higher-severity fires than existed historically. The reduction in both canopy covers as a result of fire is supported by extensive research demonstrating that fire exclusion has increased density (Camp 1999) both basal area (Russell and McBride 2001), and canopy cover (Hessburg et al. 2005, Messier et al. 2012). Findings that fire reduced the area of understory re-initiation and stem exclusion closed canopy and young forest multi-story may suggest lower-severity fires. Fire will reduce density and, in stands without vertical continuity, reduce the understory.

Logging inconsistently diminished mid-ranges of crown cover and increased early structural stages. While others have suggested that selective logging further compounded the changes resulting from fire exclusion, this study found logging altered vegetation structures uniquely from fire prevalence. Camp (1999) and Hessburg et al. (2005) found selective logging to result in younger and more densely stocked stands. Differences in results are likely due to the time period used in this analysis. In the Tapash, pre-1950 logging practices were similar to those described by Camp: focused on large and select species of trees. Logging affecting the 1949 time period would have been from truck logging carried out between 1931 and 1944. Apparent logging in 1992 would have been from commercial thinning, clearcuts and partial cuts (Wissmar et al. 1994). Unlike fire prevalence, logging reduced the amount of area with mid ranges of total and overstory crown cover and increased the area with early structural stages. This effect may have weakened or counteracted the importance of fire prevalence in predicting vegetation structure change. While past logging activity will remain a legacy of the landscape, future logging and management can target and promote desired vegetation structure.

Greater conservation protected mid-ranges of overstory crown cover but did not help to maintain old forest structures. In this regard, protected lands directly counteracted the effect of logging. Conservation status for the earlier time period was unknown, which may explain why legal protection did not help maintain old forest structures: loss of old forest structure may have occurred before areas were legally protected. Conservation status was expected to capture the importance of cumulative human disturbance. However, the relationships between conservation and structural stage were counterintuitive. Relative to fire prevalence and logging history, conservation status is of coarser scale; there is no information about specific actions promoted or prohibited within each category of conservation. As a result, it is challenging to parse out why conserved land did not protect old forest structure. The role of conservation status in altering vegetation structure and its potential for predicting future vegetation structure should be considered with caution.

High elevation sites further confounded the change in vegetation structure. As in other studies, elevation functions as a coarse scale explanatory variable (Halofsky and Hibbs 2009). Within high elevation sites, the area with 70-80% total crown cover decreased more than within lower elevation sites. The area with 90-100% crown cover, however, increased in high elevation sites and decreased at lower elevation. If greater total crown cover indicates fewer disturbances, higher elevation sites may have been naturally or intentionally protected against disturbance.

Fire prevalence, logging history, conservation status, and elevation are each correlated to different changes in vegetation structure, offering insight into how specific management can be used to meet local objectives. While there was no measure of fire severity included in this study, the effects of increased fire prevalence further support fire's role in reducing density and opening stand structure. Allowing wildfires to burn or using prescribed fire in areas not susceptible to crown fires would help to restore more open canopy structure. Though logging historically targeted midrange canopy covers, active management can be used to meet more specific targets for stand density and structure. Conservation status, unfortunately, offers little tangible insight into vegetation structure. Finally, results suggest that higher elevation sites may be on a different trajectory than their lower elevation counterparts. Active management for the Tapash should use known relationships between these processes and patterns of vegetation to help meet local objectives.

CONCLUSION

Focused on the spatial extent of the area of the Tapash Sustainable Forest Collaborative and the temporal extent of the second half of the 20th century, the objectives of this study were first, to describe the range of vegetation conditions and processes in 1949 and 1992 and second, to explore vegetation changes and their causes. Vegetation structure in the Tapash was composed of predominately 70-90% crown cover, an even distribution of overstory crown cover, two canopy layers, and early structural stages. Douglas-fir was the dominant overstory species over more than 30% of the Tapash, with the second most common species, ponderosa pine and Pacific silver fir each composing 10% of the landscape. Douglas-fir – grand fir – Pacific silver fir dominated 40% of the understory. Designated riparian-wetland areas covered 3-10% of the study area. From 1949 to 1992, average total crown cover decreased, overstory crown cover increased, the number of canopy layers decreased, and early forest structures increased at the expense of old forest structures. Cover of Douglas-fir increased as cover of ponderosa pine decreased. Designated riparian-wetland areas increased. Higher elevation sites tended to be denser, to contain old forest structures, and to have greater abundance of true-firs, hemlock, and redcedar. Low elevation sites fostered ponderosa pine. Across time, higher elevation sites became denser. Conservation status did not emerge as a powerful predictor of vegetation or vegetation change. Logging reduced mid-range canopy covers, but could be used more as an effective tool to promote desired landscape outcomes. Fire worked to maintain open stands and relatively open stand structure, but this may have been accomplished through higher severity fires than existed historically. Greater fire prevalence was associated with greater area of riparian-wetland designation. This suggests, in contrast to theories from the ICBEMP, that fire indirectly supports these areas by reducing coniferous encroachment or directly promoting fire-adapted species present in these areas. The differences between the Tapash and ICBEMP results for the Northern Cascades indicate that managers should set locally specific, rather than regionally informed, landscape objectives. The Tapash landscape is more nuanced than the typical open ponderosa forest categorization of Eastern Washington. The legacy of vegetation patterns will continue to affect future processes on the landscape, just as processes will remain forces of vegetation change.

The insignificant difference between policy-defined riparian areas and the associated uplands offers new insight into the management of these areas. This suggests that fire may be able to move through these areas. While narrower, ecologically based riparian areas likely exist on the landscape, policy-defined riparian areas are not protecting fundamentally distinctive vegetation structures. Policy-defined riparian areas may be serving as corridors of connectivity in an otherwise fragmented landscape. Careful management in riparian areas may be possible. If corridors of connectivity are not a management priority, management in riparian areas should carefully consider action on a site-by-site basis.

The rate of change in vegetation structure from 1949 to 1992 also offers unique insight for managers. The relative difference between times indicates a slow rate of change. While it is possible that this rate of change is consistent with the change in the immediate decades following fire exclusion, it is more likely that the rate of change has slowed substantially. A slower rate of change suggests we may be approaching a new stable forest state. Rather than attempt to recreate conditions prior to Euro-American settlement, management may be more effective at implementing strategies grounded in local needs and objectives.

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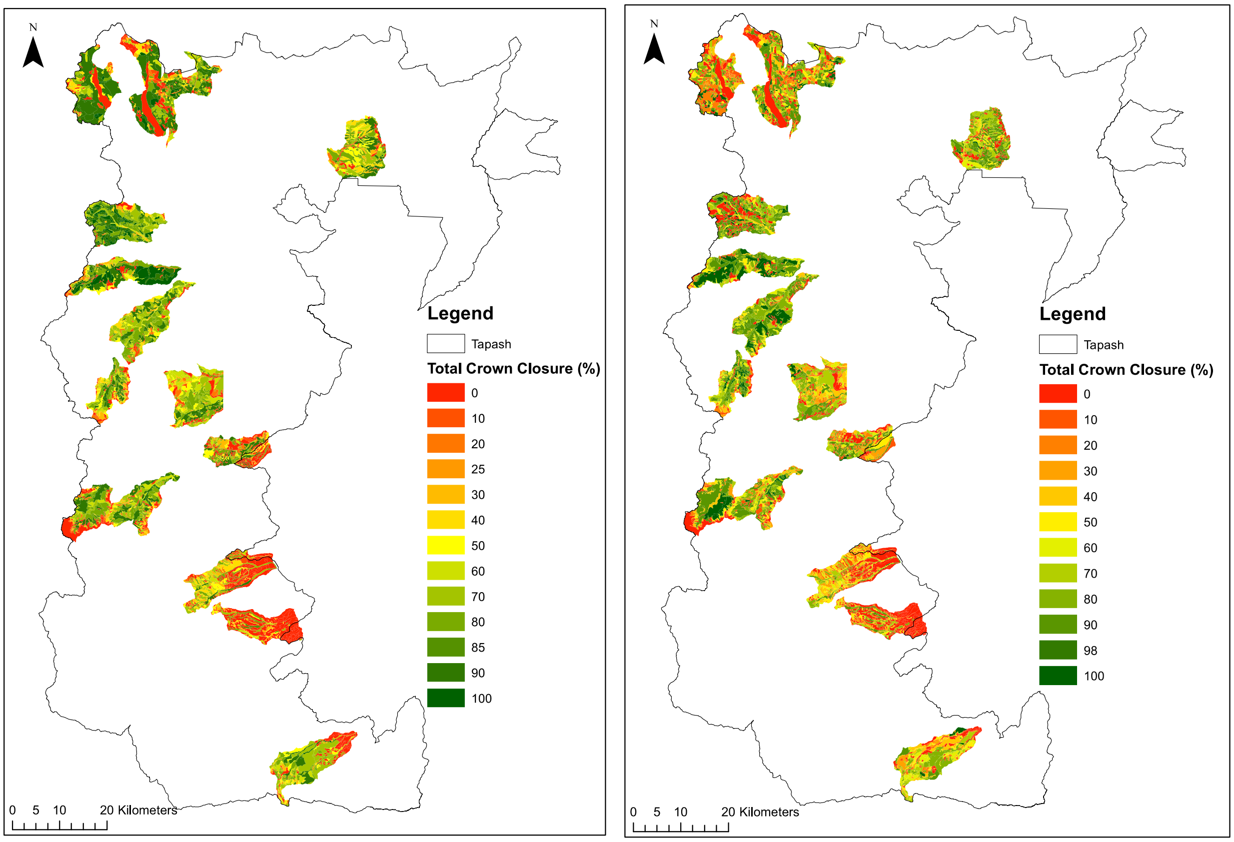
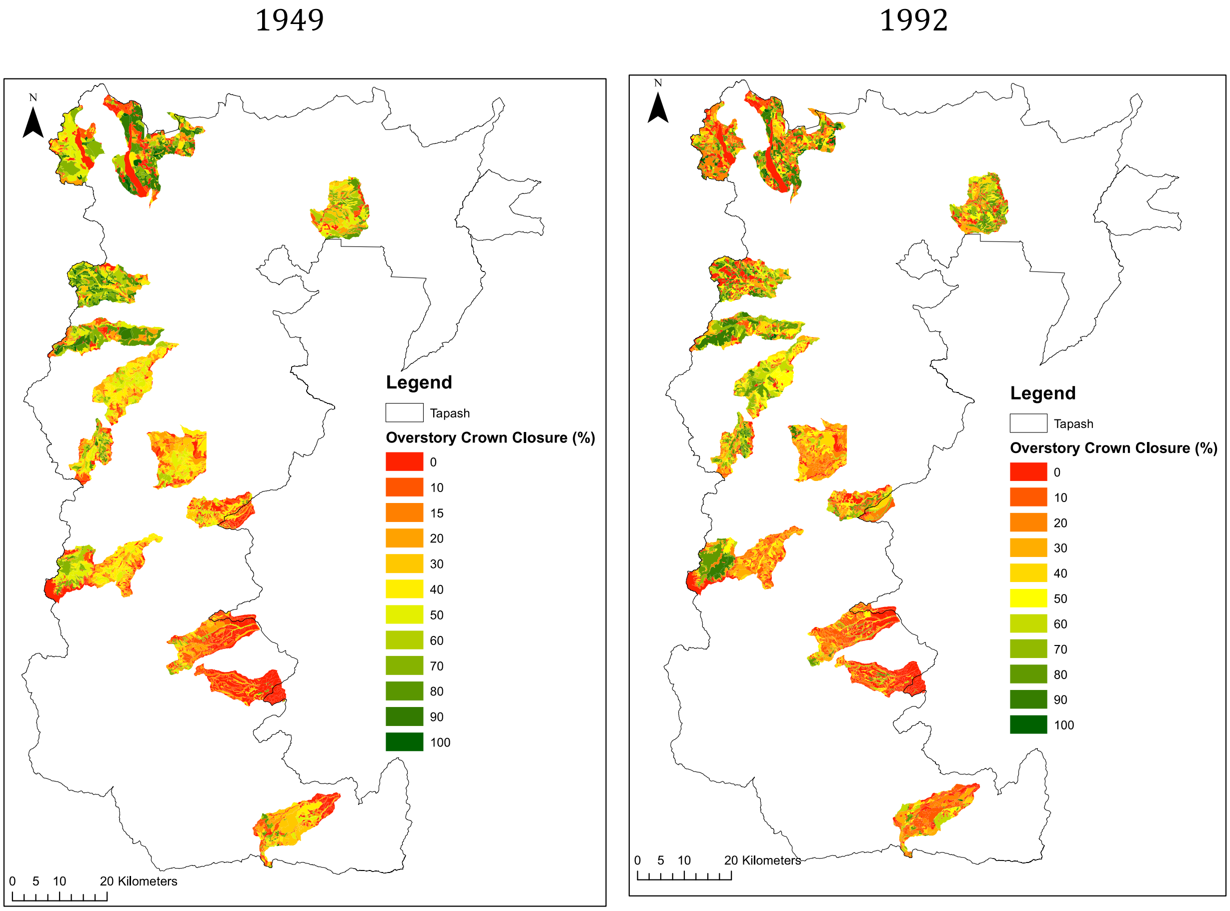
Appendix A: Spatial Distribution of Response Variables


1949

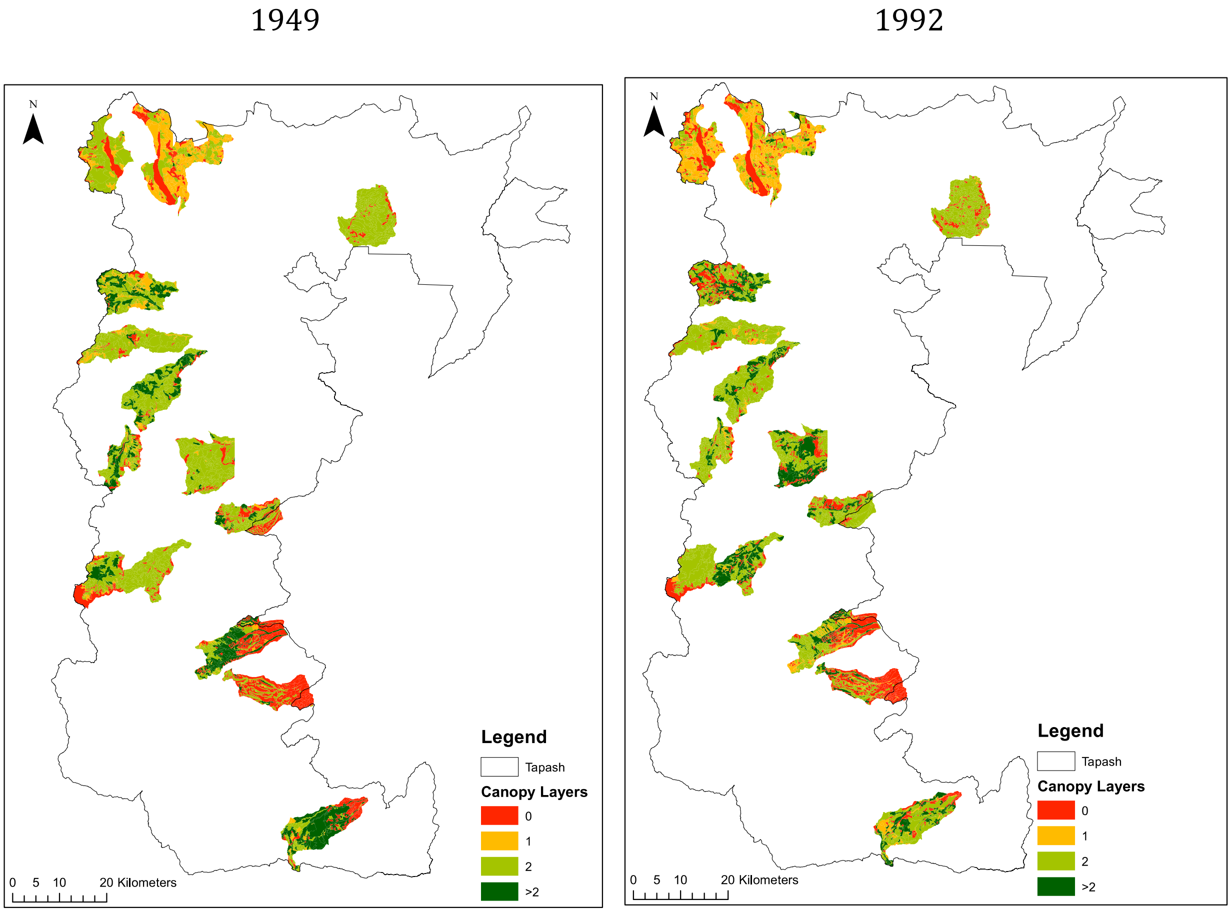
1992

Figure 34: Spatial distribution of total crown cover, 1949 and 1992.


1949

1992

Figure 35: Spatial distribution of overstory crown cover, 1949 and 1992.


1949

1992

Figure 36: Spatial distribution of number of canopy layers, 1949 and 1992.

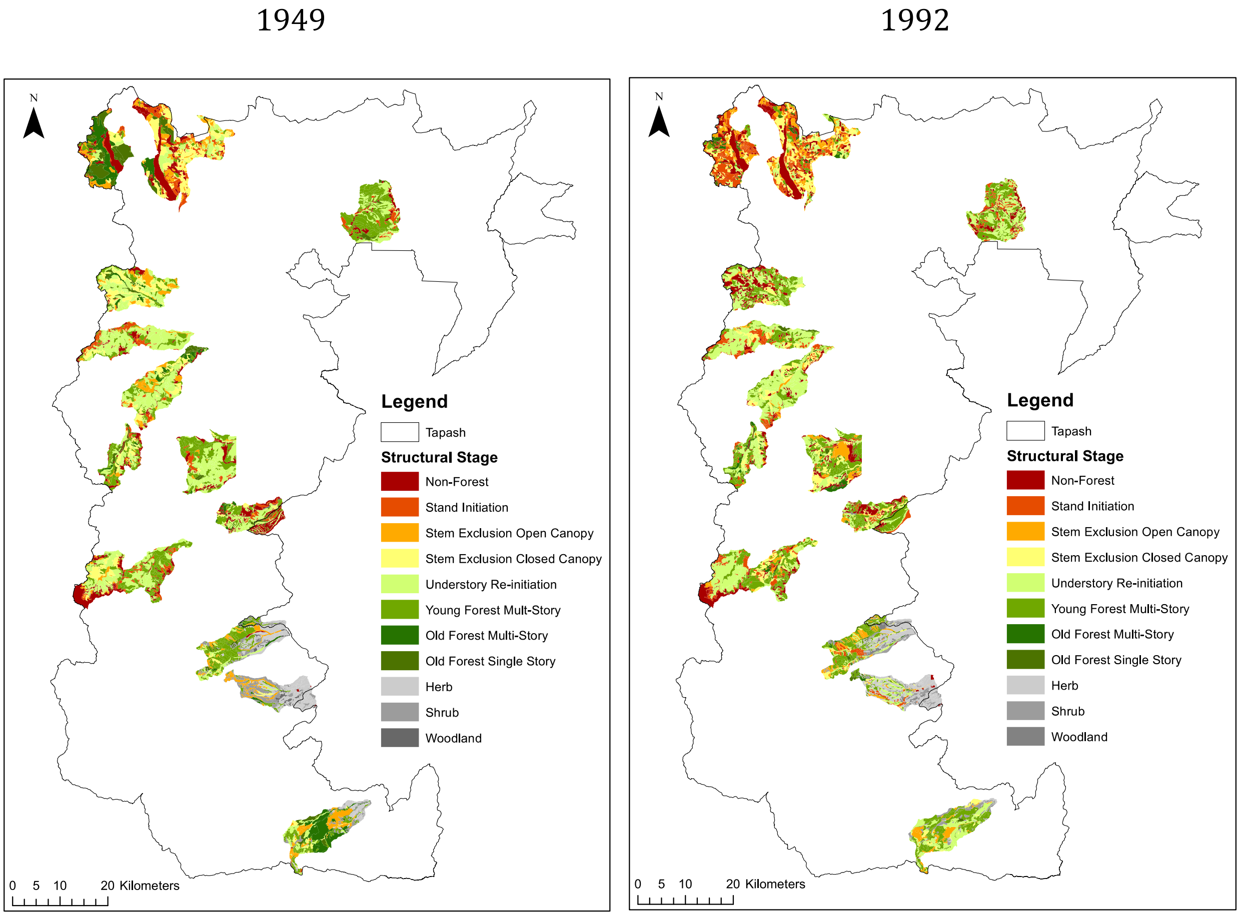
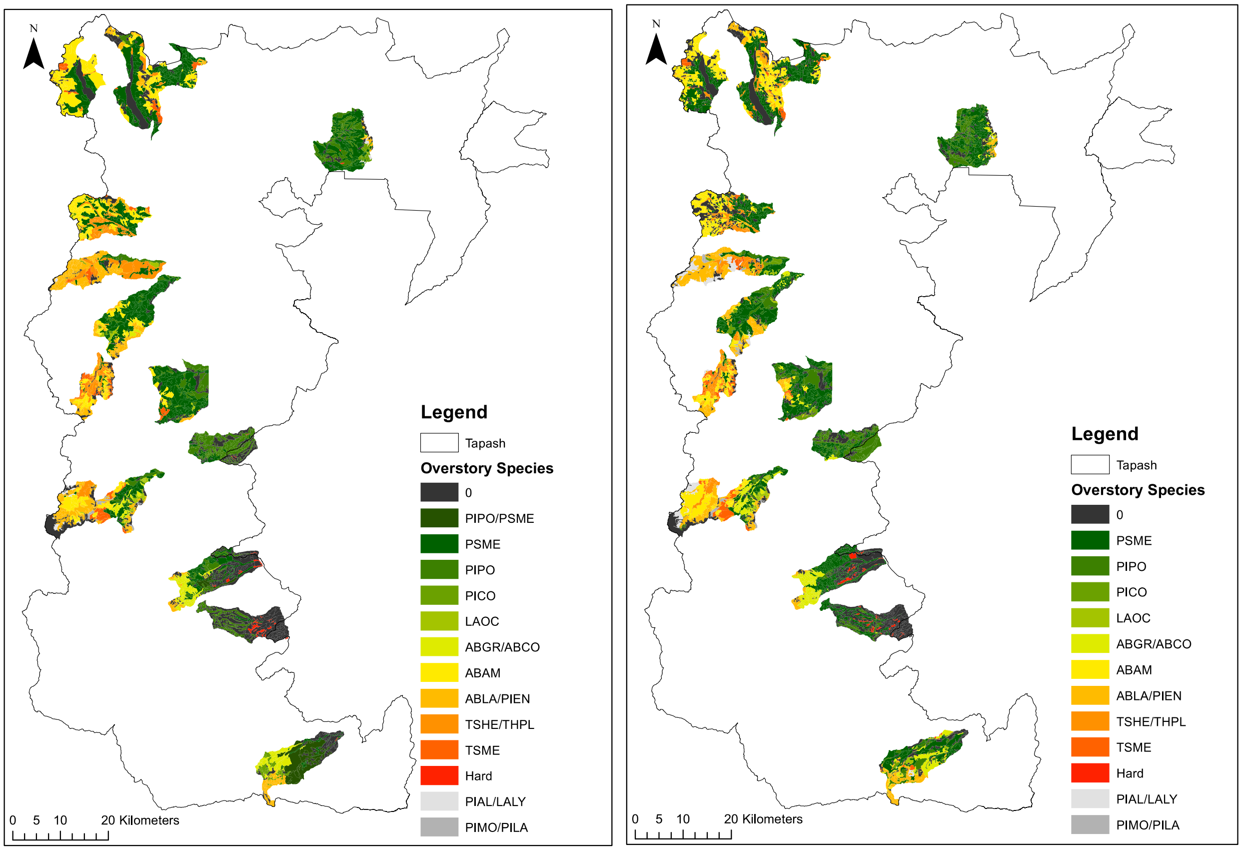
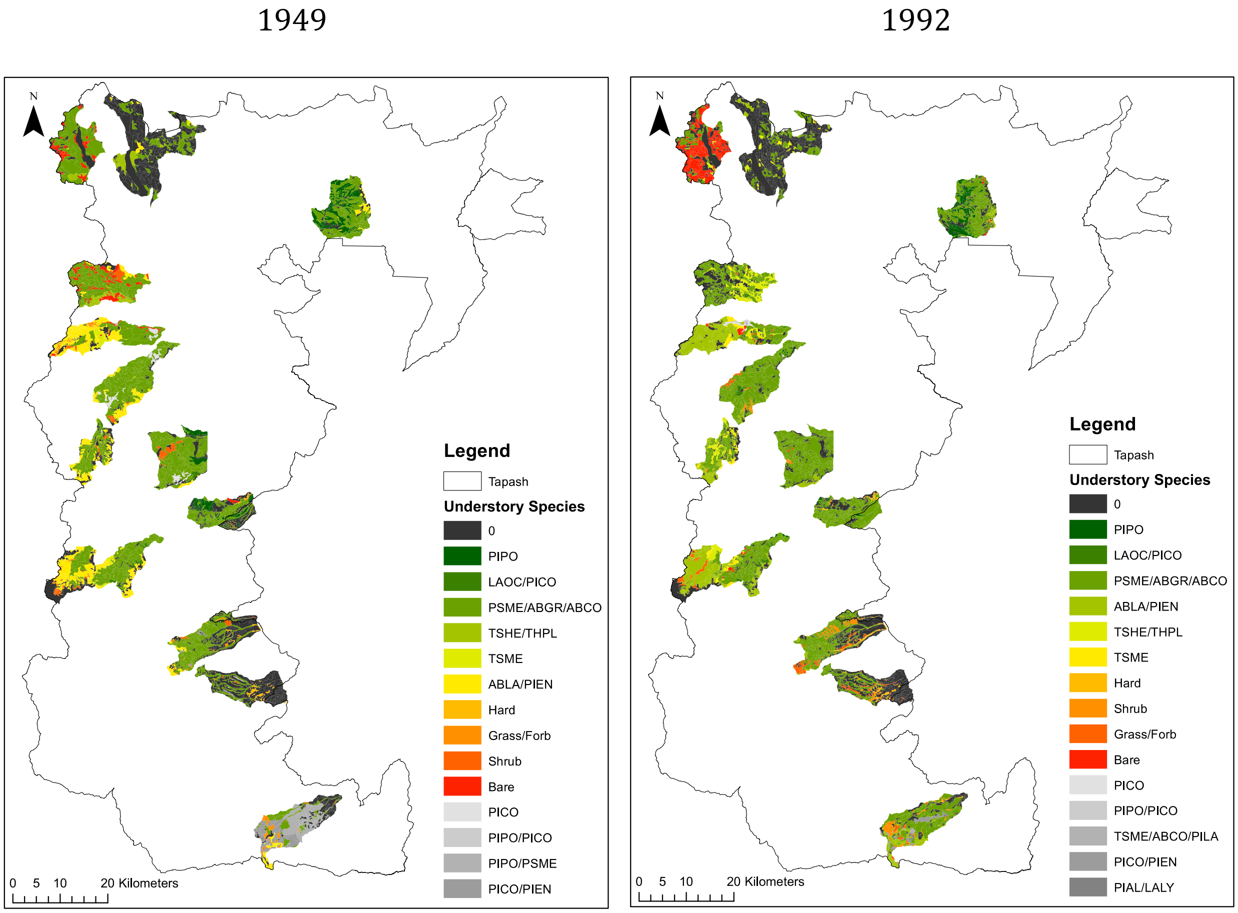


Figure 37: Spatial distribution of structural stage, 1949 and 1992.


1949

1992

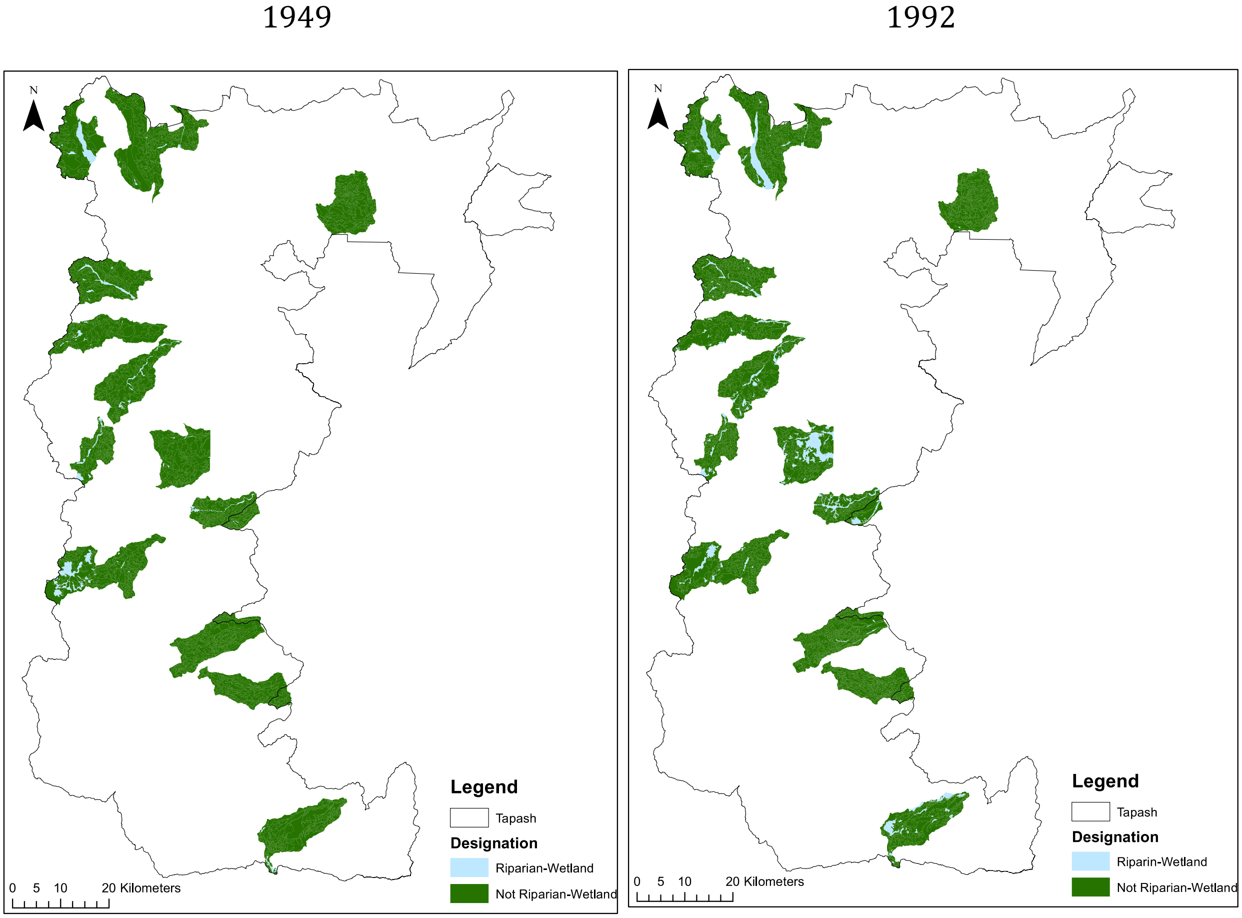
Figure 38: Spatial distribution of dominant overstory species, 1949 and 1992. Species coded in gray were not used in analysis due to rarity across subwatersheds.



1949

1992

Figure 39: Spatial distribution of dominant understory species, 1949 and 1992. Species coded in gray were not used in analysis due to rarity across subwatersheds.


1949

1992

Figure 40: Spatial distribution of riparian-wetland designation, 1949 and 1992.

Appendix B: Final PERMANOVA Models

Table 8: Final whole-plot PERMANOVA models for 1949 riparian vegetation. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

Total Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.19692	0.196918	3.7358	0.18284	0.00366 **
Fed	1	0.12629	0.126286	2.3958	0.11726	0.04001 *
Subbasin	2	0.22667	0.113334	2.1501	0.21047	0.02435 *
Residuals	10	0.52711	0.052711		0.48943	
Total	14	1.07698			1.00000	
Overstory Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.2623	0.26230	2.3205	0.15146	0.03081 *
Residuals	13	1.4695	0.11304		0.84854	
Total	14	1.7318			1.00000	
Canopy Layers						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Part. Cons.	1	0.49260	0.49260	8.5350	0.31609	0.00049 ***
Modified	1	0.20363	0.20363	3.5282	0.13066	0.02738 *
Subbasin	2	0.28506	0.14253	2.4695	0.18291	0.04329 *
Residuals	10	0.57716	0.05772		0.37034	
Total	14	1.55844			1.00000	
Structural Stage						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Part. Cons.	1	0.59557	0.59557	7.8381	0.28644	1e-05 ***
Modified	1	0.33171	0.33171	4.3655	0.15954	0.00291 **
Fed	1	0.31608	0.31608	4.1599	0.15202	0.00295 **
Residuals	11	0.83582	0.07598		0.40200	
Total	14	2.07918			1.00000	
Overstory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.58472	0.58472	4.0425	0.19926	0.00099 ***
Part. Reten.	1	0.44300	0.44300	3.0627	0.15097	0.01620 *
Modified	1	0.31559	0.31559	2.1818	0.10755	0.05990 .
Residuals	11	1.59109	0.14464		0.54222	
Total	14	2.93440			1.00000	
Understory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.22247	0.222474	2.2402	0.14699	0.09055 .
Residuals	13	1.29101	0.099308		0.85301	
Total	14	1.51348			1.00000	
Riparian/Wetland						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.031216	0.0312158	4.8926	0.27344	0.06198 .
Residuals	13	0.082943	0.0063803		0.72656	
Total	14	0.114159			1.00000	

Table 9: Final whole-wlot PERMANOVA models for 1949 upland vegetation. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

Total Crown Cover						
Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
Avg. Elev.	1	0.31155	0.311545	4.8300	0.24021	0.00187 **
Subbasin	2	0.27589	0.137943	2.1386	0.21272	0.04212 *
Residuals	11	0.70953	0.064503		0.54707	
Total	14	1.29696			1.00000	
Overstory Crown Cover						
Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
Avg. Elev.	1	0.26952	0.269516	3.1608	0.16298	0.01472 *
Leg. Prot.	1	0.22435	0.224353	2.6311	0.13567	0.03382 *
Fed	1	0.22179	0.221794	2.6011	0.13413	0.03919 *
Residuals	11	0.93796	0.085269		0.56722	
Total	14	1.65363			1.00000	
Canopy Layers						
Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
High Elev.	1	0.48881	0.48881	7.6539	0.29984	0.00128 **
Modified	1	0.22912	0.22912	3.5876	0.14055	0.02461 *
Avg. Elev.	1	0.20977	0.20977	3.2847	0.12868	0.03268 *
Residuals	11	0.70251	0.06386		0.43093	
Total	14	1.63021			1.00000	
Structural Stage						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
High Elev.	1	0.56680	0.56680	6.2638	0.24434	7e-05 ***
Modified	1	0.25592	0.25592	2.8282	0.11033	0.03542 *
Fed	1	0.50159	0.50159	5.5432	0.21623	0.00050 ***
Residuals	11	0.99537	0.09049		0.42910	
Total	14	2.31969			1.00000	
Overstory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.56450	0.56450	4.3884	0.19514	0.00079 ***
Modified	1	0.41275	0.41275	3.2087	0.14268	0.00867 **
Part. Reten.	1	0.34693	0.34693	2.6970	0.11993	0.03181 *
Fed. Own.	1	0.28225	0.28225	2.1942	0.09757	0.06077 .
Residuals	10	1.28636	0.12864		0.44468	
Total	14	2.89280			1.00000	
Understory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
High Elev.	1	0.45664	0.45664	5.0255	0.25504	0.0088 **
Modified	1	0.24349	0.24349	2.6796	0.13599	0.0601 .
Residuals	12	1.09038	0.09087		0.60898	
Total	14	1.79051			1.00000	
Riparian/Wetland						
No variable explained significant variation						

Table 10: Final whole-plot PERMANOVA models for 1992 riparian vegetation. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

Total Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
High Elev.	1	0.38602	0.38602	8.8533	0.38157	0.00020 ***
Fed	1	0.10243	0.10243	2.3491	0.10124	0.08602 .
Residuals	12	0.52323	0.04360		0.51719	
Total	14	1.01167			1.00000	
Overstory Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
High Elev.	1	0.27745	0.277448	3.2339	0.1992	0.01627 *
Residuals	13	1.11533	0.085795		0.8008	
Total	14	1.39278			1.0000	
Canopy Layers						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Num. Fires	1	0.46958	0.46958	14.3985	0.35922	0.00074 ***
High Elev.	1	0.32223	0.32223	9.8804	0.24650	0.00060 ***
Subbasin	2	0.18928	0.09464	2.9019	0.14480	0.04530 *
Residuals	10	0.32613	0.03261		0.24948	
Total	14	1.30722			1.00000	
Structural Stage						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Regen. Log.	1	0.45112	0.45112	6.8039	0.26542	8e-05 ***
High Elev.	1	0.33528	0.33528	5.0569	0.19727	0.00087 ***
Subbasin	2	0.25020	0.12510	1.8868	0.14721	0.07535 .
Residuals	10	0.66303	0.06630		0.39010	
Total	14	1.69962			1.00000	
Overstory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.53195	0.53195	5.4221	0.25821	0.00129 **
Part. Reten.	1	0.35088	0.35088	3.5765	0.17032	0.01650 *
Residuals	12	1.17730	0.09811	0.57147		
Total 14	2.06013				1.00000	
Understory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Num. of Fires	1	0.42800	0.42800	4.2085	0.19538	0.01394 *
Avg. Elev.	1	0.37284	0.37284	3.6661	0.17020	0.00738 **
Fire Area	1	0.27106	0.27106	2.6653	0.12374	0.05094 .
Residuals	11	1.11868	0.10170		0.51068	
Total	14	2.19058			1.00000	
Riparian/Wetland						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Leg. Prot.	1	0.079350	0.079350	20.291	0.6095	0.00181 **
Residuals	13	0.050839	0.003911		0.3905	
Total	14	0.130189			1.0000	

Table 11: Final whole-plot PERMANOVA models for 1992 upland vegetation. P-values are based on 99,999 permutations – “***” signifies significance at alpha <0.001, “**” 0.01, and “*” at 0.05, and “.” at 0.1.

Total Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.31747	0.31747	7.2737	0.30232	2e-05 ***
Selharv. Log	1	0.10822	0.10822	2.4794	0.10305	0.05367 .
Mng. Cons.	1	0.14432	0.14432	3.3065	0.13743	0.01855 *
Residuals	11	0.48011	0.04365		0.45720	
Total	14	1.05012			1.00000	
Overstory Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.28488	0.284882	4.7732	0.20829	0.00129 **
Leg. Prot.	1	0.23236	0.232357	3.8931	0.16988	0.00477 **
Fed	1	0.19397	0.193974	3.2500	0.14182	0.01538 *
Residuals	11	0.65652	0.059684		0.48001	
Total	14	1.36773			1.00000	
Canopy Layers						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
High Elev.	1	0.47998	0.47998	7.9175	0.33720	0.00139 **
Regen. Log.	1	0.21599	0.21599	3.5628	0.15174	0.03471 *
Residuals	12	0.72748	0.06062		0.51107	
Total	14	1.42345			1.00000	
Structural Stage						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Regen. Log.	1	0.42095	0.42095	5.4634	0.24349	0.00068 ***
Avg. Elev.	1	0.38327	0.38327	4.9744	0.22170	0.00022 ***
Residuals	12	0.92460	0.07705		0.53481	
Total	14	1.72883			1.00000	
Overstory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.52824	0.52824	6.4035	0.26476	0.00019 ***
Selharv. Log	1	0.34271	0.34271	4.1545	0.17178	0.00630 **
Part. Reten.	1	0.21676	0.21676	2.6277	0.10865	0.04488 *
Residuals	11	0.90741	0.08249		0.45481	
Total	14	1.99513			1.00000	
Understory Species						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Avg. Elev.	1	0.51792	0.51792	4.9849	0.25333	0.00123 **
Regen. Log	1	0.27977	0.27977	2.6928	0.13684	0.04252 *
Residuals	12	1.24675	0.10390		0.60983	
Total	14	2.04444			1.00000	
Riparian/Wetland						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Fire PC	1	0.015040	0.0150395	4.2453	0.24617	0.0552 .
Residuals	13	0.046055	0.0035427		0.75383	
Total	14	0.061094			1.00000	

Table 12: Final split-plot PERMANOVA models for change in riparian vegetation structure. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

Total Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
ID	14	1.45800	0.104143	4.7535	0.66467	1e-05 ***
Time	1	0.10493	0.104927	4.7893	0.04783	0.00352 **
T:Fire Area	2	0.21307	0.106536	4.8628	0.09713	0.00021 ***
T:No Log.	2	0.17081	0.085404	3.8982	0.07787	0.00165 **
T:High Elev.	1	0.04960	0.049597	2.2638	0.02261	0.07244 .
Residuals	9	0.19718	0.021909		0.08989	
Total	29	2.19358			1.00000	
Overstory Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
ID	14	2.3692	0.169232	6.0104	0.73619	1e-05 ***
Time	1	0.0937	0.093698	3.3278	0.02911	0.01572 *
T:Fire Area	2	0.2944	0.147184	5.2274	0.09147	1e-05 ***
T:No Log.	2	0.1495	0.074734	2.6542	0.04644	0.01202 *
T:Mng. Cons.	1	0.0581	0.058074	2.0625	0.01805	0.08595 .
Residuals	9	0.2534	0.028156		0.07874	
Total	29	3.2183			1.00000	
Structural Stage						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
ID	14	3.0679	0.219135	8.2455	0.79085	1e-05 ***
Time	1	0.1004	0.100445	3.7795	0.02589	0.01025 *
T:Regen. Log.	2	0.2678	0.133915	5.0389	0.06904	0.00015 ***
T:Leg. Prot.	1	0.0993	0.099264	3.7351	0.02559	0.01079 *
T:Fire Area	2	0.1046	0.052315	1.9685	0.02697	0.07196 .
Residuals	9	0.2392	0.026576		0.06166	
Total	29	3.8793			1.00000	

Table 13: Final split-plot PERMANOVA models for change in upland vegetation structure. P-values are based on 99,999 permutations – "***" signifies significance at alpha <0.001, "**" 0.01, and "*" at 0.05, and "." at 0.1.

Total Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
ID	14	1.82088	0.130063	7.1800	0.75923	1e-05 ***
Time	1	0.05126	0.051255	2.8295	0.02137	0.03671 *
T:Regen. Log.	2	0.19257	0.096283	5.3153	0.08029	0.00022 ***
T:N. Fire Yr.	2	0.11157	0.055783	3.0795	0.04652	0.00882 **
T:High Elev.	1	0.05903	0.059035	3.2590	0.02461	0.02047 *
Residuals	9	0.16303	0.018115		0.06798	
Total	29	2.39833			1.00000	
Overstory Crown Cover						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
ID	14	2.42571	0.173265	5.8988	0.78445	1e-05 ***
Time	1	0.07089	0.070887	2.4134	0.02292	0.06268 .
T:N. Fire Yr.	2	0.13675	0.068374	2.3278	0.04422	0.03117 *
T:Regen. Log.	2	0.16517	0.082586	2.8116	0.05341	0.01047 *
Residuals	10	0.29373	0.029373		0.09499	
Total	29	3.09225			1.00000	
Structural Stage						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
ID	14	3.4519	0.246564	8.7643	0.83640	1e-05 ***
Time	1	0.0786	0.078573	2.7929	0.01904	0.03676 *
T:No Log.	2	0.1545	0.077263	2.7464	0.03744	0.01394 *
T:Leg. Prot.	1	0.1326	0.132624	4.7142	0.03214	0.00324 **
Residuals	11	0.3095	0.028133		0.07498	
Total	29	4.1271			1.00000	

Appendix C: Metadata

Response Variables

Total Crown Cover

totl.0	Proportion of area with estimated total crown cover closest to 0 percent.
totl.10	Proportion of area with estimated total crown cover closest to 10 percent.
totl.20	Proportion of area with estimated total crown cover closest to 20 percent.
totl.30	Proportion of area with estimated total crown cover closest to 30 percent.
totl.40	Proportion of area with estimated total crown cover closest to 40 percent.
totl.50	Proportion of area with estimated total crown cover closest to 50 percent.
totl.60	Proportion of area with estimated total crown cover closest to 60 percent.
totl.70	Proportion of area with estimated total crown cover closest to 70 percent.
totl.80	Proportion of area with estimated total crown cover closest to 80 percent.
totl.90	Proportion of area with estimated total crown cover closest to 90 percent.
totl.100	Proportion of area with estimated total crown cover closest to 100 percent.

Overstory Crown Cover

oscc.0	Proportion of area with estimated overstory crown cover closest to 0%
oscc.10	Proportion of area with estimated overstory crown cover closest to 10%
oscc.20	Proportion of area with estimated overstory crown cover closest to 20%
oscc.30	Proportion of area with estimated overstory crown cover closest to 30%
oscc.40	Proportion of area with estimated overstory crown cover closest to 40%
oscc.50	Proportion of area with estimated overstory crown cover closest to 50%
oscc.60	Proportion of area with estimated overstory crown cover closest to 60%
oscc.70	Proportion of area with estimated overstory crown cover closest to 70%
oscc.80	Proportion of area with estimated overstory crown cover closest to 80%
oscc.90	Proportion of area with estimated overstory crown cover closest to 90%
oscc.100	Proportion of area with estimated overstory crown cover closest to 100%

Canopy Layers

cnpy.0	Proportion of experimental unit with no canopy layer.
cnpy.1	Proportion of experimental unit with single canopy layer
cnpy.2	Proportion of experimental unit with two canopy layers
cnpy.3	Proportion of experimental unit with more than two canopy layers

Structural Stage

str.si	Proportion of area classified under stand initiation
str.seoc	Proportion of area classified under stem exclusion open canopy
str.secc	Proportion of area classified under stem exclusion closed canopy
str.ur	Proportion of area classified under understory re-initiation
str.yfms	Proportion of area classified under young forest multi-story
str.ofms	Proportion of area classified under old forest multi-story
str.ofss	Proportion of area classified under old forest single story
str.herb	Proportion of area classified under herbland
str.shrub	Proportion of area classified under shrub
str.nf	Difference in proportion of area classified under other (including rock, water wet meadow/marsh, alpine meadow, dry meadow/grassland, shrubland, post logging bare ground – burned, post logging bare ground – slumps and erosion, post logging – grass/forb stage, cropland, urban/rural, pasture, grassland, woodland
str.wood	Proportion of area classified under woodland

Overstory Species (dominant species by basal area)

os.pipo	Proportion of area of ponderosa pine
os.laoc	Proportion of area of western larch
os.pico	Proportion of area of lodgepole pine
os.psme	Proportion of area of Douglas fir
os.abgr.abco	Proportion of area of grand fir/white fir
os.abam	Proportion of area of Pacific silver fir
os.abla.pien	Proportion of area of subalpine fir/Engelmann spruce
os.tshe.thpl	Proportion of area of western hemlock/western redcedar
os.tsme	Proportion of area of mountain hemlock
os.hard	Proportion of area of hardwood (maple, birch, aspect, etc)
os.pipo.psme	Proportion of area of ponderosa pine/Douglas fir
os.psme.tsme	Proportion of area of Douglas fir/mountain hemlock
os.pico.pien	Proportion of area of lodgepole pine/Engelmann spruce

Understory Species (dominant species by number of trees)

us.pipo	Proportion of area of ponderosa pine
us.laoc.pico	Proportion of area of western larch/lodgepole pine
us.psme.abgr.abco	Proportion of area of Douglas fir/white fir/Pacific silver fir

us.tshe.thpl	Proportion of area of western hemlock/western redcedar
us.tsme	Proportion of area of mountain hemlock
us.abla.pien	Proportion of area of subalpine fir/Engelmann spruce
us.hard	Proportion of area of hardwood
us.grass	Proportion of area of grass/forb
us.shrub	Proportion of area of shrubs
us.bare	Proportion of bare area

Riparian-Wetland Designation

ripr.yes	Proportion of area observed as riparian or wetland
ripr.no	Proportion of area observed as not riparian or wetland

Explanatory Variables

watershed	An identifier for the larger watershed within which the 15 smaller watersheds are nested (n=3). 4th level HUC - subbasin
time	Time period (historical or contemporary)
area	Area of analysis (riparian, upland)
ID	A unique identifier for each experimental unit
elev.high	Highest elevation present in experimental unit (center of highest band)
elev.avg	Area weighted elevation average
log.no	Proportion of experimental unit with no apparent logging apparent
log.regen	Proportion of experimental unit with evidence of regeneration (clearcut, shelterwood, seedtree harvests)
log.selharv	Proportion of experimental unit with evidence of selective harvest (select harvest, overstory removal, final removal)
log.thin	Proportion of experimental unit with evidence of thinning (commercial, precommerical)
log.pchclr	Proportion of experimental unit with evidence of patch clearcuts (clearcut patches estimated less than 10acres)
mngt1	Proportion of experimental unit that is legally protected. Encompass areas that are legally dedicated to protection and preservation of the characteristic of natural landscape (Wilderness, Congressional Reserve, National Parks). Additionally it contains management that is slightly less restrictive and may allow for more adjustments in management practices (Regional

	conservation reserves/preserves, Late Successional Reserves, Wilderness Study Areas)
mngt.3	Proportion of experimental unit that is managed for conservation. Retention of forested areas or native vegetation for a variety of reasons such as the conservation of endangered species or for maintaining forested corridors along areas of visual or biological importance (Municipal Watersheds, Corridors for visual/riparian/biodiversity, Endangered/threatened species management, Other values of importance, Private conservation areas, Wildlife Refuges).
mngt4	Partial-retention with the potential for longer rotations or more experimental management strategies (Partial retention, Adaptive Management Areas, Experimental Forests, Other wildlife areas, Primitive recreation usage).
mngt5	Proportion of experimental unit that has been modified. Major modification of the landscape and includes general forestry, developed recreation (off road vehicle use, ski areas), mining, or grazing on public land (General forestry w/ habitat modification, NWFP Matrix, developed recreation.
mngt6	Proportion experimental unit that has been privately modified. Privately owned lands which may be less restrictive than public lands may or may not remain committed towards natural resource management over time.
BLM	Proportion experimental unit that is BLM land
Fed	Proportion experimental unit that is USFS land
St	Proportion experimental unit that is state land
Priv	Proportion experimental unit that is privately owned, including National Parks
Trib	Proportion experimental unit under tribal ownership
fire.num	Number of wildland fire events per acre from 1970-1992 per hectare
fire.acres	Proportion of experimental unit which has burned in wildland fires 1970-1992
fire.num.years	Number of different years in which fires (1970-1992) occurred per hectare