Chapter 10
Fire Ecology and Management in Pacific Northwest Forests

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Abstract Fire has been an important catalyst of change in Pacific Northwest forests throughout the Holocene. The role of fire varied across this biophysically diverse region prior to European colonization, but fire exclusion and logging drastically altered forest conditions during the 19th and 20th centuries. Despite recent increases in area burned and several large wildfires with devastating social and economic consequences, area burned in recent decades remains far less than under

Ecoregions 1, Coast Range, 2, Puget Lowlands; 3, Willamette Valley; 4, Western Cascades; 9, Eastern Cascade Slopes and Foothills; 11, Blue Mountains; 77, North Cascades; 78, Klamath Mountains / California High North Coast Range

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historical regimes across most of the region. Some dry forest landscapes have experienced profound change through uncharacteristically severe fires. In moist and cold forest landscapes, wildfires have enhanced biodiversity through the creation of structurally complex early-seral habitats. Area burned is expected to double or triple in the future under a warming climate. Strategies to adapt to future wildfires vary among historical regimes and biophysical settings and will require collaborative engagement and adaptive management to facilitate ecological change at meaningful scales.

Keywords Early-seral habitat · Old-growth · Northwest Forest Plan · Fire regimes · Oregon · Washington · Northern California

10.1 Introduction

The Pacific Northwest (Oregon, Washington, and northern California – hereafter PNW) is a biophysically diverse region that encompasses several mountain ranges and spans broad environmental and climatic gradients (Fig. 10.1). Forests stretching westward from the crest of the Cascade Mountains to the Pacific Coast include some of the highest biomass terrestrial ecosystems in the world and harbor unique biodiversity dependent on old-growth habitats (Spies et al. 2018). The drier eastern, and southern parts of the region were historically dominated by mosaics of woodlands, forests, and non-forested habitats.

While old-growth forests still occur over millions of hectares, most of the PNW bears legacies of more than a century of logging and fire exclusion. Forests in the drier eastern and southern parts of the region were affected by grazing of domestic animals, fire exclusion, and selective removal of large old-growth trees in the early to middle part of the twentieth century (Hessburg and Agee 2003). Clearcutting in lower elevations of the western part of the PNW began in the late 1800s, and large wildfires associated with timber harvests and burning by early settlers affected many parts of western Oregon and Washington. Logging began on federal lands in the 1940s and peaked in the 1970s and 1980s (Johnson and Swanson 2009). Court injunctions and passage of the Northwest Forest Plan (NWFP) in 1994 drastically reduced clearcutting of older forests on federal lands within the range of the northern spotted owl (*Strix occidentalis caurina*) (Spies et al. 2019).

Our goal is to provide an overview of fire as a driver of stand, landscape, and regional forest dynamics to inform current and future management issues in PNW forests. We begin by describing the forest vegetation and biophysical settings of the region and give an overview of how climate and fire drove millennial-scale vegetation change during the Holocene. We then introduce the regional fire environment and synthesize current knowledge derived from crossdated fire histories and

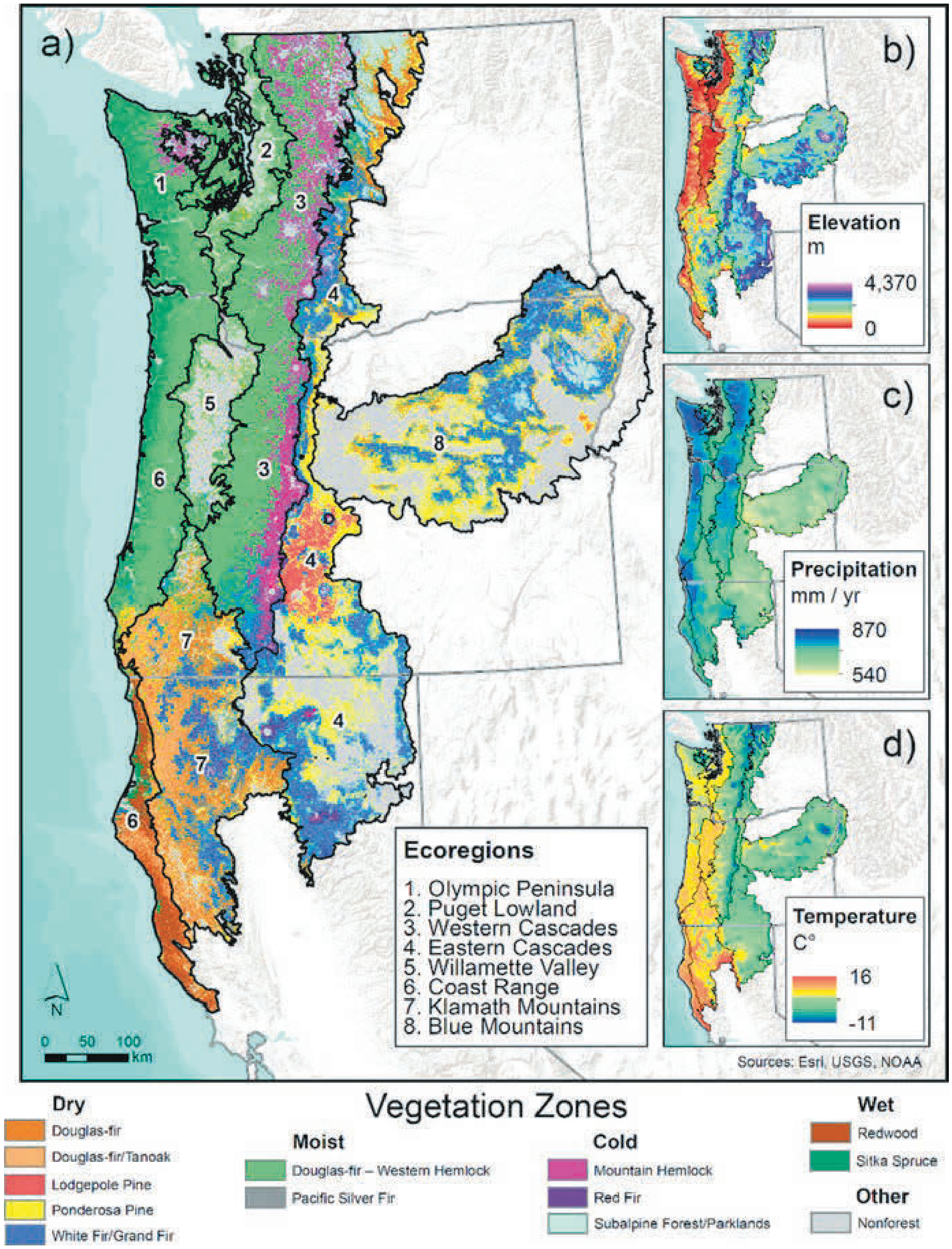

Fig. 10.1 Potential vegetation zones (Simpson 2020) and climatic setting of forested ecoregions in the PNW. Average annual temperature and average total precipitation are derived from PRISM grids (Daly et al. 2008) averaged from 1971 to 2000, obtained from the Landscape Ecology, Modeling, Mapping and Analysis group at Oregon State University

estimates of the historical range of variability (HRV) of forest conditions. We address the role of fire in promoting biodiversity and wildlife habitat, then review effects of contemporary fires and climate change in the context of current management issues.

10.2 Climate, Environment, and Forest Vegetation of the Pacific Northwest

The PNW region encompasses broad environmental and climatic gradients (Fig. 10.1). The climate is cooler and wetter towards the north with warmer, drier summers and greater inter-annual variability to the south and east of the Cascade crest (Chap. 9). Most precipitation falls during winter and the highest elevations receive significant snow which persists into June or July. Summer fog and low clouds are common along the coast and mitigate summer drought.

The broad environmental and climatic gradients are reflected in the distribution of several potential vegetation zones across the region (Fig. 10.1). These zones have similar internal biophysical conditions, as well as characteristic plant community assemblages, pathways of structural development, and historical disturbance regimes (Reilly and Spies 2015). While a few vegetation zones were traditionally characterized by one dominant fire regime, most are characterized by multiple regimes and experience low, moderate, and high-severity fire at broad temporal and spatial scales (Perry et al. 2011; Stine et al. 2014; Spies et al. 2018).

We provide a brief overview of the dominant wet, moist, cold, and dry vegetation zones in the PNW. Comprehensive characterizations of plant communities are found in Franklin and Dyrness (1973) for Oregon and Washington, and in Sawyer (2006) for northern California.

Wet forest types are dominant along coastal areas where a fog layer coming off the Pacific Ocean moderates summer temperature and drought. Sitka spruce (*Picea sitchensis*) occupies most of the coastal band from Washington to the southernmost extent of Oregon, while redwood (*Sequoia sempervirens*) becomes increasingly dominant in northern California.

Moist vegetation zones occur in Oregon and Washington west of the Cascade crest. The Douglas-fir/western hemlock zone comprises most of the moist forests at lower to middle elevations in the Coastal Ranges and western Cascades. This zone is primarily dominated by Douglas-fir (*Pseudotsuga menziesii*), with increasing abundance of shade-tolerant western hemlock (*Tsuga heterophylla*) in older stands. The Pacific silver fir zone occurs at middle elevations where much of the annual precipitation falls as snow. This zone is dominated by noble fir (*Abies procera*) and Pacific silver fir (*A. amabilis*) which generally increases in abundance in mature and late seral stands.

Cold forests zones include mountain hemlock and subalpine forests and parklands. The mountain hemlock zone is often dominated by monospecific stands of mountain hemlock (*T. mertensiana*). Lodgepole pine (*Pinus contorta*), a serotinous species primarily only at higher elevations in Oregon and Washington, is common in early seral stages of development. Western white pine (*P. monticola*) may also be an occasional component of the mountain hemlock zone in all stages of development. Shasta red fir (*A. magnifica var shastensis*) is dominant in upper montane forest of the Klamath Mountains and parts of the southern Cascades. At the highest elevations, subalpine forests and woodlands are dominated by subalpine fir (*A. lasiocarpa*), Engelmann spruce (*P. engelmannii*), western white pine, and lodgepole pine. Whitebark pine (*P. albicaulis*) is common at upper tree line in the highest mountains.

Dry vegetation zones occur across the eastern and southern part of the PNW. The ponderosa pine (*P. ponderosa*) zone occurs across much of the eastern part of the region where pure stands of ponderosa are common at lower elevations. Dry and moist mixed conifer forests occur across a broad precipitation and elevation gradient and include the grand fir, white fir, and Douglas-fir vegetation zones. Ponderosa pine is the predominant early seral species across most of the mixed conifer forests, though incense-cedar (*Calocedrus decurrens*) is common throughout and western larch (*Larix occidentalis*) may be co-dominant in some moist mixed conifer forests east of the Cascades. Grand fir (*A. grandis*) is the most common shade-tolerant species and transitions to white fir (*A. concolor*) in the southern Oregon Cascades and northern California. Mixed-conifer forests in the southern Oregon Cascades and Klamath Mountains are particularly diverse. Sugar pine (*P. lambertiana*) is a common long-lived early seral species. Knobcone pine (*P. attenuata*) is a serotinous species that may be locally abundant after fire or in the vicinity of serpentine soils. Jeffrey pine (*P. jeffreyii*) woodlands also occur on serpentine soils.

Dry vegetation zones in the Klamath Mountains also include mixed evergreen forests composed of Douglas-fir and tanoak (*Notholithocarpus densiflorus*). Other hardwood species include madrone (*Arbutus menziesii*), golden chinkapin (*Chrysolepis chrysophylla*), and canyon live oak (*Quercus chrysolepis*). Deciduous hardwoods such as black oak (*Q. kelloggii*) and Oregon white oak (*Q. garryana*) are also present in valleys and at lower elevations.

Large extents of lower elevation valleys west of the Cascades were historically dominated by Oregon white oak woodlands. Douglas-fir and grand fir were common around valley margins and on wetter sites historically but have since invaded many Oregon white oak woodlands that were historically maintained free from conifers by indigenous burning (Agee 1993). Black oak and canyon live oak woodlands are still common in parts of northern California but have also been encroached by conifers.

10.3 Paleohistory and Holocene Vegetation Change

Knowledge of vegetation changes in the PNW during the Holocene advanced considerably over the last few decades. Multiple periods of quasi-stability were punctuated by periods of transition and rapid change, catalyzed by changing climate and periods of widespread fire activity (Whitlock 1992; Walsh et al. 2015).

The early Holocene, approximately 12,000 to 8000 ybp, was a time of rapid vegetation change. The charcoal record indicates that area burned was relatively low at the beginning of the early Holocene as glaciers receded but increased and remained high until approximately 8000 ybp (Walsh et al. 2015). Cooler, wetter conditions were associated with decreasing summer insolation and area burned declined at the start of the middle Holocene (~8000 to 4000 BP) (Bartlein et al. 1998). Area burned started to increase approximately 5500 ybp and continued to increase during the late Holocene (~4000 ybp to present) despite cool and moist conditions, most likely as a result of indigenous burning (Bartlein et al. 1998; Walsh et al. 2015). Modern community assemblages established between 4000 and 2000 ybp (Whitlock 1992; Walsh et al. 2015).

Area burned fluctuated over the last 1000 years with changes in climate and indigenous populations. The warmest temperatures occurred during the Medieval Climate Anomaly (MCA) (900–1250 AD) and the coldest temperatures during the Little Ice Age (LIA) (1450–1850 AD) (Steinman et al. 2012). Fire frequency increased during the MCA in the Klamath Mountains (Daniels et al. 2005) as well as elsewhere in the Oregon and Washington mountains (Walsh et al. 2015). Declines in indigenous populations from diseases following early European contact led to greatly reduced fire frequency in moister parts of the region (Walsh et al. 2018), though dendroecological studies indicate that fire remained relatively frequent in drier parts of the region (Heyerdahl et al. 2008).

10.4 Regional Fire Environment and Presettlement Fire Regimes

Climate, ignition, and meteorology operate as "spatially varying constraints" (Krawchuk and Moritz 2011) that determine the regional fire environment and historical fire regimes (Fig. 10.2). Suitable burning conditions occur on an annual basis, even in most cold and wet vegetation zones. However, the relatively low frequency of ignitions and synoptic east wind events in the late summer and early fall limit the occurrence of fire across much of the western part of the region.

Lightning storm tracks and the distribution of indigenous populations drove historical patterns of ignition. Indigenous burning was a major source of ignition across the region and was likely most important near settlements and along river valleys and travel corridors in more remote, mountainous parts of the region (Boyd 1999; Long et al. 2018). Lightning is common throughout inland areas of the

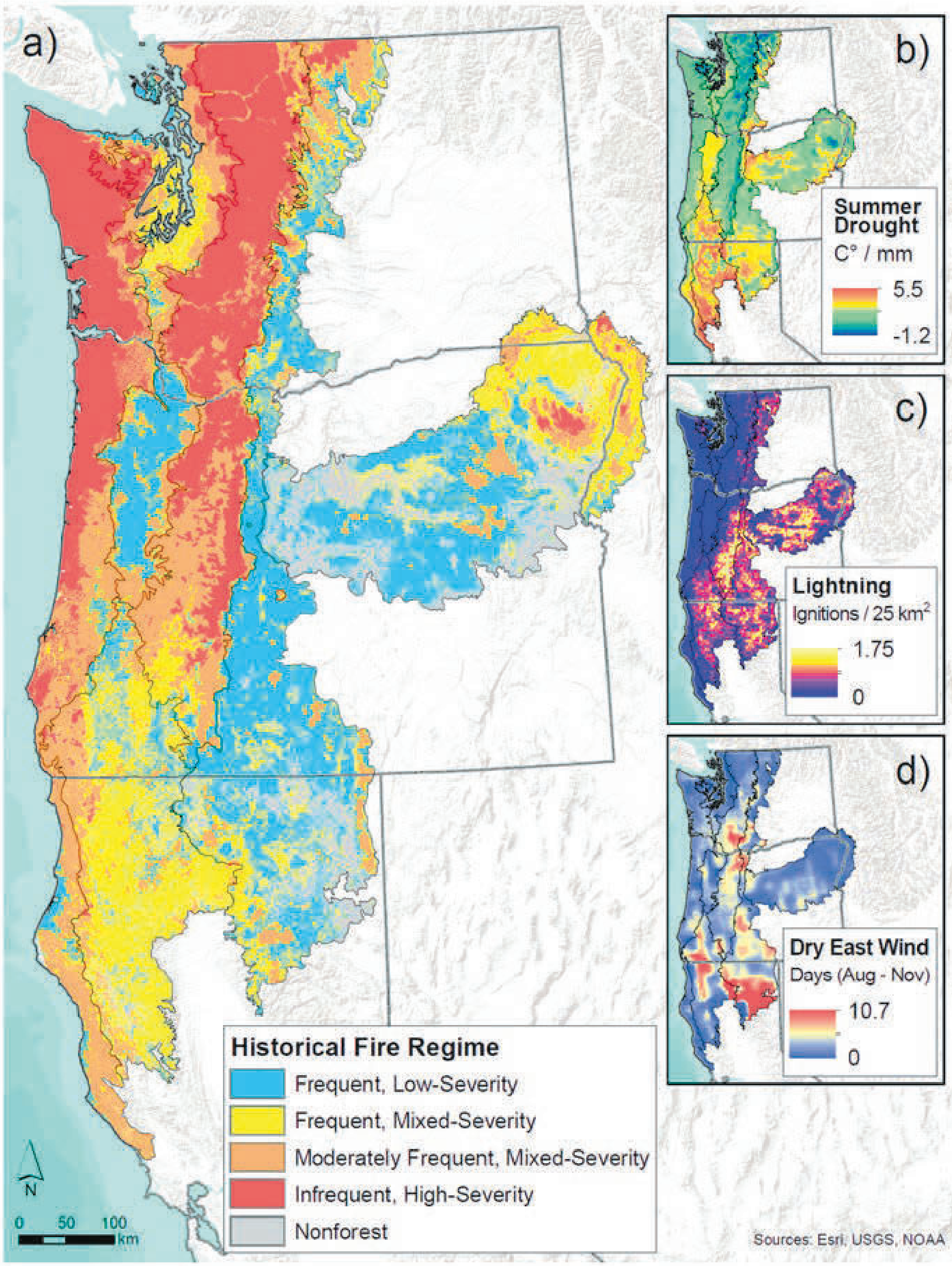

Fig. 10.2 Historical fire regimes and climatic and meteorological conditions in the PNW: (**a**) historical fire regimes; (**b**) summer (May to September) moisture stress (temperature divided by precipitation; data derived from Daly et al. 2008); (**c**) lightning ignitions (1992–2015) (data from Short 2017), and; (**d**) annual frequency of dry east wind events from August to October. The fire regime map was created using a random forest model to predict each regime based on fire history studies and historical maps of forest conditions and fire perimeters. Dry east wind events were characterized following (Cramer 1957) and were derived from GridMet data (Abatzoglou 2013) (map courtesy of Nathan Walker USFS)

southwestern and eastern part of the region, but relatively rare in coastal areas and the western Cascades of Washington.

Geographic patterns of the frequency of synoptic dry east wind events (Fig. 10.2d) contributes additional variability to the regional fire environment (Gedalof et al. 2005). Dry east winds in late summer and early fall (Cramer 1957), coincident with drought conditions and an ignition source, drove many of the large fires that occurred historically in moister and cooler forests of the PNW (Sect. 10.9).

Historical fire regimes in the PNW ranged from frequent, low-severity fires in hotter and drier parts of the region to infrequent, stand-replacing fire regimes in colder and wetter parts of the region (Fig. 10.2). These historical fire regimes are a general characterization of fire activity over the approximately 300–500 years prior to European colonization in the PNW. Fire history and HRV studies provide the foundation for fire regime classifications based on fire frequency and burn severity (e.g. tree mortality) (e.g. Agee 1993, 1998). All levels of burn severity may occur within each fire regime at some spatial or temporal scale, but the proportions and spatial patterns of burn severity become more characteristic of a regime over larger areas and longer time periods (Agee 1993). We adapt the framework of low-, mixed-, and high-severity regimes (Fig. 10.3) by dividing the broad continuum encompassed by the mixed-severity regime into two types based on the range of historical fire return intervals and gradients in productivity (Spies et al. 2018).

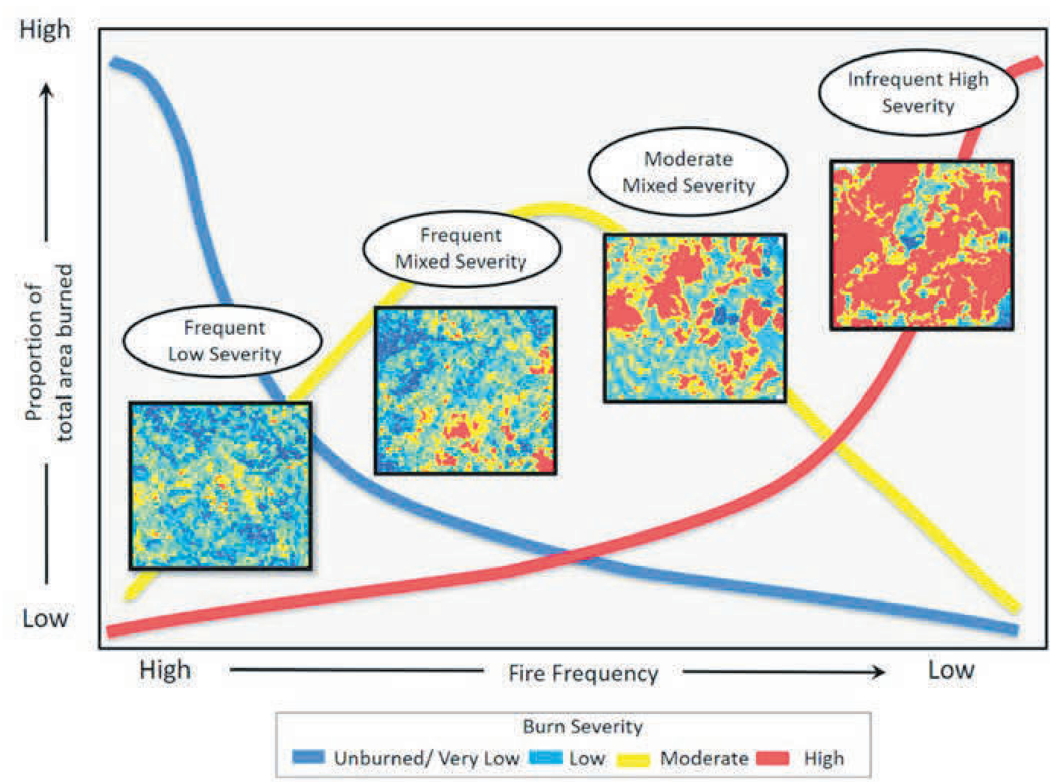

Fig. 10.3 Conceptual diagram of landscape patterns of burn severity under four idealized historical fire regimes (following Spies et al. 2018 and adapted from Agee 1998)

10.5 High Frequency, Low-Severity Fire Regimes

Frequent, low-severity fire regimes occurred across a broad precipitation gradient in the PNW. Indigenous burning was strongly linked with frequent fire across the region (Boyd 1999), especially in the oak woodlands and prairies of the Willamette Valley and Puget Lowlands where lightning is rare. In drier areas, frequent, low-severity fire occurred across the Blue Mountains, eastern Cascades, and lower elevation valleys of the Klamath Mountains. Frequent fire is also documented in low elevation Douglas-fir forests of the Puget Lowlands and western Cascades of Oregon (Bakker et al. 2019; J.D. Johnston *unpubl. data*), but less is known about the role of frequent fire in these moist forest types.

10.5.1 Dry Forests

Frequent fire is synonymous with ponderosa pine, Jeffrey pine, dry mixed conifer, and some moist mixed conifer forests in the PNW (Agee 1993). Frequent fire maintained open canopy woodlands and savannas dominated by large, shade-intolerant species and abundant perennial grasses and shrubs in the understory (Agee 1993). Trees represented a range of age classes and tree mortality from fire occurred primarily in small patches (<0.5 ha) (Youngblood et al. 2004). Fine scale variability in fire effects promoted spatial heterogeneity within stands characterized by multi-aged clumps of trees (Fig. 10.4a,b) (Taylor 2010; Larson and Churchill 2012).

Several crossdated fire history studies document mean fire return intervals (FRI) of 5–20 years in pine-dominated dry forests (Everett et al. 2000; Heyerdahl et al. 2001; Norman and Taylor 2003; Taylor 2010; Johnston et al. 2017; Merschel et al. 2018; Metlen et al. 2018; Hagmann et al. 2019). Mixed conifer forests dominated by grand fir and Douglas-fir at higher elevations and on more productive sites also experienced frequent fire. Historical mean FRIs for grand fir-dominated moist mixed conifer forests range from 12–31 years (Johnston et al. 2017; Merschel et al. 2018; Heyerdahl et al. 2019).

Prior to European colonization, fire occurrence in frequent-fire forests was strongly associated with drought driven by sea surface anomalies and synoptic weather patterns (Norman and Taylor 2003; Heyerdahl et al. 2008; Johnston et al. 2017). During below average dry conditions associated with positive values (warm phases) of the El Niño-Southern Oscillation, fires burned over large areas in the southern Blue Mountains and eastern Cascades (Heyerdahl et al. 2002; Norman and Taylor 2003; Johnston 2017; Merschel et al. 2018; Hagmann et al. 2019). Hagmann et al. (2019) document the occurrence of fires >80,000 ha every few decades in dry forests of central Oregon. Historical fires were most often smaller (<3000 ha) where topography is more complex and more barriers to spread exist (Heyerdahl et al. 2001; Taylor and Skinner 2003; Wright and Agee 2004).

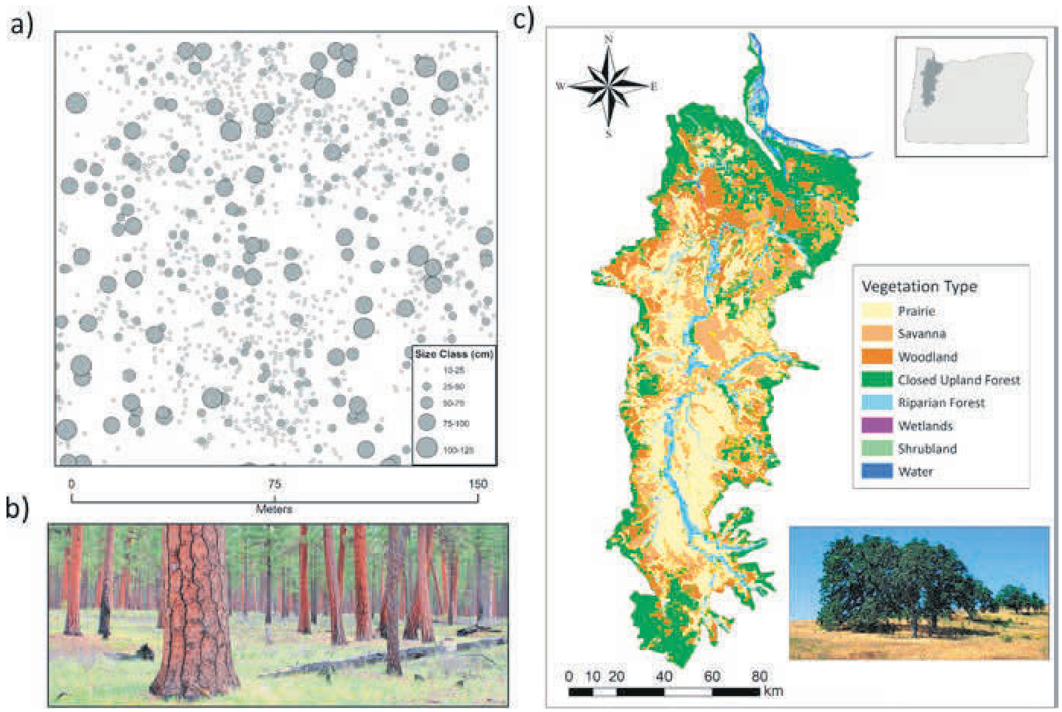

Fig. 10.4 Stand and landscape patterns in ponderosa pine and white oak woodlands: (**a**) spatial patterns of size class structure in an old-growth ponderosa pine stand in the Metolius Basin of Oregon. Ninety percent of the trees <25 cm established since the last fire in 1899 (data provided by the HJ Andrews Experimental Forest research program, funded by the National Science Foundation's Long-Term Ecological Research Program (DEB 1440409), US Forest Service Pacific Northwest Research Station, and Oregon State University); (**b**) an open old-growth ponderosa pine stand treated with prescribed fire (photo J.D. Johnston), and; (**c**) landscape patterns of vegetation in the Willamette Valley circa 1850s (data from Christy and Alverson 2011, data accessed from www.databasin.org; photo M.A. Krawchuk)

Landscape simulation model studies provide estimates of the HRV of various structural conditions and seral stages under frequent, low-severity fire regimes. In the eastern Cascades of Oregon, simulations estimate that old forests (>200 years old) made up approximately 35% of the forest landscapes with 71% of old forest in open canopy conditions (Kennedy and Wimberly 2009). Agee (2003) did not separate open from closed canopy conditions, but found that stands dominated by medium (40–64 cm diameter at breast height) and large (>64 cm diameter at breast height) trees comprised ~40 to 70% of the ponderosa pine and dry mixed-conifer in the eastern Cascades of Washington. Haugo et al. (2015) estimate that open old-growth comprised 40–65% of dry forests across Oregon and Washington. Although these studies used different methods and classifications of seral stages, their findings are consistent with early twentieth century forest inventories documenting extensive landscapes of low density, open pine forests (e.g., Hagmann et al. 2013, 2014).

10.5.2 Oak Woodlands

Early accounts of vegetation conditions from the 1800s depict large expanses of Oregon white oak savannas and woodlands in the Willamette Valley (Fig. 10.4c), Puget Lowlands, and northward into British Columbia. Lightning is rare in these areas, and indigenous burning was the primary ignition source. Indigenous burning promoted extensive prairies throughout the Willamette Valley, Puget Lowlands, and in the Klamath Mountains (Weiser and Lepofsky 2009; Long et al. 2018). Large fires lit in early fall promoted important tribal food sources including acorns and camas (*Camassia* spp.), a widely utilized plant with an edible bulb.

Despite consistency in historical accounts of oak woodlands in the PNW, there are relatively few historical fire reconstructions for Oregon white oak. Numerous authors suggest that burning every 3–5 year was optimal for maintaining oak woodlands (Tveten and Fonda 1999; Storm and Shebitz 2006; Hamman et al. 2011), but relatively few fire histories are available. Estimates of historical FRIs range from 7.4 years in the San Juan Islands in the Puget Sound (Sprenger and Dunwiddie 2011) to 26–41 years in southwestern British Columbia (Pellatt and Gedalof 2014). However, mature white oaks rarely scar, thus reconstructions likely miss fires and may overestimate FRIs (Agee 1993; Hamman et al. 2011).

Oak woodlands and prairie landscapes have suffered extensive declines due to a combination of agriculture, development, fire exclusion, and conifer encroachment. The remaining oak woodlands and prairies exist as small isolated fragments in landscapes that have been developed or become primarily forested from a lack of burning. Most remnant oak woodlands are currently in a state of decline and at risk of encroachment by shade-tolerant conifers, particularly Douglas-fir (Gilligan and Muir 2011; Schriver et al. 2018).

10.6 High Frequency Mixed-Severity Fire Regimes

Productive but seasonally dry forest landscapes experienced a frequent (~10-35 years) mixed-severity fire regime (Agee 1993; Skinner et al. 2018; Skinner and Taylor 2018). Stand and landscape dynamics were similar to those under low-severity regimes, but high-severity fire played a greater role and was linked with topography and vegetation (Taylor and Skinner 1998; Heyerdahl et al. 2001; Beaty and Taylor 2001). Occasional patches (~10–250 ha) of high-severity fire in topographically complex landscapes created coarser mosaics with early-seral habitats that were eventually colonized by shade-intolerant tree species or maintained as shrublands and meadows if reburned at short intervals.

Fire history studies of frequent mixed-severity fire landscapes indicate that FRIs were similar or slightly longer than low-severity fire regimes in adjacent landscapes. However, topographic barriers to spread increased variability in FRIs, with longer fire-free periods ranging from 11 to 49 years in frequent mixed-severity landscapes

(Heyerdahl et al. 2001; Beaty and Taylor 2001; Norman and Taylor 2003; Taylor and Skinner 2003; Kellogg et al. 2008). Fire severity patterns were primarily mixed in space, with high-severity fire more likely in different topographic settings (Taylor and Skinner 1998; Beaty and Taylor 2001; Heyerdahl et al. 2001). Differences in fire frequency and burn severity among topographic settings reinforced the underlying environmental gradients that shaped vegetation composition and structure.

10.6.1 Douglas-Fir and Mixed Evergreen Forests

The complex topography and mosaic of diverse forests at middle elevations of the Klamath Mountains exemplify stand and landscape patterns maintained by a frequent mixed-severity fire regime (Skinner et al. 2018) (Fig. 10.5a). Frequent mixed-severity fires from indigenous burning and abundant lightning shaped these landscapes for centuries (Crawford et al. 2015). Mixed evergreen forests were common on dry ridges and southwest slopes and graded into dry Douglas-fir and moist mixed conifer forests at higher elevations, and in ravines and lower slopes (Whittaker 1960). Patches of knobcone pine persisted on very xeric sites after fire and mixed with Jeffrey pine on serpentine soils. Frequent fire also maintained non-forest states including meadows and chaparral composed of sclerophyllous shrubs (Odion et al. 2010).

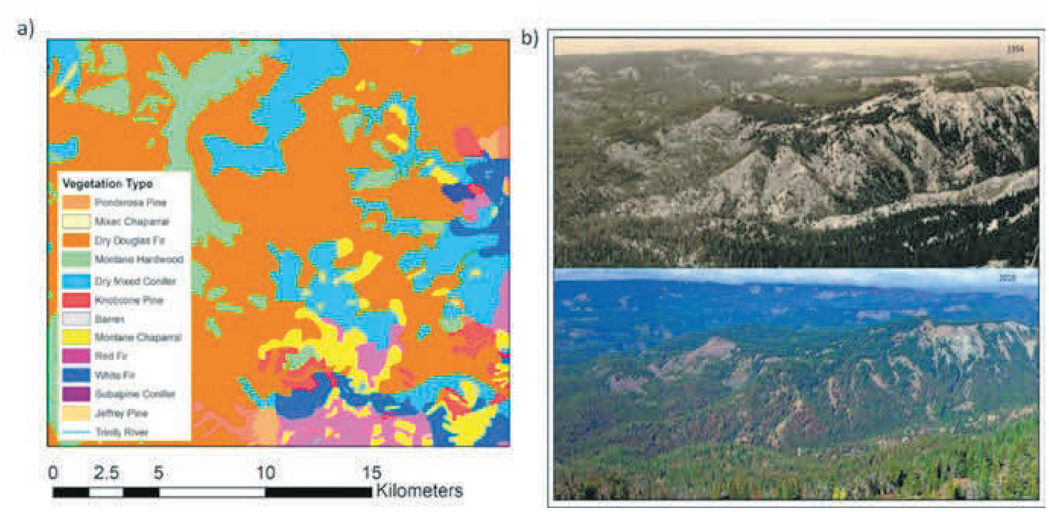

Fig. 10.5 Historical landscape patterns under frequent mixed-severity fire regimes: (**a**) 1930s distribution of vegetation types mapped by Wieslander in the Klamath Mountains of California (Images from the Wieslander Vegetation Type Mapping Collection are courtesy of the Marian Koshland BioScience, Natural Resources & Public Health Library, University of California, Berkeley, http://guides.lib.berkeley.edu/Wieslander); (**b**) Distribution of vegetation in dry mixed-conifer forests of the eastern Cascades of Washington in paired photos of Mission Peak in 1934 (photo R. Sarlin) and 2010 (photo J. Marshall) showing changes in forest mosaics resulting from elimination of historical low- and frequent, mixed-severity fire regimes

Presettlement mean FRIs ranged from 11 to 20 years in Douglas-fir and mixed evergreen hardwood forests in southwest Oregon and northern California (Frost and Sweeney 2000). Taylor and Skinner (1998) provide one of the few crossdated fire histories characterizing frequent mixed-severity regimes in Douglas-fir and mixed evergreen forests in the Klamath Mountains. Median FRIs were similar among forest types (12–19 years) but differed among slope classes and aspects. The median FRI on east facing slopes was twice as long as that on south facing slopes (16.5 years vs 8), and although minimum FRIs were similar (5 vs 4 years), east facing slopes had longer maximum fire free periods than south facing slopes (116 versus 35.5 years). FRIs were also longer and more variable on low and middle slopes than on upper slopes, which experienced twice as much high-severity fire between 1850 and 1950.

10.6.2 Mixed Conifer Forests

FRIs in some dry and moist mixed conifer forests were also generally longer and more variable than in low-severity regimes (Agee 1993; Skinner et al. 2018; Skinner and Taylor 2018). In the eastern Cascades of northern California, FRIs differed among topographic settings and south and west-facing upper slopes and ridges experienced a greater proportion of high-severity (Beaty and Taylor 2001) while riparian areas served as barriers to fire spread (Beaty and Taylor 2001, Norman and Taylor 2003). McNeil and Zobel (1980) also observed effects of topography on limiting fire spread and increasing landscape heterogeneity in mixed-conifer forests in the eastern Cascades at Crater Lake National Park, although they did not include any analysis by topographic setting. Stuart and Salazar (2000) report a median FRI of 27 years with a range of 12–161 years from 28 sites dominated by white fir across a 3750 km^2 area in the Klamath Mountains of northern California. Most of the stands they sampled were multi-aged and experienced repeated low-severity surface fires, but a few even-aged stands indicative of high-severity fire were also present.

Fire history studies from moist mixed-conifer forests of the eastern Cascades of Washington and the northern Blue Mountains document similar effects of topography on fire return intervals, but the role of high-severity fire is less resolved than in other parts of the region. Wright and Agee (2004) found mean FRIs between ~18–24 years in dry and moist mixed-conifer forests of the Teanaway Valley in eastern Washington. A fire occurred every 4 years somewhere in the ~30,000-ha watershed and though fires >5000 ha occurred occasionally, approximately 80% were <3000 ha. Patches of high-severity fire ~10–100 ha in size were inferred from even-aged stands. In another watershed in the eastern Cascades of Washington, Camp et al. (1997) estimated that less than 20% of a 47,000-ha landscape was maintained as dense late-successional habitat which occurred primarily at higher elevations or on lower slopes, benches, and headwalls.

In the northern part of the Blue Mountains, Heyerdahl et al. (2001) documented a frequent mixed-severity fire regime in two watersheds with steep slopes and complex topography. Fire frequency varied among aspects, with northern and eastern aspects experiencing fewer fires between 1798 and 1900, which the authors attributed to differences in fuel moisture, topographic setting, and vegetation composition. Postfire establishment of early seral species (lodgepole pine and larch) indicated moderate- and high-severity fire effects.

Hessburg et al. (2007) documented a greater role of high-severity fire during the early twentieth century than documented in dendroecological studies of pre-European fire regimes. Using aerial photos from the 1930s and 1940s, they found that 22% of the dry mixed-conifer forest showed evidence of low-severity fire, 59% moderate-severity (with <50% of the tree cover surviving in the most cases), and 20% high-severity. In moist mixed-conifer forest, they documented 13% low-severity, 61% moderate-severity (with <50% of the tree cover surviving in the most cases), and 26% high-severity fire.

10.7 Moderate Frequency, Mixed-Severity Fire Regimes

A moderately frequent (~35–150 years) mixed-severity regime occurred across a broad range of productivity in the PNW. Shorter duration and intensity of summer drought limited fire frequency resulting in longer fire-free intervals while greater productivity allowed for more rapid live fuel accumulation. Perennial forbs and a mix of shade-tolerant deciduous and ericaceous shrubs (e.g., *Vaccinium* spp., *Rhododendron* spp.) dominated understory vegetation, as opposed to graminoids and sclerophyllous shrubs in dry forest landscapes where fire was more frequent.

Fires in these areas historically varied in size and some parts of the landscape burned at moderate frequency, while others experienced long fire-free periods (Agee 1993). Topography played an important role in determining fire frequency and severity which were mixed in space, but large patches of high-severity fire during extreme drought or east wind events occasionally resulted in synchronization of cohort establishment over large areas. Spatially and temporally variable patterns of fire frequency and severity led to multiple successional pathways and a diversity of forest conditions (Tepley et al. 2013; Spies et al. 2018). Fire created a coarse mosaic of mixed- and even-aged stands at middle to upper elevation in moist, cold, and some dry forest landscapes dominated by Douglas-fir and true fir (*Abies* spp.). These landscapes likely had more age, structural, and compositional heterogeneity than landscapes that burned with more or less frequent fire (Spies et al. 2018).

The limited scarring potential of Douglas-fir and species of true fir makes estimates of historical fire frequency difficult in forests characterized by moderate frequency mixed-severity regimes compared to drier forest types dominated by ponderosa pine. Douglas-fir does scar, but most scars are overgrown by bark within 20 years after fire (Weisberg 2004). As a result, most available fire history studies

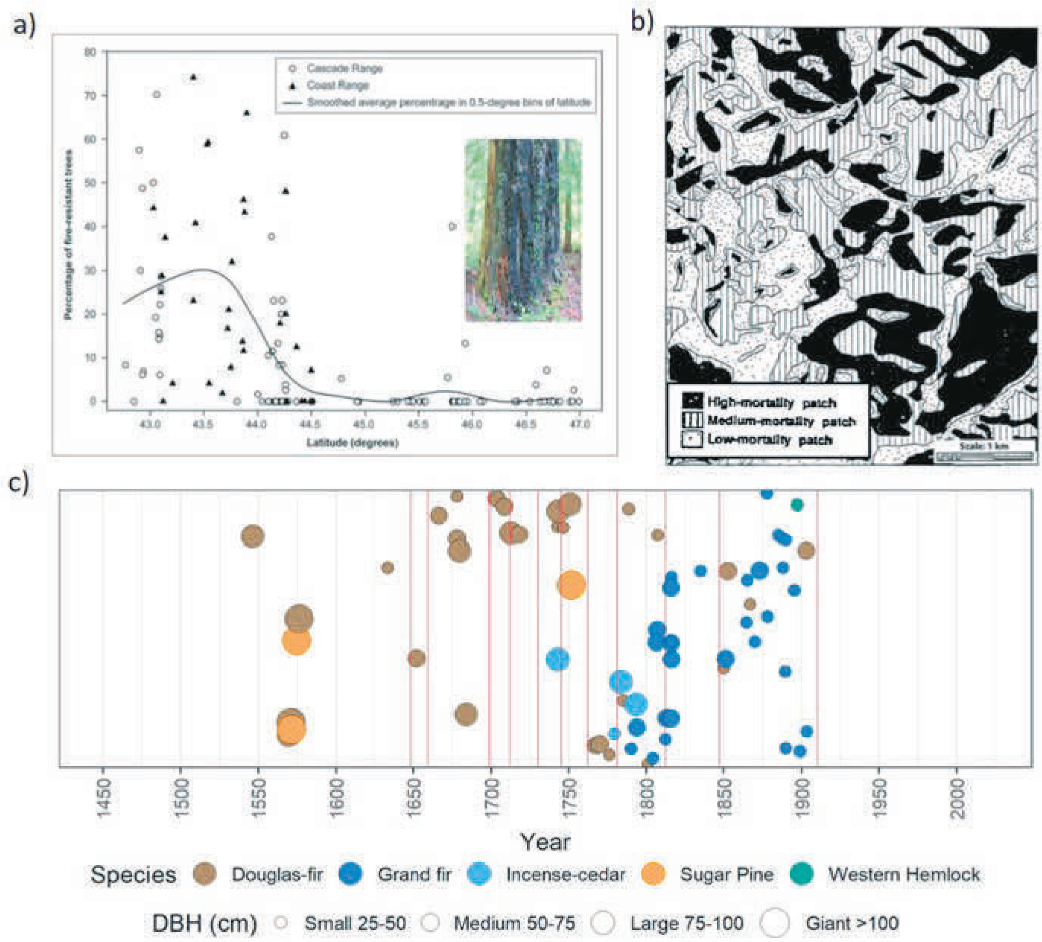

Fig. 10.6 (**a**) Percentage of fire-resistant mature and old trees with evidence of fire (scars or charred bark) in the western Cascades and Coast Range in Oregon and Washington in relation to latitude. The line is a smoothed running average in 0.5 deg. bins (from Spies et al. 2018); (**b**) mosaic of fire severity patches in a Douglas-fir and western hemlock landscape in the western Cascade Range of Oregon: black = a high mortality area (>70%), vertical lines = moderate mortality (30–70%), and stippled = low mortality areas (<30%) (from Morrison and Swanson 1990), and; (**c**) crossdated non-stand-replacing fires (vertical red lines) and tree establishment history (colored circles) depicting the development of a multi-aged stand on the Umpqua National Forest in the southern part of the Oregon western Cascades (A. Merschel, Oregon State University *unpubl. data*).

rely heavily on age structure and identification of cohorts composed of similar aged trees. Several studies based on observations from stumps and charred bark clearly document the importance of non-stand-replacing fire in Douglas-fir/western hemlock forests of the Oregon western Cascades and interior Coast Range (Fig. 10.6a) (Weisberg and Swanson 2003; Spies et al. 2018). These studies depict two major periods of synchronous fire activity prior to the 1600s and again in the 1800s until fire exclusion in the early 1900s (Weisberg and Swanson 2003). However, a lack of systematic, crossdated fire histories limits the ability to precisely link climatic drivers of fire activity over the last several centuries.

10.7.1 Moist Forests

The Douglas-fir/western hemlock zone spans a broad range of biophysical and fire environments and thus experienced different fire regimes across its distribution. Agee (1993) noted a latitudinal gradient of decreasing summer precipitation and increasing lightning frequency in the central portion of the Oregon western Cascades that drove increasing fire activity towards the south. This pattern is strongly supported by geographic patterns in the occurrence of charred bark as evidence of non-stand-replacing fire (Fig. 10.6a), suggesting a relatively abrupt shift from an infrequent, stand-replacing fire regime in the north to moderately frequent, mixed-severity regimes a farther south (Spies et al. 2018).

Differences in frequency, productivity, and adaptations of component species were manifest in different pathways of structural and successional development across the distribution of the western hemlock/Douglas-fir zone. Spies and Franklin (1991) found similar structural diversity when comparing a 400-year-old Douglas-fir/western hemlock stand and some 100-year-old stands that developed along with a shrub and hardwood component in the Oregon Coast Range. Variability in seed sources, productivity, competition with shrubs and hardwoods, and partial-stand-replacement disturbances likely led to low-density, relatively open younger forests where conifer canopy closure never occurred. These developmental pathways may be a faster route to complex older forest structure in some places than those characterized by a higher density of conifers and conspecific competition (Donato et al. 2012; Tappeiner et al. 1997).

Tepley et al. (2013) reconstructed development history in old-growth stands in the central Oregon western Cascades and found that 73% of stands experienced at least one non-stand-replacing fire since establishment. Episodic non-stand-replacing fire occurred in 63% of stands and successional development was characterized by at least two cohorts of Douglas-fir and distinct postfire cohorts of shade-tolerant species. Ten percent of stands experienced chronic non-stand-replacing fire, with multiple cohorts of Douglas-fir and smaller size classes of shade-tolerant species occurring at low abundance (e.g. Fig. 10.6c). Infrequent stand-replacing fire occurred in 27% of stands and was characterized by a single postfire cohort of Douglas-fir followed by continuous establishment of shade-tolerant species.

10.7.2 Cold Forests

Moderate frequency, mixed-severity fire regimes occurred in upper elevation forests in northern California, the eastern Cascades, and the northern Blue Mountains. Where cold forests exist in seasonally dry settings, the Pacific silver fir, mountain hemlock, subalpine fir, and Shasta red fir zones receive less annual precipitation and experience greater summer drought and more lighting ignitions than cold forests west of the Cascade Crest. Ignitions from adjacent or surrounding lower and mid-elevation dry forests occasionally spread to higher elevations where frequency was lower (Taylor 2008), but fires burning under low or moderate drought and fire weather conditions likely stopped at cold forest boundaries.

Historically, mean FRIs from moderately frequent mixed-severity regimes in cold forests of the eastern Cascades ranged from 40–70 years in red fir, mountain hemlock, and lodgepole pine in northeastern California where fires were generally small (~150 ha) (Taylor and Solem 2001; Bekker and Taylor 2010). Relatively frequent, low- and moderate-severity fire maintained small canopy gaps while occasional high-severity fire initiated cohorts of red fir (Taylor and Halpern 1991). FRIs farther north were longer and ranged from 108–137 years in mountain hemlock and Pacific silver fir in northern Washington (Agee et al. 1990). The combination of relatively frequent fire and short growing seasons promoted low density woodlands with pockets of dense forest and non-forest vegetation including subalpine meadows and shrubs that have been encroached by conifers under fire exclusion.

10.7.3 Redwood Forests

The historical role of fire in the redwood forests that blanket the foggy coastal areas of coastal northern California and southern Oregon is one of the most varied in the PNW (Stephens and Kane 2018). Given the relative rarity of lightning along the Pacific Coast (Fig. 10.2c), indigenous tribes and early settlers played an important role in ignition (Lorimer et al. 2009). Closer to the coast and to the north where there is more moisture and fog, FRIs ranged from 50–500 years (Veirs 1982; Stephens and Fry 2005). In drier, warmer inland redwood landscapes to the south, FRIs were generally <50 years (Finney and Martin 1989; Brown and Baxter 2003; Lorimer et al. 2009; Stephens and Kane 2018). Existing fire history studies document fires <1000 ha but exist only from relatively small landscapes, thus little is known about the role of larger fires (Agee 1993; Lorimer et al. 2009).

Despite extremely high levels of biomass and the flammability of redwood litter and foliage, existing evidence suggests fires were primarily low- and moderate-severity (Agee 1993). Veirs (1982) documents mixed age-class stands of redwood with multiple cohorts of Douglas-fir that established under fires severe enough to open the canopy. Occasional resprouting tanoaks and cohorts of shade-tolerant species were present, but fire-sensitive conifers including grand fir and western hemlock often dated back to the last fire. Patchy surface fires likely helped maintain perennial forbs among dense patches of understory trees, evergreen shrubs, and ferns (Lorimer et al. 2009).

Redwood stands in the drier inland are commonly interspersed with grassland and oak savannas. In these settings, redwood may be more fire-dependent as regeneration from seed is limited by soil moisture and most reproduction occurs via resprouting (Stephens and Kane 2018). Douglas-fir may be more common here too, and hardwoods are more abundant and diverse. Tanoak, madrone, and California bay (*Umbellularia californica)* all resprout and were maintained by fire. Fire exclusion since at least the early 1900s affected the drier interior parts of redwood's distribution and resulted in pulses of Douglas-fir and hardwood establishment (Wills and Stuart 1994; Brown et al. 1999).

10.8 Low Frequency, High-Severity Fire Regimes

High-severity fire regimes are characteristic of the cool, moist Coastal Ranges and the higher elevation and northern portions of the western Cascades (Fig. 10.2a) where fire-free intervals were generally longer (>150 yr), and stand-replacing fires burn very large areas (~10^4–10^6 ha) (Fig. 10.7a) (Donato et al. 2020). Fire history studies document long fire-free intervals punctuated by periods characterized by very large fires (e.g., Hemstrom and Franklin 1982; Teensma 1987), often with reburning in young stands (e.g., Gray and Franklin 1997).

Fire occurrence in low frequency, high-severity fire regimes is limited mainly by climate and weather, ignition, and regional wind patterns. Large fires were infrequent because they occur with the relatively rare coincidence of deep summer drought, lightning- or human-caused ignition, and – for the largest fires that shape

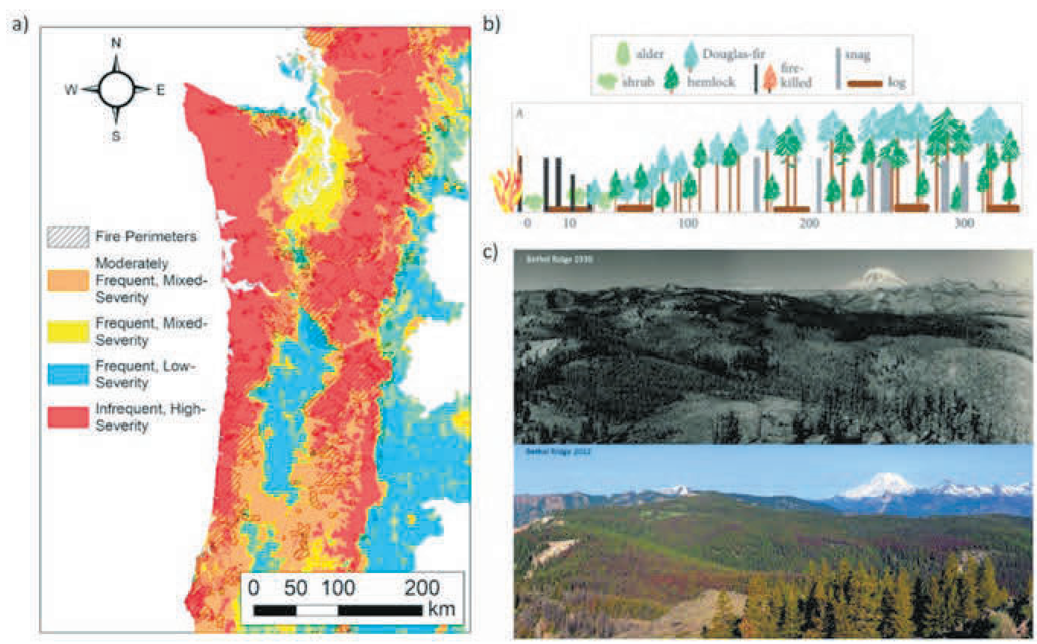

Fig. 10.7 (**a**) Historical fire regimes and patterns of stand-replacing patches present in western Oregon and Washington in 1900 and 1902 (where "destruction of timber was nearly or quite complete…areas…with only a partial destruction are not here represented"). Burned forest patches were digitized from Thompson and Johnson (1900) and Plummer et al. (1902) (data courtesy of Ray Davis US Forest Service); (**b**) a typical pathway of structural and successional development following stand-replacing fire in a Douglas-fir/western hemlock forest (from Spies et al. 2018), and; (**c**) paired photos looking west across the Cascade Crest towards Mt. Rainier on Bethel Ridge in 1936 and 2012 (photo J. Marshall)

these landscapes – major synoptic east wind events. Historically, occasional lightning ignitions and frequent indigenous burning near settlements or travel routes likely ignited small fires on a nearly annual basis. The cumulative area of these small fires would have been limited but they likely served as occassional catalysts for very large fires, driven by strong dry south or east winds.

Synoptic dry wind events are characteristic of late summer and early fall prior to the start of the rainy season (Cramer 1957). These events have a variable geographic distribution characterized by several regional hotspots that correspond with some of the large fire events during the early twentieth century (Fig. 10.2d, Fig. 10.7a). Data on these synoptic wind-driven fires are inherently rare, however evidence suggests that they can affect a substantial fraction of the region in a single fire or episode of multiple synchronous fires (Donato et al. 2020). Stand-replacing fires potentially approaching or exceeding one million ha have been described in historical land surveys (Fig. 10.7a), modern dendro-ecological studies (Henderson et al. 1989), and recent simulation models integrating literature-derived fire rotations and event frequencies (Donato et al. 2020).

Regional synchrony, or periodicity, in fire activity appears to be an important driver of landscape structure in the high-severity fire regime of the PNW. Long, relatively fire-free intervals were punctuated by periods of widespread fire activity that synchronized age structure across large portions of the region (Henderson et al. 1989; Weisberg and Swanson 2003). These cycles occurred historically every ~200–300 years, with evidence indicating major fire episodes peaking around the years 1300, 1500, 1700, and during the Euro-American settlement period circa 1850–1900 (Teensma 1987; Henderson et al. 1989; Weisberg and Swanson 2003).

10.8.1 Moist Forests

Large, east-wind-driven fires are well documented in moist forests west of the Cascade Crest. Examples in the modern record include the 1902 Yacolt Burn in southwest Washington (~200,000 ha), the 1933 Tillamook Burn in the Oregon Coast Range (>100,000 ha), and the 2020 fires in the western Cascades of Oregon. First-hand weather observations substantiate low relative humidity (25%) and average windspeeds above 30 kph during the Tillamook Fire when ~80,000 ha burned in a single 24-hour period of dry east winds in late August. Similar conditions and fire behavior were associated with the Yacolt Fire and the 2020 Labor Day fires in the western Cascades of Oregon.

Stand development following low-frequency, high-severity fire has received extensive attention in the PNW (e.g. Franklin et al. 2002) (Fig. 10.7b). The longevity and size of early-seral conifers, particularly Douglas-fir, allowed for very long periods of structural development. The duration of early-seral periods following stand-replacing fire was variable. Canopy closure could occur relatively quickly on productive sites where seed sources were abundant and competition from non-tree vegetation was minimal (Winter et al. 2002), or take up to ~80 years where tree establishment and growth proceeds more slowly (Hemstrom and Franklin 1982; Huff 1995; Tappeiner et al. 1997; Freund et al. 2014).

Reburns in young regenerating stands were an important driver of early-seral dynamics. Reburns reset succession and influenced the abundance of legacy structures, seed sources, and vegetation composition (Gray and Franklin 1997). Documented examples in the western Cascades include the Yacolt Burn that partially reburned several times (Gray and Franklin 1997) and the Tillamook Burn which reburned three times at 6-year intervals in the following two decades. Repeated burning during periods of high fire activity was likely mediated by open early seral conditions that facilitate dry fuel conditions that persist until canopy closure. In landscapes where FRIs were long, reburn allowed for longer-term persistence of early-seral associated species and habitats including meadows, shrublands, and hardwood forests.

Landscape simulation models provide important perspectives on HRV in stand-replacing fire regimes of the PNW, as empirical reconstructions over large areas are few or limited to a single time period. These studies suggest that early-seral conditions historically occurred across 12–29% of the Oregon Coast Range (Wimberly et al. 2000) and ~ 1–30% of the Washington western Cascades (Donato et al. 2020). Mid-seral structures were the least abundant landscape condition historically, varying from 12–28% (median 16%) in the Oregon Coast Range (Wimberly 2000) and ~ 10–40% (median 20%) in the Washington western Cascades (Donato et al. 2020). Both Wimberly et al. (2000) and Donato et al. (2020) reported near-identical ranges of historical late-seral conditions (~50–85%) across broad scales (>two million ha). At the finer watershed scale (~50,000 ha), late-seral conditions varied from 0–100% in both studies as fire sizes were typically greater than a single watershed or reserve.

10.8.2 Cold Forests

Fire history studies from cold forests are relatively few and limited to mountain hemlock and subalpine forests in the western Cascades. These studies are based on stand age (Hemstrom and Franklin 1982; Dickman and Cook 1989). Fire rotations span several centuries to millennia (Fahnestock and Agee 1983; Hemstrom and Franklin 1982) and tree establishment may take decades following fire (Agee and Huff 1984).

Dickman and Cook (1989) used aerial photos and stand ages to reconstruct fire history across an 18,000-ha landscape dominated by mountain hemlock in the central western Cascades of Oregon. They documented a wide range of fire sizes, but only two fires >2000 ha occurred during the last 500 years, first in the early 1600s and again in the early 1800s. Establishment histories document an early-seral period dominated by lodgepole pine for up to 200 years prior to replacement by mountain hemlock.

Long protracted early-seral periods following stand-replacing fire were dominated by shrubs, forbs, and graminoids in high elevation forests of the region

(Fig. 10.7c). Agee and Smith (1984) quantified rates of tree establishment in subalpine fir and mountain hemlock forests of the Olympic Peninsula. Dominant tree species tended to replace themselves and *Vaccinium* spp. were frequent immediately after fire. Rates of tree establishment were higher during wet summers and regeneration was more abundant near the edge of the fire perimeter. Establishment was slow and pulses of regeneration were minimal until approximately 50 years after fire.

10.9 Contemporary Fire Activity

Increased area burned in the PNW since the mid-1980s is attributed to drought and declines in summer precipitation, longer fire seasons, warmer spring and summer temperatures, and drier fuels (Halofsky et al. 2020). However, the area burned differs substantially depending on spatial scale and geographic location across the region (Miller et al. 2012; Davis et al. 2015; Reilly et al. 2017). Multiple large wildfires have occurred in most ecoregions with the exception of the Coast Range and western Cascades of Washington. The fires of 2020 were unprecedented in the last several decades with very large fires in the Klamath Mountains (August Complex 417,897 ha, Slater 63,628 ha, Red Salmon 58,549 ha) and the western Cascades of Oregon (Riverside 55,868 ha, Beachie Creek 78,336 ha, Lion's Head 82,746 ha, Holiday Farm Fire 70,170 ha, Archie Creek Fire 53,233).

Despite increasing area burned in the last three decades, there is consensus that the PNW as a whole experienced less fire than would be expected under historical conditions (Reilly et al. 2017; Haugo et al. 2019). Dry forest landscapes missed numerous fires due to twentieth-century fire exclusion, but fire exclusion likely had less influence on fire activity in wetter and cooler parts of the region where historical FRIs were longer and fire rotations are within HRV. However, given the number of ignitions and warming climate, these parts of the region have undoubtably missed many small fires that could have grown into larger fires if left to burn under extreme fire weather conditions.

Fire severity has been related to climate and drought at broad spatial scales since the mid-1980s (Miller et al. 2012; Cansler and McKenzie 2014; Reilly et al. 2017). Although annual area burned increased during this period, there is little evidence that the proportion of high-severity fires has increased in recent decades (Reilly et al. 2017). However, larger fires are associated with greater proportions of high-severity fire (Cansler and McKenzie 2014; Reilly et al. 2017). Reilly et al. (2017) found that an increase in high-severity patch size between 1985 and 2010 was associated with more area burned during drought years. At the stand scale, fire severity has been related to multiple factors including topography, stand structure, and fire weather (Dillon et al. 2011; Meigs et al. 2020). Studies indicate that dense young stands dominated by smaller trees (e.g., plantations) are more susceptible to high-severity fire than those dominated by multi-layered old-growth forests (Thompson et al. 2007; Zald and Dunn 2018).

Dry forests in Washington and Oregon experienced greater proportions and larger patches of high-severity fire in recent fires than under historical fire regimes (Reilly et al. 2017, Haugo et al. 2019). Moist mixed-conifer forests have generally been resilient to high-severity fire with regeneration peaking 5–11 years after fire (Downing et al. 2019). However, ponderosa pine and dry mixed-conifer forests at lower elevations appear to be less resilient to high-severity fire (Dodson and Root 2013; Boag et al. 2020). Shrubs can mitigate desiccation through shading and facilitate higher rates of ponderosa pine seedling establishment and survival (Keyes et al. 2009), but long-distance dispersal events will be necessary to recolonize large patches of high-severity fire.

In dry forests of the Klamath Mountains in northern California, high-severity fire accounted for approximately 10% of the area burned between 1984–2009 (Miller et al. 2012). Several studies have documented resilience of Douglas-fir to a single high-severity fire in the Klamath Mountains (e.g., Donato et al. 2009a; Tepley et al. 2017; McCord et al. 2020) which is related to the thick bark of mature trees and the ability of this species to disperse relatively long distances (Donato et al. 2009a, 2009b). Hardwoods in the Klamath Mountains are particularly resilient to wildfire due their ability to resprout (Cocking et al. 2014; McCord et al. 2020). Conifer forests dominated by Douglas-fir may transition from conifer- to hardwood-dominated forests or shrub/chaparral following short-interval reburns (Odion et al. 2010). McCord et al. (2020) found that two extremely high-severity fires in 11 years eliminated conifers (e.g., Douglas-fir), but hardwoods (e.g. tanoak, madrone) persisted and attained cover that was almost equivalent to the levels observed before the second fire within 2 years.

Wet and moist forests had experienced relatively little recent fire activity until 2020, with most contemporary fires occurring in the southern part of the Oregon western Cascades. While high-severity fire comprised 19% of the area burned in the Douglas-fir/western hemlock zone between 1985 and 2010, silver fir experienced 43% high-severity fire (Reilly et al. 2017). Multiple studies on tree regeneration following fires in the 1990s indicate that moist forests have been resilient to fire at all levels of burn severity (Larson and Franklin 2005; Brown et al. 2013; Dunn et al. 2020) with seedling abundance and richness peaking at moderate levels of severity (Dunn et al. 2020).

Cold vegetation zones, particularly in eastern Washington (Cansler and McKenzie 2014), experienced the greatest proportions of high-severity fire (~50%) in recent years with almost 70% occurring in patches ≥1000 ha (Reilly et al. 2017). Between 1985 and 2010, wildfires burned more than 30% of the subalpine zone forests in the eastern Cascades of Washington and reduced late-seral conditions by ~20% (Reilly et al. 2018). Acker et al. (2017) found sparse conifer regeneration 2 years following high-severity fire in the mountain hemlock zone in central Oregon, but seedling density was >359 per ha by 13 years postfire. Busby et al. (2020) found that subalpine forests were resilient to low- and moderate-severity fire in the southern Washington and northern Oregon western Cascades, but single and repeated high-severity fire at short-intervals reduced regeneration and shifted composition towards that of drier, lower elevation forests.

10.10 Biodiversity and Wildlife Habitat

The stand and landscape patterns of forests sculpted by fire and other disturbances provide habitat supporting the region's biodiversity, including terrestrial and aquatic wildlife. Structural elements that contribute to biodiversity in forest ecosystems include a gradient of canopy cover, single to multiple canopy strata, presence of diverse vegetative resources, snags, and dead downed wood. Changes in the abundance of these structural elements over time are manifest as unique seral stages of forest development. However, the duration and structure of these stages varies with productivity and among vegetation zones in the PNW (Reilly and Spies 2015).

Habitats associated with early-seral stages of forest development include those with open canopy conditions (<40% cover) that may be created by stand-replacing disturbance or maintained by frequent, low-severity fires that inhibits tree regeneration or recruitment into larger size classes. Old-growth forests and late seral habitats are dominated by large or old trees with complex crown structure (Van Pelt 2007, 2008), though canopy cover and abundance of dead wood vary with fire frequency. In forests where fire was frequent, old-growth structure included open woodlands dominated by large, old trees, whereas in forests with long fire-free periods, dense, multilayered forests with big trees and abundant dead wood were characteristic old-growth conditions (Spies et al. 2018).

Spatial and temporal patterns of fire severity under different fire regimes are tightly linked with structural and compositional heterogeneity at stand scales, as well as the spatial distribution and patch sizes of different forest habitats at landscape scales. A few species may be specialists in one seral stage (Swanson et al. 2014), though many generalist species with larger home ranges use a variety of seral stages or benefit from heterogeneity in fire effects at a range of spatial scales. Under frequent fire regimes, early-seral elements including open canopy gaps and big, shade intolerant tree species were present in a relatively fine-grained mosaic that supported a range of generalists and specialists (Franklin et al. 2008). The removal of fire from these forest types facilitated a transition to closed-canopy old-growth (i.e., mesophication) which now generally supports a much coarser-grained landscape mosaic. Patterns of seral diversity in landscapes with mixed- or high-severity fire regimes in moist and cold forests are primarily expressed with a coarser-grained landscape mosaic. In these regimes, specialists are more likely to occur in distinct seral patches with generalists operating along edges or areas of contrast using adjacent habitats for different functions (e.g. foraging, denning, roosting).

Early-seral and old-growth stages of forest development are the primary focus of conservation and management in the PNW due to their reduced prevalence and departure from historical conditions, predominantly from harvest activities, intensification of forest management, and changes in wildfire activity over the last century (DeMeo et al. 2018; Spies et al. 2018). The two stages are comparable in terms of the percentage of species that rely on them (Swanson et al. 2014). The loss of structurally and compositionally complex early and old-growth habitats equates to reduced landscape heterogeneity and forest biodiversity (Swanson et al. 2011, 2014;

Spies et al. 2018). Here, we focus on a subset of wildlife species that feature prominently in early seral and old-growth forests and use them as examples to illustrate the variable role of fire in on forest biodiversity across the region.

10.10.1 Early-Seral Habitats

Fire-created early-seral habitats support a number of disturbance-adapted plant and animal species associated with the open canopy conditions. In the conifer-dominated forests of the PNW, early-seral vegetation is often distinguished from later stages of development by an abundance of broadleaf vegetation (trees, shrubs, forbs, grasses) that enhances wildlife habitat, nutrient cycling (e.g., nitrogen fixation), and other ecosystem functions (Hagar 2007). However, the abundance, patch sizes, and degree of interspersion with other habitats varied among landscapes with different historical fire regimes.

Many early-seral plant species have fire-stimulated reproductive mechanisms, such as heat-induced germination (e.g., *Ceanothus*) or serotiny (e.g., lodgepole pine, knobcone pine). Hardwood tree species including red alder, quaking aspen (*Populus tremuloides*), and bigleaf maple (*Acer macrophyllum*) may establish via seed or persist by resprouting. Many forb and shrub species produce flowers, fruits, pollen, and other energy- or nutrient-rich resources at elevated rates in fire-opened sites compared to other stages of development (Campbell and Donato 2014).

The diversity and abundance of flowering forbs, shrubs, and hardwood species following fire provide essential habitat for insect pollinators in the form of larval host plants and nectar resources for adults (James and Nunnallee 2011). Pollinators in the order Hymenoptera (ants, bees, wasps, hornets, and sawflies) are also of tremendous importance in the early-seral environment. Butterflies, skippers, and moths (order *Lepidoptera*) are frequently the most visible respondents among the insects to early-seral conditions. In the Klamath Mountains of southern Oregon, high-severity post-fire environments have a higher abundance and richness of native bee species than unburned or low-severity postfire environments (Galbraith et al. 2019) due to the combination of flowering plants and cavities created in woody debris by wood boring insects (e.g. Buprestidae and Cerambycidae).

Fire-mediated injury or tree mortality often leads to colonization by woodboring or subcortical larvae of "pyrophilous insects" (Goodman and McCravy 2008). These in turn provide food resources for other organisms such as three-toed (*Picoides tridactylus*) and black-backed (*Picoides arcticus*) woodpeckers (Hutto 2008; Chap. 8, Box 8.1), which consequently increase in population for up to a decade postfire (Hutto 2008). Several birds (e.g., olive-sided flycatcher, *Contopus cooperi*, Lewis's woodpecker, *Melanerpes lewisii*) benefit from snags (especially with cavities for nesting) and early-seral vegetation providing fruits and seeds or an enhanced invertebrate prey base (Kotliar et al. 2002; Chap. 8).

Early-seral conditions are often characterized by a rich avifauna associated with or dependent on open post-fire conditions (Betts et al. 2010) and sustain a number of passerine species that rely on broadleaf shrubs and trees. Some species respond positively to broadleaf resources, and regional declines of these species are linked to loss and simplification of early-seral habitat (Betts et al. 2010). Raptors require large snags or residual live trees for perching or nesting in combination with open areas that support prey. Following disturbance, open ground-feeding birds such as mountain bluebirds (*Sialia currucoides*) thrive, while shrub-associated species such as yellow warblers (*Dendroica petechia*) increase later as shrub cover increases (Bock et al. 1978).

Many mammals benefit either from deciduous vegetation or prey associated with early-seral conditions. Ungulates such as black-tailed deer (*Odocoileus hemionus columbianus*), Rocky Mountain elk (*Cervus elaphus*), and bighorn sheep *(Ovis canadensis)* forage in early-seral habitats (Nyberg and Janz 1990; Toweill et al. 2002; Ulappa et al. 2020). Large carnivores, including wolves (*Canis lupus*) and cougar (*Puma concolor*) likely benefit from elevated populations of their prey in productive early-seral habitats. Black or grizzly bears (*Ursus americanus*, *U. arctos horribilis*) will make use of early-seral habitats in different seasons. Spring food resources include sedges (*Carex* spp), while huckleberry (*Vaccinium* spp.) or roots, tubers, seeds nuts, and grasses are important resources during hyperphagic feeding in late summer. Rodents such as pocket gophers (*Thomomys* spp), voles (*Microtus* spp), and chipmunks (*Tamiasciurus* spp) may increase in the early-seral period (e.g., Gashwiler 1970), enhancing the prey base for raptors and mammalian carnivores.

10.10.2 Old-Growth Forests

Old-growth forests of the PNW harbor many unique components of biodiversity including plants, invertebrates, amphibians, and reptiles, as well as lichens and bryophytes that are seldom found in other seral stages (Marcot et al. 2018). The diversity of vascular plants tends to increase during structural development after logging in the Douglas-fir/western hemlock zone, and peak in old-growth conditions. (Halpern and Spies 1995; Jules et al. 2008), but less is known about dynamics in other vegetation zones or following fire. Few perennial understory plant species are either absent from, or restricted to, any specific stage of successional development, although the abundance of individual species changes over time (Halpern and Spies 1995) and many late-seral plant species can persist even through short interval high-severity fires (Donato et al. 2009b). Fire exclusion, grazing, and subsequent mesophication have affected understory communities in old-growth forests in vegetation zones where fire was frequent historically (Loya and Jules 2008), but these effects are poorly understood and more research is needed.

Dry forest landscapes where fire was historically frequent were composed of a complex mixture of early-seral and old-growth structures at a range of spatial scales. Persistent openings or high-severity fire provide habitat for species like western bluebird (*Sialia mexicana*) and yellow-rumped warbler (*Dendroica coronata*) (Saab et al. 2007). Large mammals such as mule deer (*Odocoileus hemionus*) and Rocky Mountain elk also benefit from shrub, forb, and grass production in forests subject to frequent-fire and/or mechanical treatments (Long et al. 2008). Historical grazing reduced the abundance of perennial bunch grasses and forage and invasive grasses are now widespread. Due to fire exclusion, most of the open, old-growth conditions that dominated landscapes historically are now denser with closed-canopy conditions, resembling late-seral conditions in parts of the region where fire was less frequent (Hessburg et al. 2005; Reilly and Spies 2015).

Structurally complex, old-growth forests with closed-canopy and shade-tolerant species (e.g., grand fir or white fir) historically occurred in refugial settings on north-facing slopes or at stream confluences in dry forest landscapes that experienced frequent, low-severity fires (Camp et al. 1997). Large live trees, snags, and down woody debris offer roosting, denning, and foraging habitat to organisms including flammulated owls (*Otus flammeolus*), pygmy nuthatches (*Sitta pygmaea*), and northern goshawk (*Accipiter gentilis*) (DeStefano et al. 2006; Saab et al. 2007). Fire exclusion has benefitted some late seral wildlife species, enabling them to expand into landscapes where suitable habitat was restricted under historical fire regimes (e.g. northern spotted owl; Everett et al. 1997; Hagmann et al. 2017).

Structurally complex old-growth forests provide habitat for the northern spotted owl (closely related to the Mexican spotted owl; Chap. 11), which is listed as threatened under the federal Endangered Species Act (Thomas et al. 2006; USFWS 2011) across its range in the PNW. Large trees and multilayered, closed-canopy structure provide key nesting and roosting habitat, although foraging, dispersal, and non-breeding habitat can be more varied (Forsman et al. 1984). These habitats develop through a variety of different fire regimes across the region (Spies et al. 2018) in forest types ranging from wet coastal forest to dry and moist mixed-conifer forests (Lesmeister et al. 2018, Table 4–2).

Foraging habitat for the northern spotted owl varies across its range depending on habitat needs of prey species, including northern flying squirrels (*Glaucomys sabrinus*), red tree voles (*Arborimus longicaudis*), and dusky-footed woodrats (*Neotoma fuscipes*) (Lesmeister et al. 2018). Woodrats inhabit open, early-seral areas and older coniferous and mixed-conifer hardwood forests that intermingle with late-seral habitats and are the primary prey species in the Klamath Mountains (Sakai and Noon 1993). Here, frequent, mixed-severity fire regimes historically maintained meso-scale mosaics of early-seral and late-seral habitats, and owls often forage in and around edges (Diller et al. 2012). In contrast, flying squirrels and tree voles inhabit mature Douglas-fir/conifer forests and are the primary prey species for the owl farther north. Here, infrequent, high-severity fire regimes historically maintained coarse-scale mosaics of seral stages, and owls prefer interior closed-canopy habitat (Lesmeister et al. 2018).

The marbled murrelet is a small seabird that nests in coastal forests up to ~90 km from the ocean and forages in the nearshore environment, feeding on small fish and krill (Raphael et al. 2018). Suitable nesting habitat varies across its range, but large trees with a platform consisting of large, mossy branches are a key component and nesting trees may take 200–250 years to develop (Raphael et al. 2018). Murrelets prefer larger forest patch sizes with limited edge, proximity to streams, and high canopy cover. These habitat preferences suggest that the marbled murrelet is a specialist in forests with infrequent fires and may tolerate some degree of mixed-severity fire if large trees survive. However, fires that kill nesting trees and reduce cover and forest patch size result in the loss of nesting habitat and reproductive success (Agee 1993). In addition to direct loss of nest habitat to fire, more open canopy conditions may lead to increased predation on chicks and adults from birds of prey, even if the nest tree or patch persists under mixed-severity or high-severity disturbance.

Pacific marten are small carnivorous mammals that inhabit montane and coastal coniferous forests of the PNW. A close relative, the American marten (often called pine marten), is found in mid- and upper montane moist mixed-conifer and cold forests (Bull et al. 2005). Habitat preferences for marten include closed-canopy, old-growth forest conditions, but wide geographic variation in abundance is linked to prey species abundance, predators, and forest structural complexity (USFWS 2015; Moriarty et al. 2016). Structural complexity is tightly linked to resting and denning habitat, which is associated with large trees, snags, and downed logs (Slauson and Zielinski 2009). Key prey species for the Pacific marten also inhabit these conditions and include red-backed voles, flying squirrels, and Douglas's squirrels (*Tamiasciurus douglasii*). Pacific martens also inhabit areas characterized by dense shrub layers and rocky outcrops (particularly in serpentine areas of northern California and southwestern Oregon). These habitats provide sufficient resting, denning, and foraging habitat (Slauson and Zielinski 2009) but appear to be restricted to coastal fog-influenced landscapes where shrub cover is dense (USFWS 2015). Reduction of cover and structural complexity due to high-severity fire generally results in loss, degradation, or fragmentation of suitable habitat for marten, but low-severity surface fires may improve habitat by creating dead wood and increasing prey abundance (USFWS 2015).

Chinook salmon are iconic anadromous fish of the PNW with habitat networks bridging riparian areas, riverine systems, and marine environments. Fire is important to Chinook salmon across numerous life history stages due to its influence on fluvial geomorphology via wood and sediment inputs to channel networks, stream shading, water temperatures, and improved stream invertebrate productivity (Flitcroft et al. 2016). Wood delivery to stream channels as a result of tree mortality and snag fall, or transport by landslides and debris flows, provides habitat for adult Chinook before spawning by providing cover, encouraging pools to develop as cool-water refugia, and accumulating gravel for spawning (Flitcroft et al. 2016; Reeves et al. 2018). Anadromous and cold water fish appear to be adapted to historical fire regimes (Rieman et al. 2010) and some populations can rebound to higher levels than prefire (Bisson et al. 2003; Dunham et al. 2003; Flitcroft et al. 2016). However, chronic input of fine sediment from post-fire erosion reduces water quality needed for salmon egg survival (Jensen et al. 2009), and open canopy conditions from high-severity fire may increase local stream temperatures during critical egg and fry growth periods. Fish populations may decline for up to a decade or more due to uncharacteristic levels of sediment or changes in water temperature (Dunham et al. 2007; Whitney et al. 2015), and local populations may experience extirpation in highly fragmented or isolated reaches.

10.11 Climate Change: Effects, Adaptation, and Management Implications

Temperatures in the PNW increased over the last several decades and are expected to continue increasing over the next century. Compared to the recent historical period (1976–2005), global climate model projections for temperature increases in the future range from 2.0 °C to 2.6 °C for mid-century (2036–2065) and from 2.8 °C to 4.7 °C for the end of the century (2071–2100), depending on the representative concentration pathway (4.5 or 8.5) (Vose et al. 2017; Chap. 12). Warming is expected to occur during all seasons, although most models project the largest temperature increases in summer (Mote et al. 2014), and all models suggest a future increase in heat extremes (Vose et al. 2017).

Future changes in precipitation are more uncertain than those for temperature. Global climate model projections for future mean annual precipitation range from −0.7 − +13.5%, averaging about +3% among models (Mote et al. 2014). Most models project decreases in summer precipitation, but projections vary for other seasons and models agree that the length of time between precipitation events will increase (Mote et al. 2014; Easterling et al. 2017).

10.11.1 Projections for Future Fire Activity

Several studies use statistical models to project future area burned or fire potential at both global and regional scales (e.g., western USA) (Halofsky et al. 2020). All studies indicate that fire potential and/or area burned will increase in the PNW in the future with a warming climate. For the PNW, area burned is projected to increase by 300–500% (or a factor of 4–6) with a 1.2 °C increase in temperature (Mote et al. 2014). Statistical models also suggest that the annual probability of very large fires, often defined as the largest 5–10% of fires (>5000 ha), will increase in the PNW. Projections by Davis et al. (2017) suggested that the proportion of forests highly suitable for wildfires >40 ha will increase by over 20% in the next century under a high emissions scenario (RCP 8.5) for nearly all ecoregions in Oregon and Washington.

Projections of changes in fire severity are less certain than those for area burned and likelihood of large fires. van Mantgem et al. (2013), Harris and Taylor (2015), and Flannigan et al. (2013) predict increasing global and regional fire severity related to warming, drying, windier climatic conditions, larger fires, and increased fuels. In contrast, Parks et al. (2016) suggested that potential fire severity in a warming climate could change significantly and potentially decrease in the PNW because future fuels may limit future fire severity. However, they suggest that to realize predicted reductions in fire severity, land managers in the western USA would need to facilitate the transition of forest communities towards a state of equilibrium with the emerging climate via active (e.g., mechanical thinning and prescribed fire) and passive restoration strategies like managed natural fire under suitable weather conditions (Chap. 12). Resisting changes in forest composition, structure, and fuel load through aggressive fire suppression would amplify current disequilibrium conditions and likely result in increased fire severity in future decades because fuel loads will increase as the climate warms and fire danger will become more extreme (Parks et al. 2016).

Mechanistic (process-based) models (e.g. MC2) are also used to explore future changes in fire regimes. These models use mathematical relationships to represent physical and biological processes and the interactions among them. Thus, mechanistic models allow for exploration of the interactions between vegetation and fire under changing and potentially novel conditions with no past analog or equivalent. Mechanistic model simulations suggest that both fire frequency and area burned will increase in the future in the PNW, while fire severity may decrease, depending partly on future vegetation productivity (Rogers et al. 2011; Sheehan et al. 2015). Increases in productivity could result in higher fuel levels and promote high-severity fires when drought, ignitions, and extreme fire weather occur. However, none of these models incorporates wind-driven fires that play an important role in some landscapes.

10.11.2 Management Concerns, Adaptation, and Restoration

Changing climate and disturbance regimes will be a challenge to resource managers in the PNW (Peterson et al. 2011a). Although climate conditions are expected to move beyond the historical range of conditions, the concept of HRV provides information on how forests maintained resistance and resilience in the past (Spies et al. 2018). Active management can help forests adapt by restoring desired historical conditions, increasing ecosystem resilience to changing climate, and fostering both early- and late-seral biodiversity (Peterson et al. 2011a,b; Spies et al. 2018). However, restoration needs and adaptation strategies vary across the region depending on the historical role of fire and legacies of past land management (Chap. 12).

The effects of twentieth century land management and fire exclusion caused profound shifts in stand and landscape structure and composition where fire was historically frequent (Hessburg et al. 2005; Chaps 11, 12). Extensive grazing altered understory plant communities and surface fuels that promoted fire spread, and selective cutting of large ponderosa pine trees removed much of the structural backbone that promoted resilience and resistance to drought and fire (Hessburg and Agee 2003). Low-density woodlands dominated by medium and large trees are now one of the rarest structural conditions in the region (Reilly and Spies 2015). Forests are now far denser than historically (Hagmann et al. 2013, 2014, 2017, 2019; Merschel et al. 2014; Johnston et al. 2017) and much of the non-forest mosaic has been encroached by trees (Hessburg et al. 2016, 2019).

Mortality of old-growth trees and loss of habitat to high-severity fire are primary management concerns in dry forests of the PNW. Embedded within these issues of habitat conservation is a tension between forest restoration focused on returning fire to the landscape as a coarse-filter ecosystem conservation strategy (e.g., USFS 2012), and fine-filter conservation strategies focused on listed species such as the northern spotted owl, whose habitat has been reduced by logging (Spies et al. 2019). The irony is that one type of management (clearcutting) reduced the most prevalent habitat condition for old-growth forest species in wetter parts of the region, while another type of management (fire exclusion) increased that habitat in the drier part of the region. Unfortunately, the increased extent of dense, older forests in dry forest zones has also reduced forest resilience to drought and disturbance (Spies et al. 2018).

Fuel treatments in dry forests can decrease fire intensity and severity under moderate weather conditions, and can even be effective in some topographic settings in wind-driven fires (Prichard and Kennedy 2014; Prichard et al. 2020). Thinning can also decrease competition, increase vigor of residual trees, and improve resistance and resilience of trees to drought (Vernon et al. 2018; Westlind and Kerns 2020) but may lead to undesirable fire effects if surface fuels are not reduced. Prescribed fire can also be used to reduce stand densities in dry forests and increase resilience to wildfire and drought (Peterson et al. 2011a), and to promote fire-dependent habitats of tribal importance including huckleberry fields, bear grass, meadows, and masting oaks. While these treatments can promote resilient forest structure in dry forests, but they can also exacerbate invasions of non-native annual grasses that can alter disturbance regimes and catalyze shifts to non-forested states (Kerns et al. 2020; Chaps. 1, 11, 12).

To function effectively across large dry forest landscapes, the spatial scale of thinning, prescribed fire, and managed wildfire will need to increase considerably and be maintained over time (Haugo et al. 2015; Spies et al. 2019). Reilly et al. (2018) found that closed-canopy structural conditions increased in ponderosa pine and mixed confer forests of the eastern Cascades inceased between 1985 and 2010 despite recent increases in area burned and restoration treatments. The extent of fuel treatments is often limited by lack of social license, financial resources, agency capacity, and air quality constraints on prescribed burning (Spies et al. 2019). Thinning and prescribed fire treatments can be prioritized in areas where fire suppression had a large influence, where drought stress is expected to be most severe (e.g., south-facing slopes, other dry aspects and ridges), and in high-risk locations such as the wildland-urban interface (Halofsky et al. 2020). However, treating a sufficiently large area will be needed to achieve desired ecological, economic, and social benefits.

Fire exclusion has also affected forest conditions where fire was infrequent historically. These landscapes have missed numerous small fires and potentially even a few large fires, and now have simplified mosaics of forest and non-forest conditions (Spies et al. 2018; Hessburg et al. 2019). In addition, many of the wet and moist forests west of the Cascades bear the legacies of extensive clearcutting and timber harvest. While clearcut harvesting is still the primary management approach on private lands, harvesting on public lands was drastically reduced in the early 1990s in response to lawsuits and court injunctions related to listed species. The conflict over federal forest management led to the Northwest Forest Plan (NWFP) which uses an ecosystem management approach on federal lands within the range of the northern spotted owl (Spies et al. 2019). The NWFP also aimed to protect habitat for other old-growth associates, including salmonids and marbled murrelets, by establishing an extensive network of Late Successional Reserves.

Since the establishment of the NWFP, fire has been the primary agent driving losses of old-growth forests and nesting and roosting habitat for northern spotted owl (Davis et al. 2015; section 10.11.2). Much of this loss, however, occurred in dry forest landscapes where dense, closed-canopy habitat increased dramatically over the twentieth century from fire exclusion. In moist forests, losses of old-growth to fire were offset by recruitment of forests with late-seral characteristics that established following the widespread fires during the 19th and early 20th centuries. Fire suppression will continue to be an important strategy to protect remaining old forest areas in moist forests and old trees and human communities in dry forest landscapes. However, in some drier forest areas, use of wildland fire management for resource benefit could help increase resilience to climate change and fire (Barros et al. 2018). With projected increases in wildfire activity, it will be essential to protect existing old-growth patches, accelerate structural development, and increase vegetation diversity in old plantations to offset future losses to fire.

A lack of structurally complex, early-seral conditions is another management and conservation concern in landscapes with moderately frequent mixed- and high-severity fire historical regimes (Spies et al. 2019). While logging on public lands has maintained early-seral conditions, structurally complex early seral habitats with live and dead biological legacies (e.g. residual trees, snags, and downed wood) are the rarest structural conditions in wet and moist vegetation zones (Reilly and Spies 2015). Structurally complex, early-seral habitats are currently in a deficit compared to even relatively fire-quiescent historical periods (Wimberly et al. 2000; Donato et al. 2020). Recent high-severity fires have increased early-seral conditions in the Klamath Mountains and promoted the expansion of some fire-dependent early-seral species (e.g. knobcone pine; Reilly et al. 2019), but declines in early-seral habitats the Coast Range and western Cascades have had negative effects on early-seral bird species (Phalan et al. 2019). Losses of other early-seral habitats in these ecoregions include meadows and shrub fields that may have been partially maintained by fire (Skinner 1995; Takaoka and Swanson 2008; Zald 2009, Zald et al. 2012) and provide important resources for pollinators.

In wetter forest types west of the Cascade Mountains thinning and hazardous fuel treatments are unlikely to significantly affect fire behavior (Halofsky et al. 2018). Fuels recover rapidly in highly productive moist forests which would require very frequent treatment across large spatial scales. Furthermore, treatments are unlikely to mitigate fire behavior or effects because fires are typically infrequent and occur under extreme weather conditions (e.g., dry east wind events). To protect high-value resources (e.g., municipal watersheds, key wildlife habitats, infrastructure) landscape-scale fuel breaks may potentially be effective in reducing fire intensity and aiding fire suppression efforts in these wetter forests. However, fuel treatments creating more open conditions could accelerate fuels desiccation, facilitate fire spread under moderate fire weather conditions, and promote invasions of non-native species. In light of these trade-offs, promoting landscape heterogeneity in terms of species, genotypes, and stand structure could also increase resilience to disturbance (Stephens et al. 2010; Halofsky et al. 2018) and potentially increase and protect climate refugia or areas relatively buffered from the effects of climate change (Morelli et al. 2020; Krawchuk et al. 2020).

10.12 Conclusions

Knowledge of the historical role of fire in the PNW provides important context for understanding contemporary fire and anticipating potential effects of climate change and future fire. Evidence from paleoecological studies documents clear linkages between changes in climate and fire activity that drove relatively rapid and large-scale shifts in species composition. Fire history and simulation modeling studies provide a strong understanding of the HRV over the last several centuries and key insights into how forests maintained resistance and resilience over time. However, disruption of historical fire regimes and alteration of stand and landscape patterns of forest conditions have left forests vulnerable to drought and high-severity fire that could result in irreversible changes in ecosystem structure and function and loss of biodiversity, particularly in dry forests.

Although fire burned less area in recent decades than it would have historically, it has returned to many forest landscapes of the region with a range of ecological effects. Recent high-severity fires have altered landscape composition and structure and increased early-seral conditions that many species utilize or depend on and are regionally rare in moist forests. However, large patches of high-severity fire that are uncharacteristic of historical landscape dynamics have reduced old-growth conditions in dry forests and negatively impacted populations of threatened and endangered species. Regeneration failure and state changes catalyzed by short-interval reburns and non-native grasses further threaten the persistence of dry forests. While many forests of the region have been resilient to recent fires, increasing water deficits during the growing season and short-interval reburns will likely inhibit future regeneration and decrease resilience of dry and cold forests in the future.

The ongoing impacts of climate change and increasing area burned by wildfires pose a major challenge for forest management in the twenty-first century. There is a need to develop methods for fine tuning and prioritizing adaptation strategies. Active management is needed in many dry forest landscapes where fire has been absent for over a century, but challenges remain in terms of effectively building resilience and resistance to future fire and drought at large spatial scales. The 2020 fires in western Oregon came as a surprise to many people, but there is clear historical precedent for such extremely large and severe fires. Fuels treatments are unlikely to be effective in moist forests and could undermine the ecological integrity of these systems.

Moving forward, it will be essential to educate policy makers and the public on differences in historical fire regimes and to create realistic expectations on where and when fuels management can make a difference. Collaborative approaches engaging multiple stakeholders can help assess trade-offs and develop trust and social acceptance of mechanical treatments and smoke from prescribed fire. However, active management through mechanical treatment alone is unlikely to be effective in restoring dry forests at meaningful spatial scales. Dealing with fire in moist forests where human values are concentrated and large stand-replacing fires are the historical norm presents a dilemma. Protecting valued resources and conserving both early-seral and old-growth biodiversity will require new approaches that focus on building ecological and social resilience. The use of prescribed and wildland fire, particularly in remote areas where mechanical treatment is not feasible or is restricted by policy, will be essential to achieving restoration and conservation goals. Continued improvement in monitoring of treatment implementation and wildfire effects will play an integral part in adaptive management in the coming decades.

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