



Review

The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California

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ABSTRACT

Forests characterized by mixed-severity fires occupy a broad moisture gradient between lower elevation forests typified by low-severity fires and higher elevation forests in which high-severity, stand replacing fires are the norm. Mixed-severity forest types are poorly documented and little understood but likely occupy significant areas in the western United States. By definition, mixed-severity types have high beta diversity at meso-scales, encompassing patches of both high and low severity and gradients in between. Studies of mixed-severity types reveal complex landscapes in which patch sizes follow a power law distribution with many small and few large patches. Forest types characterized by mixed severity can be classified according to the modal proportion of high to low severity patches, which increases from relatively dry to relatively mesic site conditions. Mixed-severity regimes are produced by interactions between top-down forcing by climate and bottom-up shaping by topography and the flammability of vegetation, although specific effects may vary widely across the region, especially the relation between aspect and fire severity. History is important in shaping fire behavior in mixed-severity landscapes, as patterns laid down by previous fires can play a significant role in shaping future fires. Like low-severity forests in the western United States, many dry mixed-severity types experienced significant increases in stand density during the 20th century, threatening forest health and biodiversity, however not all understory development in mixed-severity forests increases the threat of severe wild fires. In general, current landscapes have been homogenized, reducing beta diversity and increasing the probability of large fires and insect outbreaks. Further loss of old, fire tolerant trees is of particular concern, but understory diversity has been reduced as well. High stand densities on relatively dry sites increase water use and therefore susceptibility to drought and insect outbreaks, exacerbating a trend of increasing regional drying. The need to restore beta diversity while protecting habitat for closed-forest specialists such as the northern spotted owl call for landscape-level approaches to ecological restoration.

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1. Introduction

In fire ecology, definitions of mixed severity fire arose from observations that many fires and fire regimes could not be neatly classified as either surface fire or stand replacement dominated disturbances. These fires occupied a middle zone in terms of first order effects leaving highly variable and mixed patterns of lethal and non-lethal outcomes. Definitions of mixed severity also arose from subtraction of more readily defined terms. Ecosystems with low severity fire were easily described as those where surface fire effects tended to dominate, and they were subsequently defined as those where less than 20% of the overstory trees or basal area is killed by the sum of all fire effects (Agee, 1990, 1993). In concept, low severity fires principally reduce the volume and distribution of the most flammable fuels via surface fire activity, and mortality effects are typically minimal (Stephens et al., 2008). At the opposite pole, high severity fires were also readily described as those where crown fire effects tended to dominate, defined by Agee (1990, 1993) as more than 70% of the overstory trees or basal area killed by the sum of all fire effects. High severity fires principally kill trees via torching and running crown fire and often significantly change the volume and distribution of surface and canopy fuels. Mixed severity fires formed the catch-all bin for what remained, by Agee's (1990, 1993) definition those where 20–70% of the overstory trees or basal area are killed by the sum of all fire effects. The broad bin of 20–70% masks a great deal of variability and would benefit from additional subdivisions. Progress toward a better scientific foundation for mixed severity fire will come by stratifying mixed severity regimes by ecological regions and proportion of high severity fire. Brown et al. (2008): stated the case for the latter "...simply to describe a historical fire regime as variable severity is by itself not useful either for characterizing fire as an ecological process or for fire management or ecological restoration purposes. For example, without reference to scale it is possible to conclude that recent variable-severity fires in ponderosa pine forests (i.e., that have included both surface burning as well as large areas of crown mortality) are within a historical range of variability even though areas of crown mortality are orders of magnitude larger than any area that occurred historically (e.g., Romme et al., 2003). We propose that future definitions of variable-severity fire regimes in ponderosa pine and related forests must be accompanied by descriptions of the maximum spatial extent and how often crown fire occurred over a defined period of time".

It is important to note that canopy damage is not necessarily the same as soil damage and the two measures of severity can be independent of each other (Jain and Graham, 2007; Safford et al., 2009). In general, the severity of impacts cannot be generalized across different components of an ecosystem (e.g. soils, trees, understory vegetation, streams).

Mixed severity fire regimes are poorly understood and poorly documented but in all likelihood were widespread both in the western and eastern US. For example, Schoennagel et al. (2004) estimate that mixed severity regimes account for 17–50% of the major forest types of the Rocky Mountains.

Key ecological and management questions associated with historic¹ mixed-severity regimes center on implications of structurally diverse and temporally variable landscapes for habitats, animal movements, and propagation of disturbances. Consistent with the *intermediate disturbance hypothesis* (Connell, 1978; Petraitis et al., 1989), mixed severity regimes (by definition) produced rich intermediate scale beta diversity, providing a wide variety of habitats across landscapes. Forests in which mixed severity regimes were the norm were likely to support plant and animal species that prefer closed or nearly closed conditions for at least a part of their life history (Spies et al., 2006), as well as early successional and mid-successional specialists, and species that used both early and late-successional conditions [e.g. the California spotted owl (Bond et al., 2009) and the northern spotted owl in the Klamath Mountains (Franklin et al., 2000)].

In this paper we discuss: (i) the likely extent and location of historical forests of the mixed severity fire regime in Oregon, Washington and California, and variation in fire ecology within this large class (ii) the environmental factors that produce mixed-severity fires; (iii) changes to mixed severity landscapes during the 20th century and threats to biodiversity resulting with those changes; and (iv) uncertainties in the knowledge base and research needed to address those uncertainties. In a companion paper we discuss management approaches to reducing losses to remaining old trees and the habitat they represent; and to maintaining an appropriate mix of early, mid, and late successional habitats across landscapes.

2. Ecology and spatial geography of mixed severity disturbance

What exactly is a mixed severity disturbance? At a broad regional scale all wildfire is mixed severity, a fact that limits the usefulness of such scales for ecological interpretation. Moreover, all disturbance processes exhibit heterogeneity at one spatial scale or another, which may manifest within stands, across landscapes, or in some combination of the two. Within the spectrum of possible patterns mixed severity regimes grade into low and high severity regimes without distinct thresholds or patterns. To better understand the nature of mixed-severity regimes, we must look to the ecology, the spatial geography, and the variability of fires and their effects.

Mixed-severity fires create a patchiness of forest structure, composition, and seral status that can be observed and quantified at an intermediate or meso-scale, with patch sizes ranging from a few hundredths up to tens or hundreds of ha, depending on locale and climatic drivers (Fig. 1a). In forest types that were historically dominated by mixed severity regimes, surface and canopy fuels, topography, climatic conditions, and ignitions worked in concert to influence variation in fire frequency, severity, spatial extent, and seasonality. The result was a complex spatio-temporal mix of low, moderate, and high severity patches.

As we discuss in more detail later, the scale of patch sizes and the envelope of burn severity vary with forest type and across the region, however there are also widespread similarities. Studies in both Washington and California have found that patch sizes in mixed severity regimes followed a negative power law

¹ In the context of this paper, "historic" refers to the period prior to settlement by Euro-Americans.

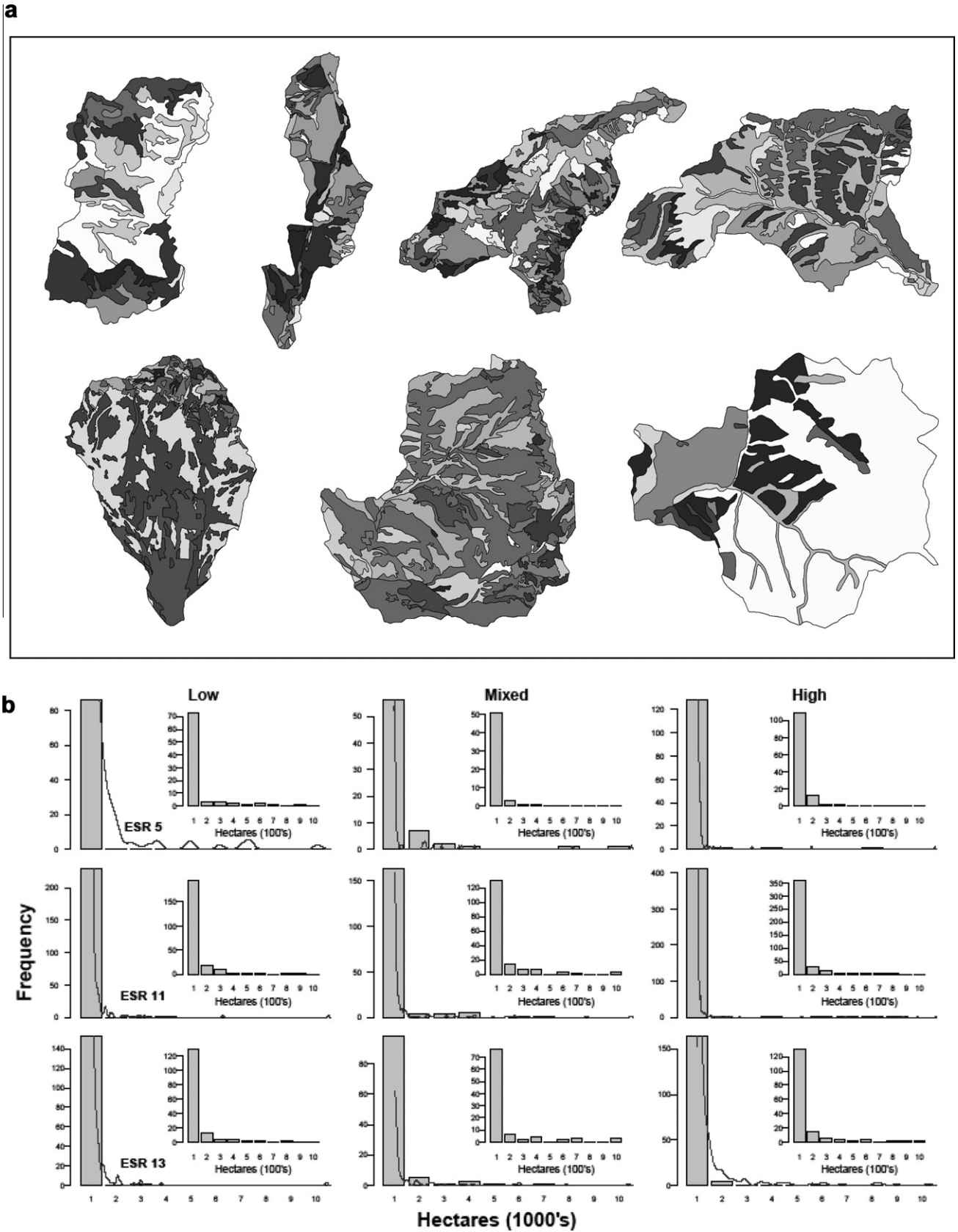


Fig. 1. (a) A sample of 7 historical (ca. 1900) maps of combined cover type and structural class conditions from subwatersheds of the eastern Washington Cascades. Gray tones indicate unique cover type-structural class combinations. Note the highly variable patch sizes. (b) Frequency-size distributions of reconstructed historical (ca. 1900) fire severity patches in three ecoregions of the eastern Washington Cascades. *Low*, *mixed*, and *high* denote severity corresponding with <20%, 20–70%, and >70% of the overstorey crown cover or basal area killed by fires, respectively. Data are from Hessburg et al. (2007). (See Hessburg et al., 2000 for complete details).

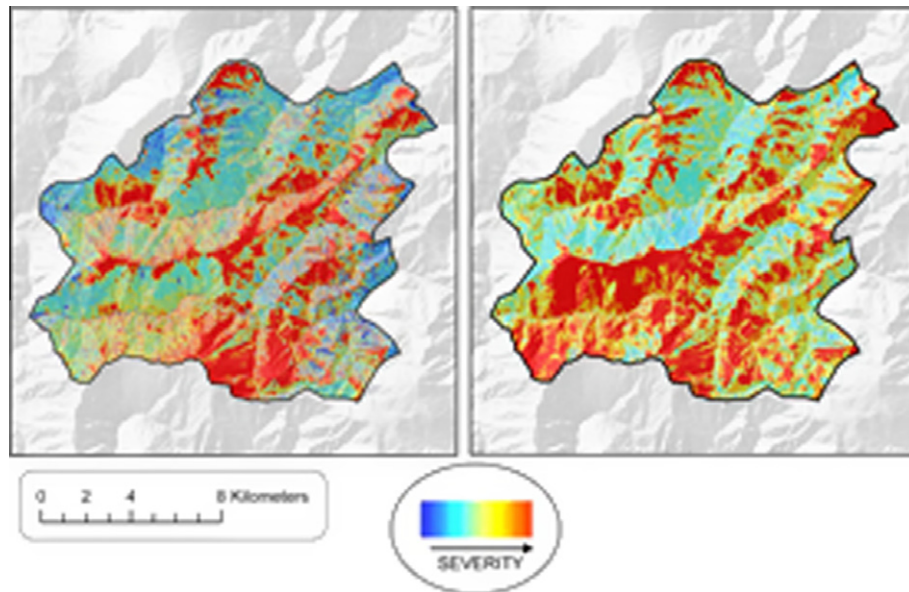


Fig. 2. Comparison of fire severity between the 1987 Silver fire (left) and the 2002 Biscuit fire, which burned through the same area (Thompson et al., 2007).

approximating a Pareto distribution (i.e. many small patches and a few large forming a long tail to the right in the frequency-size histogram). That was the case in two recent fires in Yosemite National Park (central California) where stand replacement patch sizes ranged from .05 (the lower limit of determination) to 90 ha (Collins and Stephens, 2010). In another California study, landscapes exhibited multi-scale patterns of fire sizes that followed a power law distribution for both the meso-scale (50–5000 ha) and for smaller patches embedded within the larger (Moritz et al., 2010). Smaller patch sizes were thought to be driven by endogenous processes, larger by rare or extreme events. Similar results were found in eastern Washington, where patch sizes of low, mixed, and high severity fires ranged from ~1 (the lower limit of determination) to 10,000 ha (Hessburg et al., 2007, Fig. 1b).

The large amount of edge and clumpiness in forest structure, composition, and seral status within and among patches provides a rich intermingling of habitats for early, mid-, and late-successional specialists as well as variety for individual species. As an example of the latter, California spotted owls prefer unburned or lightly burned mixed conifer forests with large trees for roosting and, probably because of prey abundance, moderately or severely burned forest for foraging (Bond et al., 2009). Similarly, Franklin et al. (2000) found that a mosaic including both old forests and early successional patches provided optimal habitat for northern spotted owls in California.

Mixed-severity systems exhibit temporal as well as spatial variability. Depending on climate-vegetation interactions, the proportion of low to high severity patches might vary between fires in a particular locale (e.g. Heyerdahl et al., 2002; Gedalof et al., 2005; Marlon et al., 2009), and the characteristic power law pattern of patch sizes may be altered by extreme fire weather. A recent example is the contrast between the 1987 Silver Fire in SW Oregon, which created a mosaic of low to moderate severity patches, and the 2002 Biscuit Fire, which burned the same area with a preponderance of high severity patches (Fig. 2). The median crown damage (i.e. scorch and consumption) in the Silver fire, which burned under relatively mild weather conditions, was about 16% while the median crown damage for the Biscuit fire, which burned under much hotter and windier conditions was

63% (Thompson and Spies, 2010). Another factor contributing to the higher severity of the Biscuit fire was the high amount of early seral patches produced by the Silver Fire. As we discuss in more detail later, some early seral community types have a high probability of burning severely (Odion et al., 2004; Stephens and Moghaddas, 2005; Thompson et al., 2007). In general, legacies from past fires, as well as from other natural disturbances and land uses, influence fire behavior in a given area, a point we return to later in the paper.

2.1. Where are the forests of the historical mixed severity fire regime?

Fig. 3a shows the geographic distribution of mixed-severity forests in the Pacific Northwest, while Fig. 3b illustrates variation among the forest types in the modal characteristics of fires (because of temporal variation as discussed above, the ratios shown in Fig. 3b should be understood as approximations of central tendencies). In the Interior West (east of the Cascades crest), the Klamath Mountains, low to mid elevations on the western slopes of the Cascades (depending on latitude), portions of the eastern slopes of the Coast Range, and in the Northern and Central Sierra Nevada, forests characterized historically by mixed-severity fire regimes occupied a broad range of environments between forests with predominantly surface fire regimes (dry ponderosa pine, pine-oak, and oak) and subalpine forests dominated by stand replacing regimes.

Spies et al. (2006) grouped forest types that were historically influenced by mixed-severity fire regimes into ponderosa pine (dominated by low severity but experiencing occasional mixed severity in some locales), mixed-conifer/evergreen on dry sites (includes the Douglas-fir zone and driest parts of the other zones), and mixed-conifer/evergreen on mesic sites. Using forest types as defined by Cowlin et al. (1942) for eastern Oregon and Washington, mixed severity fire regimes were probably common in the “pine mixture”, “upper slope mixture”, “Douglas-fir”, and “white fir” types, all four being mixed conifer forest types occupying relatively cool and mesic environments above the forest-shrub land ecotone. The pine mixture and upper slope mixture are distinguished by a relatively high proportion (20–50%) of ponderosa pine, while the other two types have a greater proportion of either Douglas-fir or



Fig. 3a. Bailey Sections and Subsections in Oregon, Washington, and California with forest vegetation types that display mixed severity fire regimes (Bailey, 1995, 2009, http://svinetfc4.fs.fed.us/clearinghouse/other_resources/ecosubregions.html). Section M261A has been modified along the Southwest Oregon coast according to Frenkel (1993) to exclude an area of mostly high severity regimes. Most Sections also contain areas of either low-severity or high-severity regimes (or both). Section alphanumeric codes are: M242B (Western Cascades), M242C (Eastern Cascades), M261A (Klamath Mountains), M261B (Northern California Coast Ranges), M261C (Northern California Interior Coast Ranges), M261D (Southern Cascades Section), M261E (Sierra Nevada), M261F (Sierra Nevada Foothills), M261G (Modoc Plateau), M332G (Blue Mountains), and M333A (Okanogan Highlands).

white fir (Cowlin et al., 1942). Western larch is a common component, particularly in the latter two types.

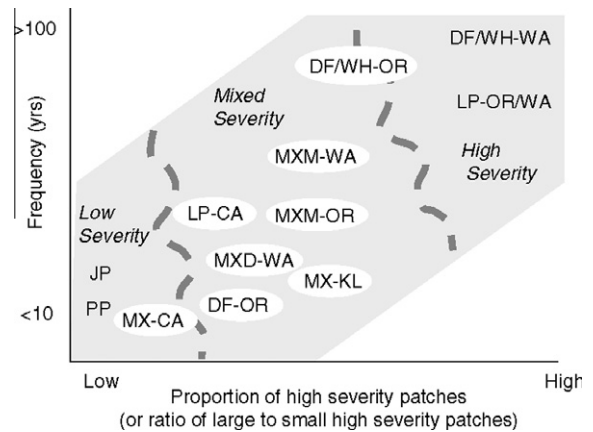


Fig. 3b. General distribution of low, mixed, and high severity disturbance regimes in relation to proportion of high severity patches and frequency of fire for the Pacific Northwest and northern California. The centers of the distributions of a few of the major forest types are shown to illustrate variation. Geographic modifiers illustrate that disturbance regimes of a forest type can vary geographically. PP = ponderosa pine, JP = Jeffrey Pine, DF = Douglas-fir, MX = Mixed conifer, WH = western hemlock; LP = lodgepole pine. WA = Washington, OR = Oregon, KL = Klamath region of California and Oregon, CA = California Cascades and Sierra Nevada.

In the eastern Washington Cascade Mountains and across the Okanogan Highlands, forest types we classify as having predominantly mixed severity regimes (Fig. 3) represent about 30% of total forest area, while in eastern Oregon they represent about 13% (Cowlin et al., 1942). The total area of mixed regime types is similar between the two states (except for the Douglas-fir type, which is concentrated largely in Washington), however, eastern Oregon has more total forest area and a four-fold greater area of dry ponderosa pine types.

In the southern Cascade Range northern Sierra Nevada, and Klamath Mountains, mixed severity fire regimes are associated with mesic mixed conifer/hardwood forests, Douglas-fir, and red fir forest types (Skinner et al., 2006; Skinner and Taylor, 2006; Collins and Stephens, 2010). Relatively mesic Douglas-fir/hemlock forests in low to mid elevations of the western central Cascades may also have experienced mixed severity fire regimes, occasionally with more surface fire than stand replacing effects, but generally the converse was true (Morrison and Swanson, 1990).

Within a given forest type the characteristics of mixed severity fires vary spatially over environmental gradients that often follow large and small topographic features. In both the eastern Cascade Mountains and the Okanogan Highlands of eastern Washington, Hessburg et al. (2007) found that mixed severity fires occurred in both the mesic and the dry forests of the Douglas-fir and grand fir zones during the pre-suppression era, representing about 58% of that region. In moist mixed conifer, they found that stand replacement fire effects were slightly more widespread in patches than surface fire effects, while in dry mixed conifer, surface fire effects were more widespread by nearly 2:1. Similarly, whereas all of the Klamath Mountains can be classed as having a mixed severity regime, surface fires became more dominant as one moved from the mesic western portions to the dry eastern portions of the range. (The Biscuit fire burned in the relatively mesic northwestern portion). This same pattern likely holds over moisture gradients in any subregion, and across the north-south moisture gradient within the region, with the result that forest type alone is not a good predictor of the proportion of low and high severity patches that

may occur within mixed severity regimes of the region. Some forest types that are typified by mixed severity regimes in Washington fall into a low severity regime in California. That is the case with dry Douglas-fir and mixed conifer types, which in California are typified by low-intensity surface fire rather than mixed severity (Skinner et al., 2006; Skinner and Taylor, 2006).

2.2. What influences the relative proportions of high and low severity?

Any given fire regime is influenced to one degree or another by both top-down and bottom-up forces. From the top-down, spatio-temporal patterns of regional climate influence fire frequency and severity through patterns of seasonality, temperature, and precipitation (Littell et al., 2009). To a certain extent throughout the region, but especially in California and southwestern Oregon, top-down climatic control is exerted largely through the Mediterranean climate of long, dry summers that provide for conditions where fires can readily burn in mixed conifer forests regardless of variation in total annual precipitation (Minnich, 2006). However, fire activity varies year to year, which Littell et al. (2009) correlate with variations in either summer precipitation or summer Palmer Drought Severity Index and other researchers associate with large scale atmospheric phenomena that alter winter precipitation (Norman and Taylor, 2003; Gedalof et al., 2005; Taylor et al., 2008, 2006; Trouet and Taylor 2009, 2010; Trouet et al. 2010). Years with low winter precipitation and high fire risk are associated with a strong atmospheric ridge that blocks moisture from moving onshore (the Pacific North American teleconnection pattern, or PNA), however the strength of this effect varies with phases of both the Pacific Decadal Oscillation (PDO) and the El Niño Southern Oscillation (ENSO). Wet-dry patterns are not necessarily synchronous across the region. In particular, ENSO and the PDO exhibit a dipole between the northwestern and southwestern US with the fulcrum shifting north or south in the vicinity of the Klamaths on a decadal time scale (Westerling and Swetnam, 2003). In consequence, dry years in the Sierras and Klamaths may or may not correspond to dry years further north (Skinner, 2006; Trouet et al., 2006). Over longer time scales, a 2000 year record of sediment cores from the Oregon Siskiyou shows that large sediment pulses occurred frequently during the Medieval Warm Period, with long periods of low sediment input immediately before and after (the latter corresponding to the Little Ice Age) (Colombaroli and Gavin, 2010). Questions remain about the degree to which that work can be generalized and the relation between sediment yields and fire characteristics.

From the bottom up, local factors (e.g. stand and landscape structure, topography) exert a strong enough influence that locales may burn quite differently even under the same top-down conditions (Skinner et al., 2006; Skinner and Taylor, 2006; Colombaroli and Gavin, 2010). Regional climate is filtered and shaped by broad-scale geologic, vegetative, and geomorphic conditions. For example, Hessburg et al. (2000b, 2004) found that patterns of fire severity eastern Washington were best explained by grouping into eco regions with similar biogeoclimatic influences. The moisture regime of each biophysical setting (precipitation + soil depth + soil organic deposits + evapo-transpiration) interacts with local biotic factors (e.g. fuel bed characteristics, stand composition and structure) and biotic patterns at the landscape scale to determine fire severity regimes (Miller, 2003). In eastern Oregon and Washington, white fir types, so named because land cover was dominated by white or grand fir (50% or more by volume), commonly occurred on relatively cool and moist topographic positions (e.g. north slopes) within the elevation range of ponderosa pine (Cowlin et al., 1942). These provided potential habitat for species that prefer relatively closed forests, and may have been important seed source areas for the invasion of white and grand fir into ponderosa pine dominated patches following the modern era of fire exclusion (e.g. Camp et al., 1997).

Because of their relatively high fuel moisture, riparian zones tend to buffer the spread of fires, but with their relatively high biomass may change from fire suppressors to fire corridors if fuel moisture drops sufficiently low (Pettit and Naiman, 2007).

Humans significantly altered fire regimes even before the EuroAmerican era. In some areas of the Northwest, burning by Native Americans altered the dominant effects of climate and may have converted potentially mixed-severity regimes to frequent, low-intensity ones. For example, in the Little River watershed of the Umpqua National Forest (Oregon), the relationship between fire occurrence (as measured by bole scars) and precipitation (as measured by tree ring widths) changed in the mid-19th century, coincident with declining populations of Native Americans (Carloni, 2005). Fire scars from 1590 to 1820 were not correlated to precipitation, whereas between 1850 and 1950 they were. Similarly, tree regeneration was uncorrelated with fire events between 1590 and 1820, but between 1850 and 1950 there was a highly significant positive correlation. Similar patterns were probably found in areas with high densities of Native Americans in California (Anderson 2005, Stephens et al., 2008; Skinner et al., 2009).

In the more mesic northerly parts of the region, cool, moist northerly aspects may burn with mixed severity while adjoining southerly aspects burn with low severity, or both may burn with mixed severity with stand replacement fire dominating on the northerly aspects and surface fire dominating on southerly. In the more arid Klamath Mountains the opposite is seen, patchy fires dominating on south and west facing aspects and low severity fires dominating on north and east facing aspects (Taylor and Skinner, 1998). Severe weather conditions can override topographic effects to at least some degree. For example, aspect effects were weak in the Biscuit fire, perhaps because the hot, dry winds that drove the fire during its blow-up period came from the NE and drove the fire against aspects that are often considered refugia (Thompson and Spies, 2010). However, in the Megram fire (Northern California, 1999) under similar severe conditions, topography was significantly associated with fire severity patterns (Jimerson and Jones, 2003).

2.3. Vegetation type and structure

Within a given climatic regime, and even within a given fire, densely stocked, uniform forests have a relatively high probability of burning with lethal effects dominating. However, several caveats go with this. In the case of plantations, flammability has been found to depend on the degree and kind of slash treatment during site preparation (Huff et al., 1995; Weatherspoon and Skinner, 1995). Weatherspoon and Skinner (1995) found that techniques which encouraged the growth of grasses (machine piling) resulted in greater fire damage, while those that produced a forb cover (broadcast burning) resulted in less and plantations in which logging slash had not been treated suffered heavily. As fully-stocked stands of shade intolerant species mature, self-pruning raises crown base height and shading discourages the development of other fuel ladders, lessening the chances of fire propagating from ground to crowns (but vulnerability to crown fire via fuel ladders in adjacent stands remains). Such stands are on their way to becoming the mature closed conifer stands that were the most resistant vegetation type in the Biscuit fire (Thompson and Spies, 2009, 2010). There are significant variations on that theme; if stands are too dense individual tree growth is retarded and movement toward a resistant mature stand may be impeded, while the

vegetation that develops beneath an open stand may act as fire suppressants rather than fuel ladders (Agee et al., 2002).

With the exception of extreme fire weather conditions (≥ 95 th percentile), forests composed of large and very large fire tolerant species tend to burn at low or mixed severity with surface fire effects dominating even when overstory canopies are dense, in part at least because trees are tall with live crowns relatively far above the surface (Stephens and Moghaddas, 2005; Thompson and Spies, 2009; Thompson and Spies, 2010). However, that depends on the dominant tree species, which in turn reflects site characteristics and probably fire history. In the 1987 fire complex in Northern California, stands dominated by ponderosa pine experienced higher severity than those dominated by Douglas-fir or hardwoods, which Weatherspoon and Skinner (1995) attribute to “the fuelbed, usually warmer and drier sites, and generally more open stand structure of ponderosa pine-dominated stands”. Weatherspoon and Skinner also suggest that ponderosa stands, with their past history of frequent surface fires, were more impacted by fire exclusion during the 20th century than Douglas-fir stands. In central Oregon’s B & B fire, however, ponderosa pine stands burned with lower severity than mixed-conifer, perhaps because the latter had increased fuel loading as a result of recent insect and disease mortality.

Stands dominated by hardwoods tend to burn with lower intensity than conifer-dominated stands (Skinner and Chang, 1996; Skinner et al., 2006), and there are anecdotal examples of mid story hardwoods protecting conifers in the Siskiyou (Perry, 1988; Raymond and Peterson, 2005). Hardwood-dominated stands suffered higher levels of damage during the Biscuit fire than closed conifer stands (Thompson and Spies, 2010), however, crown damage does not necessarily correlate with propagating flames to adjacent crowns (e.g. when damage is due to scorch rather than consumption). In the Biscuit fire, when hardwoods were intermixed with conifers “the hardwood subcanopy affected fire behavior in ways other than serving as a ladder fuel” (Raymond and Peterson, 2005). Raymond and Peterson speculated that mature hardwoods shaded dead fuels and slowed their desiccation, reduced wind speed within stands, and blocked the propagation of heat upwards into conifer canopies. A conifer subcanopy would also produce the first two effects, however the third depends on flammability, a function of chemical content (esp. monoterpenes), hydration, and leaf structure, factors in which conifers and hardwoods differ (Agee et al., 2002). In their study of foliar moisture content in Pacific Northwest species, Agee et al. (2002) concluded that understory grasses would have a dampening effect on flame lengths into September and understory shrubs would have a dampening effect into October. On the other hand, conifers suffered the worst crown damage in the Biscuit fire when in open forests with a shrub understory (Thompson and Spies, 2009). Species composition matters; shrubs in the Thompson and Spies study were predominantly sclerophyllous species that, as we discuss below, may burn readily.

Depending on species composition and age, early successional stands can be quite flammable. In the 2002 Biscuit fire, stands that originated from the 1987 Silver fire (predominantly *Ceanothus* and *Arctostaphylos* shrubs, with intermixed sprouting hardwoods and young conifers) experienced significantly more canopy damage than older, closed conifer forests (Thompson and Spies, 2010). Similarly, in their study of recent fires in Yosemite National Park, Collins and Stephens (2010) found that stands were most susceptible to high severity reburn when they were between 17 and 30 years old. In contrast, in their youngest stages early successional stands have been found to be less flammable and constrain the extent of fires. For example, recently burned forest patches in mesic Sierran mixed conifer forests constrained the extent of subsequent fires when the time since previous fire was 9 years or less (Collins et al., 2009). The period of relatively low flammability likely varies with a number of factors such as the rate at which flammable

biomass accretes and interactions between weather and topography. Post-fire management may also have an effect. As mentioned earlier, stands that were salvage logged and planted to conifers following the 1987 Silver fire reburned more severely in the 2002 Biscuit fire than stands that had not been salvaged and planted, although the difference was not large (Thompson et al., 2007; Thompson and Spies, 2010).

2.4. Landscapes: context, fences and corridors, self-organization

The complex mosaic resulting from variety in successional and structural conditions across a broad spectrum of patch sizes potentially affects patterns of burning in at least two ways. Intuitively, fire severity within patches can depend on the larger landscape context, and research supports this idea (Weatherspoon and Skinner, 1995; Fites-Kaufmann, 1997). For example, patches that for environmental and structural reasons are conditioned to burn with mostly stand replacing effects may burn with moderate severity if embedded within a landscape dominated by low-moderate intensity fire (Fig. 4). Likewise, stands conditioned to burn with mostly surface fire effects dominating may burn with mixed or even high severity if embedded within a landscape prone to high-intensity fire (Hessburg et al., 1999a, 1999b). Fire frequency may also depend on context, with mixtures of short- and long-interval types resulting in the frequency of each shifting toward the other (Agee et al., 1990). At a more dispersed level, the variable grain and pattern of the mixed-severity mosaic act as a patchwork quilt of “fences and corridors” that interact with topographic complexity and top-down climatic drivers to either facilitate or resist the movement of fires (or insect outbreaks or species migrations) (Moritz et al., 2010).

What is the dynamic of this pattern? Is it a shifting mosaic, and if so is there a landscape-level self-organizing² aspect that constrains overall patterns within a certain envelope (Moritz et al., 2010)? Or are there stand-level self-organizing aspects in which certain structures tend to perpetuate themselves and maintain a semi-static mosaic (Perry, 1995; Skinner and Taylor, 2006; Odion et al., 2009)? The answer to all three questions is probably yes; the mixed severity dynamic is too complex to be neatly pigeon-holed, and different mechanisms may operate at different temporal and spatial scales (Holling, 1992; Perry, 1995; Moritz et al., 2010).

As we have discussed, even within shifting mosaics the patterns of natural wildfires are constrained within certain envelopes by climate and topography. Current studies also support the existence of self-reinforcing community structures, or to use Peterson’s (2002) terminology, memories of past disturbances influence responses to future disturbances. In the Biscuit fire, for example, the strongest predictor of relative crown damage was crown damage in the Silver fire, which burned 15 years previously within the same area (Thompson and Spies, 2010). Followed to its logical conclusion, and depending on fire return intervals, system memory would tend to push the landscape toward a binary condition of early successional shrub fields and older closed conifer forests. Because fires that are sufficiently severe have some impact even on relatively resistant forests (Thompson and Spies, 2010), repeated fires at sufficiently short intervals could erode the binary landscape structure over time, however Moritz et al. (2010) argue that lagged effects of past fires and recovery rates (sensu Peterson, 2002) would prevent that from happening and maintain structural diversity on the landscape. Moreover, variability in fire return intervals

² Self-organization refers to the tendency for system dynamics to emerge from internal interactions and structure rather than outside forces. “Self-reinforcing” is a similar concept in which system structure leads to processes that tend to maintain the structure. The dynamics of any system are likely to be driven by both external and internal forces.

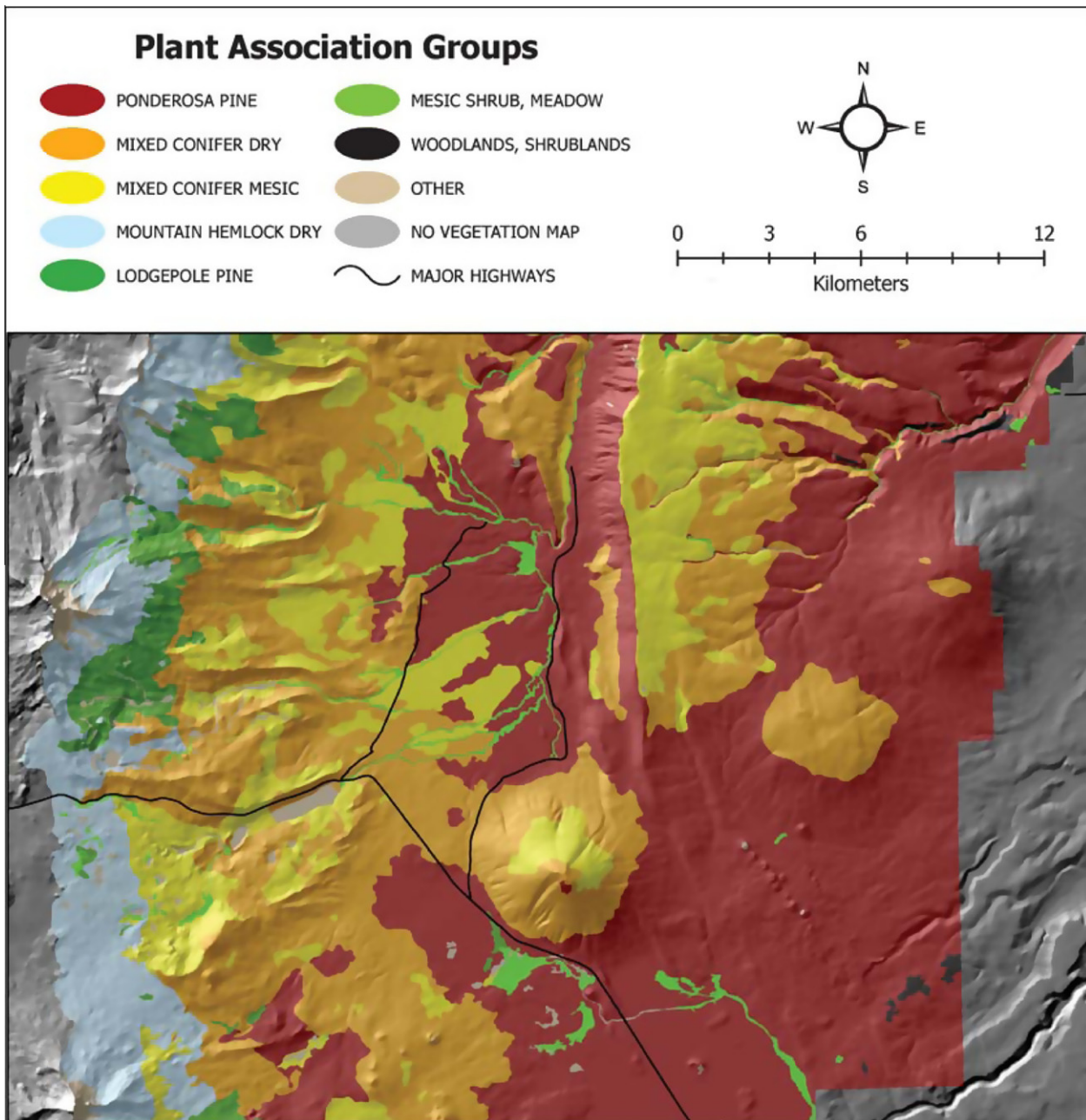


Fig. 4. Relationship between plant association groups and topography on a portion of the Deschutes National Forest, Oregon. Note the intermingling of forest types that occupy different positions on the mixed-severity gradient (refer to Fig. 3). From Spies et al. 2006.

at the landscape scale would allow some areas to develop greater resistance (e.g. thicker bark, higher crowns) and thereby lower severity.³

The two clearest examples of self-reinforcing memory in the Pacific Northwest are montane *Ceanothus/Arctostaphylos* shrub fields (chaparral) and forests dominated by large, fire resistant tree species. Skinner and Taylor (2006) hypothesize that because of the frequency with which it burns, chaparral disrupts the normal successional processes that act to bring forest back. Topographic position, edaphic conditions, and less frequent, but more intense fires contribute to long-term persistence of chaparral in the landscape (Nagel and Taylor, 2005; Odion et al., 2009), especially on the upper

third of slopes and ridgetops, topographic positions prone to more severe fires (Weatherspoon and Skinner, 1995; Taylor and Skinner, 1998; Beaty and Taylor, 2001). The chaparral growth habit of mostly live material with little surface fuel hinders fire from burning under all but the most severe conditions, but when it does burn it tends to crown and kill intermixed conifers (Thompson and Spies, 2009). In contrast, the neighboring conifer stands produce ample needle cast and small dead material to carry fires more frequently under more benign burning conditions.

Patchy but abundant conifer regeneration has been documented within early successional shrub/hardwood communities in the Klamath Mountains (Shatford et al., 2007; Donato et al., 2009), at least some of the patchiness determined by whether or not the broadleaves and conifers share mycorrhizal species (Horton et al., 1999). However, the time required for conifers to

³ We are indebted to an anonymous reviewer for pointing this out.

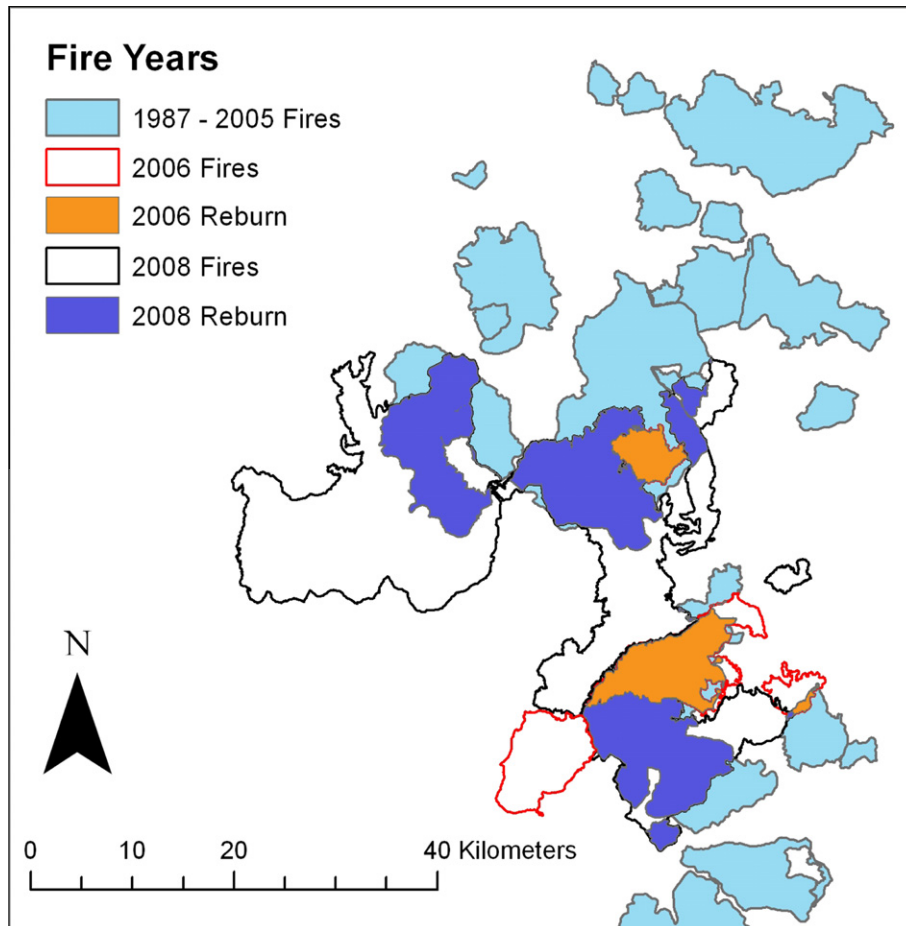


Fig. 5. Map of recurring fires in the Klamath Mountain portion of the Shatford et al. (2007) study. Light blue are areas burned from 1987–2005. The orange areas reburned in 2006, while the dark blue areas reburned in 2008. The dark blue area near center is the location of several of their data sites (see Shatford et al., 2007, Fig. 1, p. 140). Base map by B. Estes.

achieve a size sufficient to survive subsequent fires reduces the chances they will eventually replace chaparral (e.g. Fig. 5), although shrub seed banks and *Arctostaphylos* skeletons in mature conifer stands indicate that succession from shrub dominated communities to closed conifer forests is not uncommon (and has probably become more so in the era of fire suppression). The pathway followed by a given site is likely to depend on a variety of factors, including environment, history (e.g. the timing of a reburn), composition of the shrub community, and initial shrub density. This diversity in pathways provides for heterogeneity of habitats across the landscape (Nagel and Taylor, 2005).

It is well known that short-term fluctuations in weather can strongly influence fire behavior, however both Thompson and Spies (2010) and Collins and Stephens (2010) found that, while weather was clearly a factor, self-reinforcing dynamics resulting from fire history and vegetation type were more important determinants of fire severity. It may take changes in climate over relatively long intervals to produce shifts in self-reinforcing components of the mosaic. Long periods with low or no fire activity would increase the probability of conifers replacing shrub fields and in many forest types long fire-free periods could also allow shade-tolerant fuel ladders to develop and increase the probability of stand-replacement fire in closed forests. For example, in their analysis of factors influencing stand-replacing patches created by mixed-severity fires in Yosemite National Park (fires had not been suppressed in certain areas of the park since 1975), Collins and Stephens (2010) found that the largest patches occurred in forests

where *Abies* spp. were intermixed with lodgepole pine, perhaps indicating succession to the more shade tolerant firs. Taylor and Solem (2001) found that *Abies* spp. are replacing lodgepole, ponderosa, and Jeffery pines in California's Caribou Wilderness.

However, fire-free period is not by itself a good general metric for susceptibility to severe fire. Collins and Stephens (2010) found that larger stand-replacing patches in pine and shrub-dominated vegetation types occurred in areas that had burned 17–30 years previously. They attributed the relatively small patch sizes in older stands of those types in part at least to discontinuous fuel beds and the presence of natural fire breaks. Both Odion et al. (2004) and Thompson and Spies (2009) found that stands with the longest fire-free periods in the Klamaths burned with the lowest severity. Stand-development pathways in mixed evergreen forests of the Klamaths are likely to have different implications for fire susceptibility than in other regions, in part because of the large hardwood component. For example, many of the stands studied by Odion et al. (2004) had subcanopies dominated by tanoak. Various factors may play a role in the degree to which vegetation strata function as fuel ladders or fire suppressors (e.g. through foliar characteristics or by suppressing solar radiation and wind speed), and given the wide range of environments occupied by mixed-severity forests these functions probably vary significantly throughout the region. Proximity to seed sources for shade-tolerant tree species is one likely factor. It is possible that more productive sites with relatively high closure in the upper canopy retard the establishment and growth of even shade-tolerant tree species, however

on the east slopes of the Oregon Cascades understory *Abies* spp. were abundant in stands with basal areas up to $26 \text{ m}^2 \text{ ha}^{-1}$ in large (>50 cm DBH) early seral tree species (Perry unpublished). There, *Abies* stocking was influenced primarily by mean annual precipitation. Nevertheless, selective logging or natural processes that open the upper canopy and allow light to penetrate potentially stimulate development of fuel ladders in some stands.

In summary, extended periods with relatively low fire activity have the potential to trigger shifts in the self-reinforcing landscape mosaic, but the dynamic is likely to be complex and such shifts are not a foregone conclusion.

Riparian zones have been little studied with regard to fire; however they represent a significant landscape feature that in at least some cases affects fire behavior at larger scales. In the Klamath Mountains, Skinner (2003) found that, while the range of fire return intervals (FRI's) were similar between riparian (along perennial streams) and upslope areas, median FRI's were approximately twice as long in the former as in the latter. Skinner et al. (2006) concluded that, in the Klamaths, "...riparian areas along perennial watercourses served as effective barriers to spread of many low-intensity and some moderate-intensity fires and strongly influenced patterns of fire occurrence beyond their immediate vicinity". Olson and Agee (2005) found a similar pattern on the western slopes of the Cascades in southern Oregon, however median FRI's differed much less between riparian and upslope than they did in the Klamaths and were statistically insignificant. More work is needed on this topic.

3. Biodiversity threats associated with contemporary conditions

Logging and fire suppression during the 20th century have increased the density of young conifers and in many cases triggered a shift from shade-intolerant to shade-tolerant species, putting some components of biological diversity at risk (Perry et al., 2004; Hessburg et al., 2004; Haugo et al., 2010; Naficy et al., 2010). EuroAmerican settlement and management exacted an enormous toll on the large tree structure of the forests of the historical mixed severity regime. Not only were old forests clearcut, but in many areas large and very large remnant emergent trees that made up the upper crown classes of forest patches were selectively harvested (Hessburg et al., 2000a, Hessburg and Agee, 2003). The area of old forest habitat in eastern Oregon and the interior Columbia Basin has been sharply reduced (Henjum et al., 1994; Hessburg et al., 2000a, Wisdom et al., 2000), and the remainder is threatened by wildfires, drought, and insects. For example, about 3 per cent (>5500 ha) of older forest on the east slopes of the Cascades was burned by stand-replacing fires between 1994 and 2003 (Moeur et al., unpublished data). During the same period in the Oregon Klamath province about 11 per cent (>32,500 ha) of older forest burned at high severity (Moeur et al., unpublished data).

Particularly in the dry portions of the mixed conifer zone, decades of fire suppression have accelerated successional processes and set the stage for resistant forest structures and landscape patterns to be weakened and overcome. Young conifers are poised to dominate many early successional shrub-hardwood communities and have established in relatively high numbers beneath older

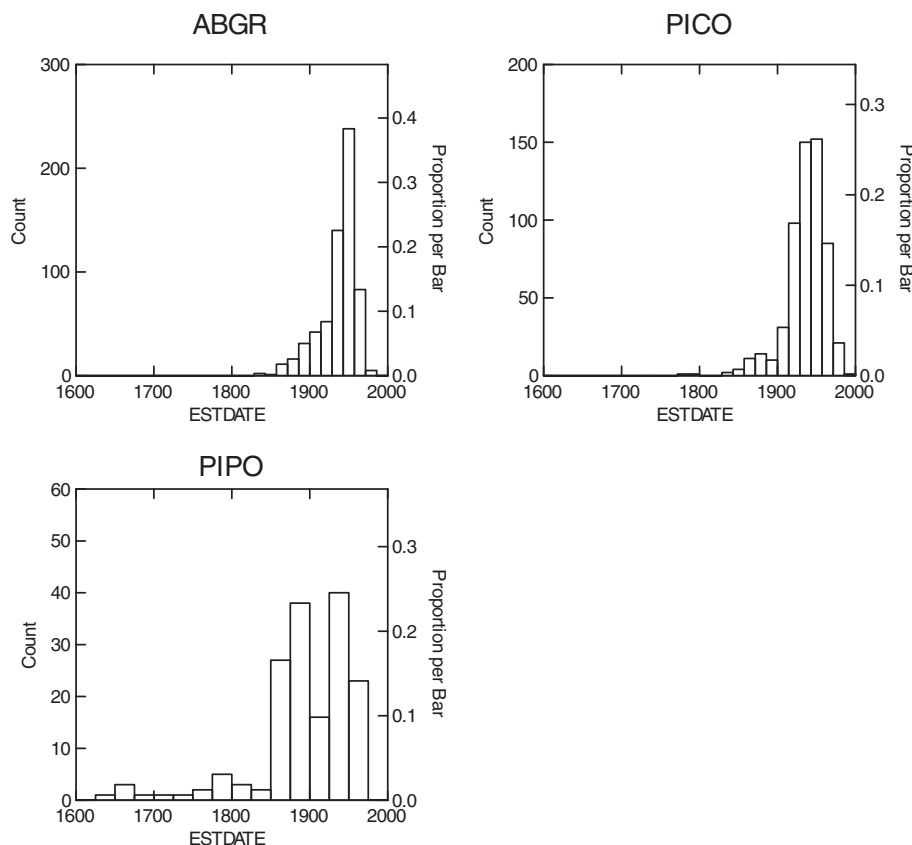


Fig. 6. Establishment date (at breast height) for ponderosa pine (PIPO), grand fir (ABGR), and lodgepole pine (PICO) in old growth forests within the mixed-conifer zone on the Deschutes National Forest, Oregon. Note different Y-scales. Adapted from Perry et al. (2004).



Fig. 7a. Top: Jeffrey pine-white fir and red fir stands in Lassen Volcanic National Park in 1925. Patches of mature trees of variable size are intermixed with areas dominated by shrubs. This vegetation pattern is the result on mixed severity fire effects that burn areas at low, moderate, and high severity. Shrub cover is much lower in 2009 (bottom) and the shrub fields have been invaded by mixture of white fir, Jeffrey pine, red fir, and western white pine. Overall, the forest is now more dense and the forest cover is more homogenous than in 1925. Fires burned frequently in this landscape until fire suppression became effective in 1903 (Taylor, 2000).

stands of early successional, fire resistant trees (Figs. 6 and 7). The latter may be accompanied by a dramatic shift in tree species composition. For example, a study in the mixed conifer zone on the eastern slopes of the central Oregon Cascades found that, while 89 percent of trees older than 150 years were either ponderosa pine, western white pine, or Douglas-fir (all relatively fire resistant after the sapling stage), 90 per cent of trees younger than 100 years were either grand fir or lodgepole pine (Perry et al., 2004).

Relationships between conifers and shrubs are not solely antagonistic. Through their ability to recover quickly (from sprouts or seed banks) and stabilize soils, shrubs and hardwood trees play essential roles in ecosystem resilience (Perry et al., 1989). Ectomycorrhizal species (e.g. manzanita, oaks, madrone) stabilize mycorrhizal fungi and perhaps other soil biota that are important to conifer recovery (Amaranthus and Perry, 1989; Borchers and Perry, 1990; Perry et al., 1989), and *Ceanothus* spp. replenish soil nitrogen. In the Klamaths, both the density and relative growth rate of conifer regeneration correlate positively with density of broadleaves in recovering burns within the Douglas-fir and Douglas fir/tanoak vegetation series (Shatford et al., 2007; Irvine et al., 2009). These associations are negative in the white fir series; however, Shatford et al. (2007) found abundant conifer regeneration within shrub fields in that zone.

Increased stocking densities resulting from invasion by Douglas-fir, grand fir, white fir and lodgepole pine have increased fire risk in some forest types, especially the dry eastern slopes of the Cascades, western slopes of the southern Cascades, and lower to midslopes of the Sierra Nevada. Significant increases in stocking density due to fire suppression are less likely in the more mesic to wet western slopes of the central and northern Cascades and eastern slopes of the Coast Range in Oregon and Washington. In the highly diverse Klamath Range, topographic and vegetation complexity make generalizations difficult. However there, as elsewhere, the effect of ingrowth is locally modified by topography and associated environmental conditions. Moreover, in some cases trees that are potential fuel ladders may have the opposite effect and reduce fire intensity by creating shaded cooler conditions and blocking wind, a poorly understood effect not necessarily restricted to the Klamath region.

The fire risks posed by ingrowth vary with species and forest type. We have discussed broad-leaved hardwoods in this respect. On the eastern slopes of the Oregon Cascades stocking density of *Abies* spp., which increases with mean annual precipitation, is a significant predictor of crown fire risk, but density of *Pinus* spp. is not (Perry et al., 2004, Perry unpublished),⁴ reflecting in part the long crowns maintained by shade-tolerant *Abies*. By virtue of hydration and foliar chemistry, some species are less flammable than others (e.g. Weatherspoon and Skinner, 1995). Improved understanding of interactions among plant species, fire behavior, and climatic context are key research questions.

Threats to the biodiversity of mixed-severity ecosystems are exacerbated by various factors that homogenize landscapes, reducing beta diversity and potentially synchronizing fires and insect outbreaks. The spread of fuel ladders out from topographically-protected areas sets the stage for fires to burn with more uniform high severity than had probably been the case in the past (Schoenagel et al., 2004). A possible example of that effect is the B & B fire in central Oregon, where dry and moist mixed conifer burned with similar severity. Increased evapotranspiration by densely stocked stands reduces water available to streams, which in turn likely effects fuel moisture in riparian zones and could shift riparian areas from fire barriers to fire corridors.⁵ Large wildfires homogenize the landscape, and uniform fuels reduction potentially does so as well. While mixed severity forest types contained dense patches of young trees in the past and experienced some high severity fire, both the abundance of young trees and the likelihood of large, high severity fires have increased. The predominance of densely stocked plantations in some areas has in all likelihood altered the landscape disturbance dynamic, although exactly how is unclear.

Even where fires are patchy, the increased predominance of late successional tree species has altered the composition of the seed rain and, depending on survival probabilities, may shift species composition of the regenerating forest from a dominance by early-successional to a dominance by late successional tree species. Fire suppression has resulted in fewer and smaller naturally-recovering, early successional gaps and patches being created or maintained (Skinner, 1995).

Fire risk is not the only issue. Drying and warming due to climate change is poised to dramatically alter the environments many forests now experience (Neilson et al., 2005, 2007; McKenny

⁴ Multiple regression relating the critical wind speed for producing a crown fire (predicted by NEXUS) to crown bulk density, crown base height, stocking density of *Abies*, and stocking density of *Pinus* accounted for 97% of the variation among plots (plot variables were described by Perry et al. 2004). All variables correlated negatively with the critical wind speed (i.e. as they increased the threshold for crown fire decreased), and all except stocking density of *Pinus* entered the model with a probability of at least .005 (*Pinus* had a probability of .227). The difference between species was not related to differences in overall stocking density.

⁵ Frank Lake, personal communication.



Fig. 7b. Young grand fir beneath old growth ponderosa pine. Deschutes National Forest, Oregon. Plots within old-growth forests in the mixed conifer zone of the Bend Ranger District show that 90 percent of trees older than 150 years are ponderosa pine, Douglas-fir, or western white pine, while 90 per cent of trees younger than 100 years are grand fir or lodgepole pine (Perry et al., 2004).



Fig. 7c. Young Douglas-fir beneath older ponderosa pine. Rogue River National Forest, Oregon.

et al., 2007; Brown, 2008; Marlon et al., 2009). For example, in Washington State, Littell et al. (2010) concluded that “climate will be inconsistent with the establishment of Douglas-fir, ponderosa pine, and lodgepole pine in many areas by the middle of the twenty-first century”. Models show that northeastern British Columbia, currently occupied by boreal forest, will have a climate more suitable for ponderosa pine by 2080 (Hamann and Wang, 2006). In all likelihood fire behavior will be altered along with climate (Bachelet et al., 2007; Marlon et al., 2009; Littell et al., 2010); in fact, an analysis of Canadian fires since 1970 shows that climate warming already is producing increased fire activity

(Gillett et al., 2004). One implication is that the characteristic boundaries between high-, mixed-, and low severity fire regimes will shift.

All trees in densely-stocked stands are threatened by drought, which has been and is predicted to continue increasing in the western US (Dai 2010). A recent study found that 72 percent of gauging stations in the Pacific Northwest experienced significant declines in 25th percentile flows between 1948 and 2006, i.e. dry years are getting drier (Luce and Holden, 2009). A significant increase in non-fire mortality of old growth trees over the past several decades is probably due to increasing water deficits (Guarin and

Taylor, 2005; van Mantgem et al., 2009 Overstocking undoubtedly contributes significantly to this problem. On Blacks Mountain Experimental Forest in Northern California, an average of 63 percent of large trees (>60 cm DBH) were rated at high risk to mortality in unthinned plots, compared to 16 per cent in heavily thinned plots (Ritchie et al., 2007).

It is not only trees that are threatened by overstocking. Densely stocked stands alter the light environment and significantly impact understory diversity and cover. On the Stanislaus National Forest (Northern California), studies on permanent plots showed that between logging in 1929 and remeasurement in 2008, the cover of understory shrubs went from 28.6% to 2.5%, with *Ceanothus* and *Arctostaphylos* almost completely dropping out (Eric Knapp personal communication). The number of stems of herbaceous species dropped from an average of 4.0 to 0.9 m⁻², but there was great deal of variability around those averages. In 2008, tree density was approximately double the historic norm on these sites. Historically, such high densities may well have occurred as patches in mixed severity regimes, but not uniformly across the landscape.

Replacement of early successional shrub-hardwood communities by closed forests in the absence of fire significantly impacts landscape diversity. Shatford et al. (2007) recorded 47 species of shrubs and hardwoods in early successional communities of the Klamaths. Fontaine et al. (2009) found that broad-leaved hardwoods and shrubs played a major role in structuring bird communities in the Klamaths, and concluded that “extended periods of early seral broadleaf dominance and short-interval high severity fires may be important to the conservation of avian biodiversity”. Not surprisingly, however, they also found that closed forests and early-successional communities were characterized by different avian guilds. As we pointed out earlier, it is the diversity of successional stages across a landscape that creates the high species richness typical of mixed-severity types, not any one particular community type.

4. Research needs

- (1) More needs to be known about the biodiversity costs associated with loss of open canopied forest or early successional patches, and the landscape mix that best accommodates diverse habitat needs.
- (2) Better estimates are needed of the relation between stand density/ species mix and water use, and particularly the degree to which older trees are water stressed by the presence of younger trees within a stand.
- (3) Topographically-related patterns of burning vary significantly from north to south across the region. Although history is no longer necessarily a reliable guide to the future (Millar et al., 2007), it seems likely that historic topographic relations to fire will be preserved in a warming climate. Because they provide insights into landscape strategies, more needs to be known about historic patterns in specific locales.
- (4) The ecological functions of hardwoods in the Klamath region should be clarified, especially with regard to their role in fire (their importance as both habitat and rapid-response soil-stabilizers seems clear). While there is considerable evidence that hardwoods reduce fire severity when intermixed with conifers, results from the Biscuit fire appear not to fit that pattern. Why the difference?
- (5) Regional variation in mixed severity fire regimes and their ecological effects needs to be characterized more systematically and in greater ecological and spatial detail. We have highlighted some of the major differences in this paper but further work is needed to create a solid foundation for

conservation and restoration. For example, we do not know how to spatially stratify fire regimes and restoration needs at subregional-landscape scales based on topography, potential vegetation, and current vegetation.

5. Summary

1. The defining element of mixed severity regimes is spatial and temporal variability in fire effects and ecological responses. Regimes vary regionally in the mean proportion of high severity patches and the frequency with which fires occur. However, some aspects of spatial patterning seem relatively constant, particularly the occurrence of a Pareto-type distribution of many small and few large high severity patches.
2. Consistent with the intermediate disturbance hypothesis, the diversity of patch types typical of mixed-severity regimes results in high levels of beta diversity in both plants and animals.
3. Wildfire behavior in mixed severity types is influenced by both top-down and bottom-up factors. From the top-down, regional climate, shaped by large scale atmospheric processes and modified by large scale geomorphic features, plays a key role. From the bottom up, local topography, vegetation type, and disturbance history influence burning patterns. Vegetation types (species composition and structure) that are either relatively vulnerable or resistant to stand-replacing fire can result in a self-reinforcing dynamic and consequent partial decoupling from the top-down effects of climate.
4. A combination of logging older forests and fire suppression has produced landscapes with many more young conifers than was likely to have been true prior to the 20th century.
5. Two or more canopy layers do not always mean higher risk for crown fire. It depends on region and species composition. Hardwoods respond differently to fire than conifers. In many cases they can help to reduce the intensity of a fire. In other cases, when they occur as dense young vegetation, they can help carry fire into crowns of adjacent conifers under extreme weather.

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