Chapter 8
Fire Ecology of Rocky Mountain Forests

Sharon M. Hood, Brian J. Harvey, Paula J. Fornwalt, Cameron E. Naficy, Winslow D. Hansen, Kimberley T. Davis, Mike A. Battaglia, Camille S. Stevens-Rumann, and Victoria Ann Saab

Abstract Fire is a dominant driver of ecosystem patterns and processes across the Rocky Mountains. This chapter describes fire ecology and fire-related management for the major forest types in the Rocky Mountains. Major forest types included are ponderosa pine, Douglas-fir, mixed-conifer, lodgepole pine, spruce-fir, five-needle pines, and aspen. For each forest type we describe historical fire regimes, interactions between fire and other disturbances, departures from historical patterns, and projected future patterns. We explain fire resistance and postfire recovery patterns. We also include projected alterations to fire regimes and ecological implications due to climate change, with common silvicultural and fuel treatment options for restoration and wildfire mitigation. This information provides a comprehensive examination of contemporary fire ecology and management options in the Rocky Mountains, couched in a historical perspective.

Keywords Interactions · Montane forests · Subalpine forests · Climate change · Restoration

---

Ecoregions 15, Northern Rockies; 16, Idaho Batholith; 17, Middle Rockies; 19, Wasatch and Uinta Mountains; 21, Southern Rockies; 41, Canadian Rockies

---

S. M. Hood (✉)
USDA Forest Service, Rocky Mountain Research Station, Fire, Fuel, and Smoke Program, Missoula, MT, USA
e-mail: sharon.hood@usda.gov

B. J. Harvey
School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA
e-mail: bjharvey@uw.edu

P. J. Fornwalt
USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA
e-mail: paula.fornwalt@usda.gov

C. H. Greenberg, B. Collins (eds.), *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*, Managing Forest Ecosystems 39, https://doi.org/10.1007/978-3-030-73267-7_8

8.1 Forest Biogeography

The Rocky Mountains of the USA (RCKS) has large elevational and latitudinal gradients that drive complex patterns in fire regimes and fire ecology. In this chapter, we describe past, present, and future fire regimes and fire ecology of RCKS forests. We move from low to high elevation, recognizing that forest zone elevations are contingent on latitude across the region (Fig. 8.1). We describe forests included in the Level III Ecoregions within the Cool Temperate Forest & Woodland Formation, Rocky Mountain Forest & Woodland Division of the Terrestrial Classification System (Chap. 1, Table 1.1) and further divide the region into the Northern, Central, and Southern RCKS. While large, these biogeographic sub-regions still allow for comparing broad patterns across the RCKS. Landscape context is important, as there is no single fire regime for the RCKS; low-, mixed-, and high-severity regimes are common in each of the three sub-regions. Understanding historical fire regimes is essential to understanding how forests evolved with wildland fire and for anticipating how forests will respond to management, altered fire regimes, and climate change.

We organize this chapter to focus on the major forest types (Fig 8.1), grouped into dry montane, mesic montane, and subalpine forest zones. We describe each forest type and its dominant climate and fire regime, drawing on LANDFIRE

C. E. Naficy
Department of Forest Ecosystems & Society, College of Forestry, Oregon State University,
Corvallis, OR, USA
e-mail: cameron.naficy@oregonstate.edu

W. D. Hansen
Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY, USA
e-mail: hansenw@caryinstitute.org

K. T. Davis
Department of Ecosystem and Conservation Sciences, University of Montana,
Missoula, MT, USA
e-mail: kimberley.davis@umontana.edu

M. A. Battaglia
USDA Forest Service, Rocky Mountain Research Station, Forest and Woodland Ecosystems
Program, Fort Collins, CO, USA
e-mail: michael.battaglia@usda.gov

C. S. Stevens-Rumann
Department of Forest and Rangeland Stewardship, Colorado State University,
Fort Collins, CO, USA
e-mail: C.Stevens-Rumann@colostate.edu

V. A. Saab
USDA Forest Service, Rocky Mountain Research Station, Wildlife and Terrestrial Ecosystems
Program, Bozeman, MT, USA
e-mail: victoria.saab@usda.gov

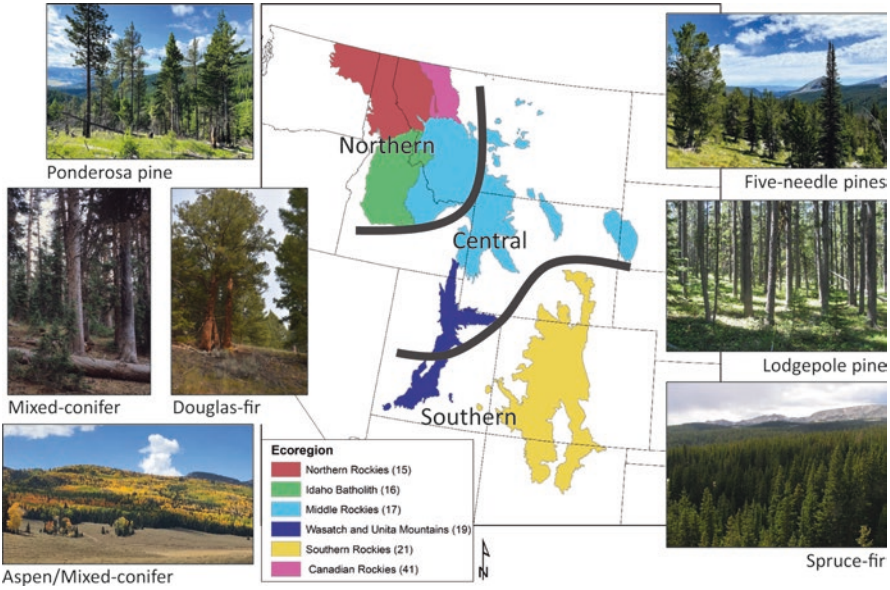


Fig. 8.1 The three sub-regions (Northern, Central, and Southern) used to delineate the US Rocky Mountains in this chapter, by Level III Ecoregion name and number, as well as the various forest types described in this chapter. (Photo credits: Spruce-fir J. Frank; Aspen/Mixed-conifer M. Varner; all others by chapter authors)

terrestrial ecological classifications (NatureServe 2018). The Northern RCKS are lower in elevation and influenced by a maritime climate that moderates temperatures and produces more rainfall in winter than the Central and Southern RCKS. Summers are hot and dry. The Central and Southern RCKS have a continental climate, with cold winters, hot summers, and portions that are influenced by monsoons. In the dry montane zone, forests are dominated by ponderosa pine (*Pinus ponderosa* vars. *ponderosa* and *scopulorum*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Mixed-conifer forests form in mesic portions of the dry montane zone, as well as in the mesic montane zone. The subalpine zone consists of lodgepole pine (*Pinus contorta* var. *latifolia*) forests at lower elevations, transitioning to forests of subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*), Engelmann spruce (*Picea engelmannii* var. *engelmannii*) ("spruce-fir"), and five-needle pine species (i.e., whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), Great Basin bristlecone pine (*Pinus longaeva*), and Rocky Mountain bristlecone pine (*Pinus aristata*)) with increasing elevation. Aspen (*Populus tremuloides*) forests can occur across all forest zones.

8.1.1 Forest Types

8.1.1.1 Dry Montane and Mesic Montane Forests

The dry montane forests of the Rocky Mountains consist of ponderosa pine, Douglas-fir, and dry mixed-conifer forest types. Ponderosa pine and dry mixed-conifer forests occupy the lower treeline to mid-slope positions in areas of warm, dry climate, whereas Douglas-fir forests fill these landscape positions in colder, dry areas where a shorter growing season length excludes ponderosa pine.

Ponderosa pine grows throughout the RCKS (also see Chaps. 9, 10, and 11) and occurs in almost pure stands to stands where it is only a minor component. Two varieties are recognized in the RCKS: *Pinus ponderosa* var. *ponderosa* occurs west of the Continental Divide in Idaho and Montana, while *P. ponderosa* var. *scopulorum* occurs east of the Continental Divide in Montana, south to Mexico (Oliver and Ryker 1990). Ponderosa pine forests generally form the lowest elevation forests in the RCKS, at the ecotone with grassland and sagebrush-steppe ecosystems and occur at progressively higher elevations moving from northern to southern latitudes. RCKS ponderosa pine forests can be either climax (will persist in the absence of disturbance) or seral (will transition to dominance by other species in the absence of disturbance) depending on the location. Ponderosa pine is generally only a climax species in the driest portion of its range, where it co-occurs with few other species (e.g., juniper (*Juniperus*) spp., Gambel oak (*Quercus gambelii*)). In most of the rest of its range, ponderosa pine is a seral species that maintains dominance over co-occurring species largely as a result of recurrent fire. Fire exclusion has increased the relative abundance of Douglas-fir on sites with intermediate moisture and a combination of Douglas-fir and other co-occurring species (lodgepole pine, grand fir (*A. grandis*) in the north, and white fir (*A. concolor*) in the south), on moister sites.

Douglas-fir has a broad distribution along the RCKS, from Canada southwards into Mexico. It grows under wide-ranging climate and edaphic conditions. Douglas-fir's range is fairly continuous in the Northern RCKS. In the Northern RCKS and portions of the Central RCKS, including much of the Greater Yellowstone Ecosystem (GYE; an intact northern temperate ecosystem located in portions of Wyoming, Montana, and Idaho), almost pure Douglas-fir forests form at lower elevations in dry, cold areas as open forests interspersed with sagebrush grasslands. Due to its wide ecological amplitude, Douglas-fir can co-occur with ponderosa pine on more mesic, warm sites at low elevations, through the upper montane in mixed-conifer forests. Douglas-fir dominance in mixed-conifer and ponderosa pine forests varies greatly depending on disturbance history.

The dry mixed-conifer forest type is highly variable depending on sub-region and fire history. Dry mixed-conifer forests are typically dominated by ponderosa pine and/or Douglas-fir. In the Northern RCKS, other seral species such as western larch (*Larix occidentalis*), grand fir, lodgepole pine, and western white pine (*Pinus monticola*) are common. Without fire, grand fir, subalpine fir, and Engelmann spruce gradually become increasingly dominant. In dry mixed-conifer forests of the

Southern RCKS, white fir is common and blue spruce (*Picea pungens*) can occur, while western larch, western white pine, and grand fir are absent.

Mesic montane forests are dominated by the moist mixed-conifer forest type, sometimes co-mingled with the true mesic forest type in the wettest portions of this zone. Moist mixed-conifer forests are composed of a diverse mixture of species that vary within and between sub-regions. Ponderosa pine may be present, but these stands are often co-dominated by a mix of Douglas-fir and moist-site species such as lodgepole pine, western larch, western white pine, and true firs in the Northern RCKS or aspen, spruce and subalpine fir in the Central RCKS, and white fir and southwestern white pine in the Southern RCKS. Moist mixed-conifer forests dominate in middle elevations. Mesic forests in the Northern RCKS are dominated by western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*), with components of Douglas-fir, western white pine, lodgepole pine, grand fir, subalpine fir, Pacific yew (*Taxus brevifolia*), and western larch. These mesic forests are concentrated in topographic sites that create consistently cool, moist conditions (e.g., narrow valleys, topographically sheltered sites), or in areas influenced by Pacific maritime climate that receive high rainfall totals, sometimes termed interior rainforest (Gavin et al. 2009).

8.1.1.2 Subalpine Forests

The upper montane and subalpine forests of the RCKS consist of lodgepole pine, spruce-fir, high elevation five-needle pine, and aspen forest types.

Lodgepole pine forests are extensive, growing from Canada to the Southern RCKS in Colorado. Lodgepole pine has one of the widest ranges of environmental tolerance of all North American conifers, surviving in frost pockets where other tree species do not (Lotan and Critchfield 1990). Lodgepole pine forests can be seral to mixed-conifer and spruce-fir forests, or climax on poor sites where it is the only tree capable of growing. Nearly pure stands of lodgepole pine in the Northern RCKS occur between the upper limit of Douglas-fir and the lower limit of subalpine fir. In Montana, lodgepole pine stands are especially well developed on broad ridges and high valleys near and east of the Continental Divide (Arno 1980) but occur widely throughout much of the region. Because of its wide ecological amplitude (both in latitude and elevation), lodgepole pine grows from nearly pure stands to mixed stands with many associated species. In cool, dry environments, even-aged, single-storied, near-monospecific stands originating from high-severity fire are common. In some cases, it grows as two-aged, multistoried, almost pure stands (Anderson 2003). Lodgepole pine also forms an important component of mixed-conifer forests.

Subalpine forests dominated by Engelmann spruce and subalpine fir occur generally in the elevational band above moist mixed-conifer and pure lodgepole pine forest types throughout the RCKS from Canada south to New Mexico (Peet 2000). In many locations, spruce-fir forests can extend upward to the upper treeline in *krummholz* form (i.e., stunted, mat-like growth). Spruce and fir occupy a high elevation zone of the RCKS that is among the coldest and wettest of the continental USA, with high winter snowfall totals (>500 cm) and potential for frost at any time of year; frost-free periods are generally short (30–60 days/year) (Alexander et al. 1990; Alexander and Sheppard 1990).

Five-needle pine forests form the highest elevation forest type (for review see Tomback et al. 2011). Limber pine has the broadest distribution and ecological amplitude, occurring throughout the RCKS and growing from lower to upper treeline. In the upper subalpine to treeline, whitebark pine occurs in the Northern RCKS and GYE, Rocky Mountain bristlecone pine in the Southern RCKS and Great Basin bristlecone pine in Utah. These species can occur as almost pure stands or as a component in cold spruce-fir and lodgepole pine forests. At the highest elevations, five-needle pines form scattered patches of krummholz amid rock scree. The introduced white pine blister rust (*Cronartium ribicola*) and native mountain pine beetle (*Dendroctonus ponderosae*) have caused high levels of five-needle pine mortality in the RCKS (Tomback et al. 2011).

The aspen forest type is difficult to characterize because it occurs throughout the RCKS owing to aspen's broad ecological amplitude; we include it with subalpine forests, but it is also often found in montane forests. Aspen forms extensive forests in portions of the Southern and Central RCKS, with smaller clones found along riparian areas and localized mesic sites in the Northern RCKS (Shinneman et al. 2013; Rogers et al. 2014). Aspen exists as both an early seral component of mixed-conifer or spruce-fir forests and as relatively stable, climax pure forests, depending on soil type and climate. Mueggler (1989) estimated approximately two-thirds of aspen stands are seral. In the Central and Southern RCKS, aspen-mixed-conifer forests occur in colder environments of the dry montane zone and in the mesic montane to subalpine zones. These former forests typically consist of aspen along with Douglas-fir, ponderosa pine, and/or white fir; on more mesic sites, subalpine fir and blue spruce occur. In mesic montane aspen/mixed-conifer forests, Engelmann spruce and lodgepole pine typically co-occur with aspen. Aspen is unique among other common RCKS tree species in that it largely relies on vegetative reproduction, forming genetically identical clonal ramets through suckering. Disturbance is needed to stimulate suckering and rejuvenate the clone. In areas of stable aspen, regular disturbance allows clones to persist for thousands of years. In the absence of disturbance, the health of the clone declines with little-to-no suckering occurring. In seral aspen, conifers will encroach and outcompete aspen without disturbance. Lack of fire and age-related senescence is associated with widespread aspen decline in Utah and Colorado. In areas of high ungulate populations, heavy browsing of suckers also contributes to aspen decline.

8.1.2 Climate-Fire Interactions

Climate and its effect on wildland fire changes greatly from the Northern to Southern RCKS. The Central RCKS is located around a critical north-south transition zone of major synoptic climate patterns that influences interannual patterns of drought and fire (Brown et al. 2008). As a result, fire seasonality and synchrony with the Northern or Southern RCKS are quite variable. When monsoons bring summer precipitation to Southern Utah and Colorado, fire activity is often minimal. Years when monsoons fail to materialize are often associated with large wildfires in the Central and Southern RCKS, especially when preceded by wet years that create abundant herbaceous fuels (Swetnam and Betancourt 1998; Veblen et al. 2000). Wildland fires typically occur late July through October, when seasonal rains and snow end the season (Littell et al. 2009). In lower elevation forests, where snow cover is more ephemeral, fuels are typically dry enough to burn by late spring, although most fires typically occur mid-to-late summer. Fire season in higher elevation forests is typically later in the summer, after snow melt, and can continue into the fall until snowpack accumulates.

Fire behavior and subsequent fire effects depend on fuels, weather, and topography, as well as adaptations of local vegetation to fire. Fire regimes in the RCKS are governed by both top-down climatic factors and bottom-up factors of topography, population density, and fine-scale forest mosaics (Falk et al. 2011). Schoennagel et al. (2004) review how fire, fuels, and climate interact across the RCKS to influence forest structure and composition. In lower elevation, dry montane forests of the RCKS, weather conditions conducive to fire occur for several months in most years. Fires in this zone were historically relatively frequent, with intra-regional variability driven by a combination of the abundance of lightning ignitions, indigenous fire use practices, and fire-fire interactions. In contrast, in the subalpine forest zone there is typically enough fuel to support fire, but in most years, weather conditions are such that fuels are not easily ignited.

Area burned in forests across the RCKS is strongly positively correlated with low precipitation, negative Palmer Drought Severity Index (i.e., dry conditions), and high temperatures, but there are some sub-regional differences (Heyerdahl et al. 2008; Littell et al. 2009). In the Northern RCKS, regional fire years are associated with warm springs and warm, dry summers; antecedent year climate is uncorrelated with regional burn patterns (Heyerdahl et al. 2008). Fires in lower montane forests, but not upper montane forests, of the Southern RCKS are heavily influenced by antecedent year climate – with area burned positively related to moist conditions that allow fine fuels to accumulate occurring two years prior to a dry year (Sherriff and Veblen 2008). Regional fire years in the Southern RCKS are associated with higher winter temperatures and lower winter and spring precipitation (Littell et al. 2009).

The influence of the El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) on fire switches around 40° N (Brown et al. 2008). In the Northern RCKS, ENSO La Niña years typically have higher snowpack and are associated with years of low regional fire activity (Heyerdahl et al. 2008). In contrast, regional fire years in the Colorado Front Range are closely tied to ENSO events, where the warm El Niño phase increases moisture during spring, resulting in higher plant production that causes a spike in fires several years later. In Colorado, La Niña causes dry springs and is associated with widespread fire the same year (Veblen et al. 2000; Schoennagel et al. 2005). Years with positive PDO during El Niño are strongly associated with large fires in the Central RCKS, while large fires years in the Southern RCKS are more likely when negative PDO is combined with La Niña (Schoennagel et al. 2005). In Utah, La Niña conditions are associated with regional fire years and El Niño conditions tend to be non-fire years (Brown et al. 2008).

8.2 Historical Fire Regimes

Fire regimes are useful constructs for describing general domains of fire dynamics (Agee 1993). Many characteristics (e.g., fire size, seasonality; see Chap. 1) can be included in fire regime descriptions; we focus principally on fire severity and frequency as two foundational characteristics that highlight key differences among forest types. Despite some variability in wildfire seasonality across the RCKS, modern fires and fire scar records suggest that historically, peak fire season was late summer to early fall in the Northern RCKS (Heyerdahl et al. 2008), and prior to the arrival of midsummer monsoons in the Southern RCKS. As in most western forests, a small fraction of total fires were responsible for the majority of area burned (Strauss et al. 1989), likely occurring in large fire complexes during drought years. Written historical documents, fire atlases, and fire scar data attest to major fire years in the Northern (1889, 1910, 1919), Central (1785), and Southern RCKS (1851, 1859, 1879) that burned hundreds of thousands to millions of hectares (Brown and Wu 2005; Brown 2006; Sherriff and Veblen 2006; Heyerdahl et al. 2008). In addition to fire, insect outbreaks also exerted large influences on forest structure and landscape patterns (Sect. 8.4).

In contrast to regional fire regime patterns, fire severity and frequency varied at finer scales as a function of forest vegetation, topography, and cultural fire use practices. Numerous tribes occupied the lands known today as the United States (US Forest Service Tribal Connections Viewer: https://usfs.maps.arcgis.com/apps/webappviewer/index.html?id=fe311f69cb1d43558227d73bc34f3a32). For millennia, and still today, indigenous communities actively manage vegetation for an array of objectives through burning, although the colonization of western North America by Euro-Americans in the 1800s has drastically reduced the extent of indigenous fire use (Pyne 1982; Kimmerer and Lake 2001; Yazzie 2007). Fire is widely used as a tool for land clearing for settlements, hunting, and improving crop production. The influence of Native American fire use on vegetation structure and composition is increasingly documented through better incorporation of indigenous knowledge into western frameworks of fire ecology, though much progress is needed (Kimmerer and Lake 2001). In many areas of the RCKS, Native American burning increased fire frequency, altered the season of burning, and expanded the geography of fire into places that may not have otherwise burned regularly (Kimmerer and Lake 2001).

8.2.1 Dry Montane and Mesic Montane Forests

Historical fire regimes of the dry, warm montane forests of the RCKS varied from frequent, low-severity to moderate-frequency, mixed-severity. The frequent, low-severity fire regime characteristic of southwestern ponderosa pine forests (Chap. 11) was not as ubiquitous in the Rocky Mountains, largely being confined to the lowest elevation, driest portions of the range of this forest type (Kaufmann et al. 2004).

In the Northern RCKS, ponderosa pine at lower-elevation, drier sites typically experienced a low-severity fire regime, with average fire-free intervals of 5–25 years. Maximum fire-free intervals ranged from 21–30 years (minimum 3–4 years) (Arno 1980). Frequent low-severity surface fires were most common, but infrequent high-severity fires also occurred (Arno et al. 1995a). In areas of intermediate moisture, ponderosa pine and dry mixed-conifer forests experienced moderate-frequency, mixed-severity fire regimes. Mean fire return intervals (FRIs) ranged from 15–40 years with maximum fire-free intervals of approximately 35–70 years (Arno 1980; Barrett et al. 1991; Naficy 2017). The mixed-severity fire regime of these forests created a diversity of disturbance histories, successional trajectories, ages, and stand conditions resulting from different sequences and timing of high- and low- to moderate-severity fires (Barrett et al. 1991; Arno et al. 1995a; Naficy 2017). For example, old multi-aged dry mixed-conifer stands resulted from two alternative pathways; one dominated by recurrent lower-severity fires and another where an older high-severity fire was followed by a mix of low- and moderate-severity fires. These older forests were interspersed with younger, even-aged and multi-aged patches that resulted from a mix of more recent high-severity fire followed by subsequent non-stand-replacing fires. In the absence of fire, the density of Douglas-fir and moist-site species (e.g., lodgepole pine, grand fir) increased and the proportion of grasslands, shrublands and open canopy forest patches decreased (Arno et al. 1995b; Dickinson 2014).

The Black Hills region of the Central RCKS supports an isolated ponderosa pine forest covering almost 15,540 km^2 surrounded by the Great Plains (Shepperd and Battaglia 2002). Fire history studies and historical accounts document fire frequencies ranging from 10 to 35 years, depending on elevation (Shepperd and Battaglia 2002; Jain et al. 2012). Most fires occurred in the late growing season or fall (Brown and Sieg 1999). A mix of variable-frequency, low-severity surface fire and moderate-severity fire created a matrix of lower and higher density forest patches (Brown and Sieg 1999). In some areas, high-severity fires may have killed large patches of trees, initiating even-aged (Shinneman and Baker 1997) and multi-aged stands (Lentile et al. 2005). Even-aged patches of ponderosa pine may also have resulted from optimal climatic conditions leading to regionally synchronous recruitment (Brown 2006).

In the Southern RCKS, the fire regime was dominated by moderate- to high-frequency, low- to mixed-severity fire regimes (McKinney 2019). Sherriff and Veblen (2007) estimated approximately 20% of ponderosa pine forests along the

Colorado Front Range experienced a low-severity fire regime, and 80% burned under a mixed-severity fire regime. Sites <2100 m likely burned with low-severity surface fires with 10–30-year FRIs; at higher elevations FRIs ranged from 30 to 100+ years. Fires in higher-elevation forests of the Colorado Front Range occurred mostly during extreme drought; about 62% were moderate severity (21–79% tree survival), and 38% high severity (≤20% tree survival) (Schoennagel et al. 2011). Battaglia et al. (2018) estimated that historical fire regimes in the Colorado Front Range created and maintained relatively low-density forests, with ~100 trees/ha in the lower montane and ~160 trees/ha in the upper montane, although variability was high in the lower montane. In southwestern Colorado, a similar pattern of more frequent, lower-severity fire at lower elevations, transitioning to mixed-severity fire regimes with increasing elevation has been documented (Brown and Wu 2005; Tepley and Veblen 2015).

Fire regimes in dry, colder montane forests of the Northern and Central RCKS were historically of mixed severity, forming complex patterns typically dominated by Douglas-fir. In lower elevation Douglas-fir forests, fire was recurrent (median 20–45 years), with highly variable FRIs (Barrett 1994; Heyerdahl et al. 2006). This fire frequency limited establishment of Douglas-fir and lodgepole pine in portions of the lower ecotone, thereby maintaining and expanding grasslands, and creating a mosaic of non-forest, open-canopied savannas, and dense regenerating postfire forest (Arno et al. 1995b).

In contrast to ecotonal Douglas-fir forests, fire regimes in montane Douglas-fir forests of the Central and Northern RCKS had intermediate FRIs (median 35–70 years) and more severe mixed-severity regimes. Naficy (2017) documented a mixed-severity fire regime dominated by moderate- and high-severity fire effects across 80% of the area, with low-severity effects in the remaining 20% in montane Douglas-fir forests from two adjacent mountain ranges in northern Yellowstone. This regime resulted in a mix of predominantly intermediate-aged single and multi-cohort stands, with a small amount of old multi-cohort forest. At a mid-elevation site in Wyoming in the Central RCKS, Douglas-fir forests had a historical FRI of 47 years that likely burned as mixed-severity based on growth increases on surviving trees and continuous recruitment (Brown et al. 2020). The fire regime in Douglas-fir dominated forests in small, isolated mountain ranges of southwestern Montana west of the Continental Divide was characterized by moderate-severity fires (50% of total area burned), with some low-severity (39%) and stand-replacing (11%) burns. Fires were smaller and more likely to burn as moderate-severity compared to east of the Divide, where lodgepole pine dominated. The more complex west-side historical fire regime is attributed to more heterogeneous topography and interspersion of forested and non-forested patches (Murray et al. 1998).

Substantially less is known about the historical fire regimes of moist mixed-conifer forests than other forest types in the RCKS. This is due to numerous factors, including high variability of fire-free intervals, greater prevalence of severe fire that consumes evidence of previous fires, abundance of fire-sensitive tree species that serve as poor fire recorders, and higher site productivity that results in faster wound healing, faster dead wood decomposition, and increased frequency of embedded fire scars that are difficult to locate and sample. Median FRIs in moist mixed-conifer forests ranged from 30–45 years, tending to be somewhat longer and more variable than in neighboring dry mixed-conifer forests (Barrett et al. 1991; Romme et al. 2009; Tepley and Veblen 2015; Naficy 2017). This combination of short- and longer-interval fires interacting with insect outbreaks resulted in greater diversity of successional phases, age structures, and patch sizes. Fire severity in moist mixed-conifer forests across the RCKS was highly variable, likely due to variability in FRIs that influenced fuel abundance and continuity, topographic complexity, and the diverse species assemblages that comprise these forests. A relatively high proportion of the landscape consisted of young- to intermediate-aged, multi-cohort stands (Tepley and Veblen 2015; Naficy 2017) that resulted from recurrent moderate-severity fires or alternating stand-replacing and non-stand-replacing fires. These younger, multi-aged stands were often intermixed with older multi-aged and even-aged stands, resulting in a complex landscape patchwork.

8.2.2 Subalpine Forests

Fire regimes in lodgepole pine forests were dominated by infrequent, stand-replacement fire (Schoennagel et al. 2004), but mixed-severity fire regimes were also common in drier portions of the range, especially in the northern RCKS (Arno 1980; Barrett et al. 1991; Agee 1993). Historically, weather and fuel availability limited fire in many lodgepole pine forests, such that the FRI was 120–400 years and typically occurred as stand-replacement crown fires driven by dry, hot, and windy conditions (Romme 1982; Sibold et al. 2006). Lodgepole pine forests with a mixed-severity fire regime experienced more frequent fire (25–50 year FRI), dominated by low- to moderate-severity surface fires, with some high-severity fire (Arno 1980). This variation in frequency and severity created multi-aged structures and a fine-grained mosaic of young even- and mixed-aged lodgepole pine forests (Barrett et al. 1991; Arno et al. 1993).

Historical fire regimes of spruce-fir forests were infrequent (FRIs ~100–550 years) and largely stand-replacing (Aplet et al. 1988; Sibold et al. 2006). The broad variability in FRIs is partly due to the extensive distribution of spruce-fir forests across diverse topographic, geographic, and geological gradients. Long FRIs and the predominance of high-severity fire erases most information about previous patterns of forest conditions, and limits insights into the drivers of fire and ranges of variability in subalpine forest systems. Romme (1982) suggested that non-equilibrium dynamics characterized subalpine forests in western Yellowstone, where a few large, infrequent (~300 year FRI) severe fires initiated long-term change. Studies from subalpine forests in Colorado document different spatial patterning of fire, including both coarse- and meso-scale mosaics (Buechling and Baker 2004; Sibold et al. 2006). This variation in the spatial patterning of fires in spruce-fir forests contributed to heterogeneity of landscape conditions, wildlife habitat, and ecosystem resilience to disturbances (Turner and Romme 1994).

Fire history reconstructions of high-elevation five-needle pine forests suggest high variability of historical fire regimes (Romme and Walsh 2003; (Larson et al. 2009). A synthesis of studies from the Northern RCKS describes the historical fire regime of whitebark pine as mixed-severity, with fires of variable size and FRIs of 30–144 years, but sometimes up to 300 years (Morgan et al. 1981). There are few fire history reconstructions in Rocky Mountain bristlecone pine forests and limber pine forests, but it seems that fire was frequent enough to support both low-intensity surface fire (Brown and Schoettle 2008; Coop and Schoettle 2011) and some variable high-severity fire that facilitated pine regeneration (Coop and Schoettle 2009). Even less is known about historical fire regimes in Great Basin bristlecone pine.

Aspen can be stable or seral in the RCKS, leading to varied historical fire regimes (Shinneman et al. 2013; Rogers et al. 2014). Stable aspen occurs in areas that lack conifers due to topographic isolation, or edaphic site conditions that give it a competitive edge; fire did not have a large influence in these areas historically (Shinneman et al. 2013). Seral aspen depends on fire for persistence, as it promotes extensive aspen suckering and kills competing conifers. Large patches of aspen have been shown to reduce burn probability or fire spread patterns due to high fuel moisture content of over- and understory vegetation and low conifer fuel loading. Fire history reconstruction in aspen is difficult because aspen typically do not form fire-scars, deteriorate quickly, are short-lived, and high-severity fires can eliminate evidence of past fires. Most aspen studies in the RCKS occur in the Central and Southern subregions, and few can reconstruct long-term fire frequency (Shinneman et al. 2013). In southwestern Colorado, the historical FRI ranged from 10 to 45 years (mean 18 years) in aspen/mixed-conifer forests (Tepley and Veblen 2015). Aspen forests often burned less frequently than adjacent or intermixed conifer forest types (Shinneman et al. 2013). Fires were typically moderate- to high-severity (Tepley and Veblen 2015), resulting in relatively young aspen sometimes across large areas (Binkley et al. 2014). Extensive areas of aspen-dominated forest in areas that could support more conifers suggest the possibility of fairly large-scale, fire-driven alternative states between aspen and conifer forest (Romme et al. 2009). Pollen records show aspen states have historically shifted over long time scales driven by concomitant changes in climate and fire frequency (Carter et al. 2017; Morris et al. 2019).

8.3 Contemporary Fire Regimes

8.3.1 Euro-American Colonization and Altered Fire Regimes

Euro-American colonization of the RCKS altered fire regimes both indirectly through domestic grazing, mining, road building, timber harvesting, and removal of Native Americans from their lands, and directly through fire suppression efforts. The onset of fire exclusion varied across the Northern, Central, and Southern RCKS due to differences in socio-political histories and geographical settings, and within them due to gradients of topography and forest types that limited the types or extent of possible land uses and settlement. Euro-American colonization of the RCKS was punctuated by the development of major settlement routes, mineral discoveries prompting local population swells, construction of transcontinental railroads that created high demand for timber and more permanent settlement, and introduced heavy grazing by domestic animals (Madany and West 1983; Malone et al. 1991). Euro-American colonization greatly reduced Native American populations (O'Fallon and Fehren-Schmitz 2011) and was accompanied by relocation of tribes to reservations and prohibition of cultural fire use (Yazzie 2007). Effective fire exclusion often paralleled these major developments with a lag of several decades, drastically reducing the annual area burned across the RCKS between the 1860s and 1930s (Brown and Sieg 1999; Heyerdahl et al. 2006; Naficy 2017). Federal policies initiated in the early 1900s began an era of direct fire suppression that largely continues to this day (Pyne 1982). Advancements in fire suppression activities (e.g., installing fire lookouts; smokejumping) facilitated fire suppression even in remote areas beginning in the 1940s (Pyne 1982).

The ecological legacy of Euro-American colonization differs across forest types, although broadly speaking, it has homogenized the spatial patterning of non-forest and forest vegetation types and reduced forest age and structural diversity. In dry montane forests, fire exclusion effects interact with the effects of other post-colonization activities such as timber harvesting. Historical timber harvesting was quite extensive in these forests, particularly near human communities (Veblen and Lorenz 1986; Brown et al. 2019). These forests, especially, have experienced lengthened FRIs and thus greater change in stand structure, composition, and fuels. Where timber harvest did not occur, stand-level responses to fire exclusion are contingent on site-level disturbance history. In historically open-canopy, multi-aged stands created by recurrent, non-stand-replacing fire, fire exclusion has led to increased tree density and shifts in species composition towards more shade-tolerant species such as Douglas-fir, true firs, or lodgepole pine (Arno et al. 1995b; Brown and Cook 2006; Naficy et al. 2010; Schoennagel et al. 2011; Battaglia et al. 2018). In denser stands that were already recovering from severe fire at the onset of fire exclusion, structural and compositional shifts have been much more limited due to the negative feedback exerted by the closed canopy overstory on understory regeneration. Where timber harvest removed many large, old trees the structural and compositional shifts initiated by fire exclusion have been greatly exacerbated and accompanied by reductions in age structure diversity (Brown and Cook 2006; Naficy et al. 2010; Battaglia et al. 2018). In cold, dry montane Douglas-fir forests at the lower forest ecotone, fire exclusion has caused stand densification and encroachment of Douglas-fir into grasslands, resulting in significant homogenization of landscape patterns (Heyerdahl et al. 2006). However, above the lower ecotone, where higher severity fire was an important component of the fire regime (Naficy 2017), fire exclusion effects are most evident as reduced landscape diversity of age classes. Fire exclusion has had a more muted effect in moist mixed-conifer forests. An important contrast with drier forests is the greater abundance of shade-tolerant species that increases understory tree densities and vertical structural homogenization, even in more closed-canopy stands. Here, the most important landscape-scale changes resulting from fire exclusion are reduced landscape diversity of stand ages, successional stages, and structural types. For subalpine forests, Euro-American land use also has had more subtle effects (Romme 1982; Sibold et al. 2006). Fire exclusion has lengthened FRIs in some cases (Buechling and Baker 2004), but not always (Romme 1982; Sibold et al. 2006). Stand- and landscape-scale changes include shifts to more advanced forest successional stages, infilling of subalpine meadows, and some loss of landscape mosaic diversity, but these effects are generally considered more limited in scope, magnitude, and ecological impact compared to lower elevation forests (Schoennagel et al. 2004).

As fire is sensitive to climate across the western USA, anthropogenic climate change is now altering contemporary fire regimes. More frequent, larger, and more severe fires are occurring due to unusually hot and dry conditions (Rocca et al. 2014; Abatzoglou and Williams 2016; Parks and Abatzoglou 2020). Concurrent with warming and drying, fire frequency in the RCKS has increased by roughly 500% since the 1970s, and burned area has increased 1700% (Westerling 2016). Evidence is growing that climate change from anthropogenic emissions account for half of the increases in burned area (Abatzoglou and Williams 2016). These changes in climate and fire regimes have ecological consequences for postfire resilience and recovery (see Sects. 8.4 and 8.6.1 for additional detail). For example, increasing fire severity has slowed recovery of understory plant species adapted to cool, mesic environments (Stevens et al. 2019), and climatic conditions are now unsuitable for tree recruitment after fire at many dry, low-elevation sites in the RCKS (Davis et al. 2019). Drier conditions in the first few years following fire have been associated with lower regeneration densities of Engelmann spruce and subalpine fir in the Northern RCKS (Harvey et al. 2016c). Recruitment pulses of these species in Colorado are linked to years with high soil moisture availability, which has declined in the past 30 years due to reduced snowpack, higher summer temperatures, and moisture deficits (Andrus et al. 2018). People also account for a substantial portion of ignitions in the RCKS, particularly in areas of the wildland-urban interface (WUI) (Balch et al. 2017). In many regions of the RCKS, population growth has been rapid in recent decades; the WUI has expanded by 33% in the USA (Radeloff et al. 2018).

8.3.2 Resumption of Active Fire Regimes in Large Protected Areas

The RCKS contain some of the largest, most ecologically intact, and iconic protected forested landscapes in the contiguous USA. These areas present unique opportunities for the ecological study of biodiversity, landscape disturbance, and land use change that are generally not possible in smaller, more fragmented protected areas close to human population centers (Miller and Aplet 2016). They also present the opportunity for more flexible fire management approaches, including prescribed fire, that has resulted in a resumption of active fire regimes and a larger annual area burned than in unprotected areas.

Historically, large protected areas in the RCKS were subject to the same management paradigms that caused abrupt regional declines in area burned. However, due to their large size, remoteness, and low road densities, wildfires continued in many of these areas for several decades after declines began near major settlements (Arno et al. 2000; Naficy 2017). The intentional return of fire to forested ecosystems in the RCKS occurred first in the National Parks in the late 1960s and soon afterwards in National Forests in the early 1970s, following policy changes within each agency and the initiative of local managers (van Wagtendonk 2007; Miller and Aplet 2016). The return of fire in the RCKS was gradual, and political, institutional, and operational support for wildland fire use policies has varied over time (Miller and Aplet 2016).

Collectively, the resumption and maintenance of fire regimes in large protected areas has provided key insights regarding effects of land use change on fire regimes, landscape resilience, and vegetation responses to climate change. Prior to this, many were concerned that forests, especially at low- to-mid-elevations, were ecologically vulnerable to resumption of fire as a result of increased fuel amount, continuity, and landscape homogenization (e.g., Hessburg et al. 2005). However, studies conducted in the Northern and Central RCKS have shown that high-severity fire represents a small portion of total area burned, with landscape patterns that are broadly consistent with our understanding of historical fire regimes (Larson et al. 2013; Harvey et al. 2016b; Naficy et al. 2016). For low-mid elevation forests in the Southern RCKS, which largely exist outside protected areas, properties of resumed fire regimes will ultimately emerge from the joint effects of historical fire exclusion, extensive timber harvest, continued fire suppression efforts and climate change and will require additional study (Sherriff et al. 2014; Fornwalt et al. 2016; Rodman et al. 2020a).

8.4 Disturbance Interactions

Fire and other natural disturbances (e.g., insect outbreaks, windthrow) are an integral part of the structure and function of Rocky Mountain forests. These disturbances have occurred and interacted for millennia (e.g., Millspaugh and Whitlock 1995; Brunelle et al. 2008) and continue today (e.g., Baker and Veblen 1990; Bebi et al. 2003). However, since the late 1990s, the extent and severity of native insect outbreaks (Raffa et al. 2008; Meddens et al. 2012) have sharply increased concurrently with fire activity (Westerling 2016), raising concerns about how fire interacts with multiple other disturbances (Parker et al. 2006). Here, we focus on how fire interacts with insect outbreaks and with past fires when short interval “reburns” occur. The occurrence of one disturbance can be linked to another (Simard et al. 2011). Linked disturbances can be positive (facilitating the incidence or spread of a subsequent disturbance, or amplifying the intensity) or negative (impeding the incidence or spread, or reducing the intensity) (Kane et al. 2017). Disturbance interactions can also produce compound or cascading effects on ecosystem response to disturbance (Buma 2015). Interactions between fire and other disturbance types can occur in any sequential order; fire can be affected by or affect other disturbances – including other fires.

8.4.1 Fire-Insect Interactions

Outbreaks of native insects, including bark beetles (Coleoptera: Curculionidae, Scolytinae) and western spruce budworm (*Choristoneura freemani*), have been widespread, synchronous, long-lasting, and severe since the 1990s (Raffa et al. 2008; Flower et al. 2014), although linkages with altered fire regimes are variable. Outbreaks are driven by widespread drought and the abundance of suitable host trees. The effects of altered fire regimes on beetle outbreaks is associated with the concomitant changes in stand structure and forests in many areas of the RCKS. In lower-elevation dry montane and mesic forests with historically more frequent, low- and mixed-severity fire regimes, fire suppression and exclusion has driven increases in density and increased landscape homogeneity – all factors that can increase outbreak potential (Fettig et al. 2007). Douglas-fir beetle (*Dendroctonus pseudotsugae*) and mountain pine beetle outbreaks in Douglas-fir, ponderosa pine, and dry mixed-conifer forests are more severe and linked to increases in dense stands with high basal area of larger-diameter host trees (Negrón and Popp 2004; Graham et al. 2019). In subalpine forests with infrequent, stand-replacing fire regimes, it is changing climate, rather than alterations in fire regimes, that has driven recent outbreak severity (Baker and Veblen 1990; Negrón and Huckaby 2020).

The concurrent recent increases in fire activity and bark beetle outbreaks in the RCKS has led to concerns that outbreaks increase the likelihood, size, and severity of subsequent fires. Several reviews summarize beetle outbreak effects on fuels, fire occurrence, fire size, and fire severity, as well as operational concerns and ecological response (e.g., Hicke et al. 2012; Jenkins et al. 2014; Kane et al. 2017). Beetle outbreaks can substantially alter fuel profiles by killing the dominant overstory trees and stimulating understory vegetation production. This is well documented in ponderosa pine forests (Hoffman et al. 2012; Crotteau et al. 2020), Douglas-fir forests (Donato et al. 2013), lodgepole pine forests (Klutsch et al. 2011; Simard et al. 2011; Schoennagel et al. 2012), and spruce-fir forests (DeRose and Long 2009). In general, trends follow a similar pattern among forest types. The first 1–2 years (red stage) after beetle outbreaks start are characterized by changes to fine fuels in the canopy through a steep drop in foliar moisture and increased needle flammability as trees die. This decrease in canopy moisture is counteracted by reduced canopy fuels as needles drop from dead trees. The next 3–10 years (gray stage) are characterized by decreased crown fire hazard as available canopy fuels remain lower, while surface fire hazard fuels increase as fallen branches accumulate on the forest floor.

Finally, 1–3 decades after beetle outbreaks (silver stage), coarse fuels accumulate on the forest floor as snags fall, and canopy fuels redevelop as shade tolerant or later seral trees ascend to the canopy. The degree and magnitude of these changes is dependent on the mix of host and non-host species (Hicke et al. 2012).

Despite the relatively consistent changes to fuel profiles caused by beetle outbreaks, strong evidence of linkages between outbreaks and subsequent fire is lacking. The occurrence of fire throughout the 1900s (Kulakowski and Jarvis 2011) and mid-1980s–2010s (Meigs et al. 2015) was unrelated to prior bark beetle outbreaks, instead driven by antecedent drought conditions. Area burned at the annual scale (Hart et al. 2015) and daily scale (e.g., within fire events, Kulakowski and Veblen 2007; Hart and Preston 2020) since the early 2000s was also unrelated to prior bark beetle outbreaks across the western USA. Regardless, post-outbreak fire-prone forests inevitably burn. When they do, most measures of fire severity (e.g., fire-killed basal area) are not strongly linked to prefire outbreak severity (e.g., beetle-killed basal area). For example, fire severity was unrelated to prefire beetle outbreak severity in gray stage Douglas-fir forests or gray stage spruce-fir forests (Harvey et al. 2013; Andrus et al. 2016). In lodgepole pine stands, the effects of mountain beetle outbreaks on fire severity have generally been minor but also depended on the time since outbreak and weather at the time of fire. Fire severity was largely unrelated to prefire outbreak severity when it burned through red stage outbreaks, but burn severity decreased with gray stage outbreak severity under moderate weather conditions and increased modestly with outbreak severity under extreme weather conditions (Harvey et al. 2014a, b). Even with fairly modest effects of outbreaks on burn severity, dead trees killed by beetle outbreaks (or other factors) have more of their branches consumed in a fire, and typically exhibit deep charring on snags (Harvey et al. 2014b; Talucci and Krawchuk 2019).

Whether or not beetle outbreaks and subsequent fire produce compound effects on postfire forest recovery (e.g., tree regeneration) depends strongly on the regeneration traits of the host tree species (Sect. 8.5.2). For example, lodgepole pine recovery, where serotinous, is generally minimally affected (Harvey et al. 2014a,b; but see Rhoades et al. 2018), as it maintains a viable canopy seedbank that can persist >10 years on beetle-killed trees (Teste et al. 2011). Species without a canopy seedbank (i.e., produce seed that is released upon maturity) may be more affected postfire, as seed source postfire and microclimate conducive for seedling germination could be lacking (Carlson et al. 2020). For example, Douglas-fir exhibits lower postfire seedling regeneration in areas affected by prefire beetle outbreaks than unaffected areas (Harvey et al. 2013). However, because non-seedbanking species like Douglas-fir regenerate over a longer postfire window, effects may be transient as differences are erased with time (Stevens-Rumann et al. 2015).

Operational concerns around fire behavior and firefighter safety in relation to beetle outbreaks are also a key research priority. Resistance to control is affected by fire behavior and safe navigability – both factors that could be more challenging in forests impacted by severe beetle outbreaks (Page et al. 2013). Firefighter observations in the RCKS have reported surprising fire behavior in post-mountain pine beetle outbreak stands across stages (red, gray, silver) (Moriarty et al. 2019).

However, a systematic study of more than 300 fires in the western USA that intersected prior mountain pine beetle outbreaks did not detect an effect of outbreaks on daily area burned (a proxy for rate of spread) or observed fire behavior (Hart and Preston 2020).

Fire and bark beetles can also interact in the opposite direction, with fires impacting subsequent bark beetle outbreaks. Severe fires kill abundant host trees required to sustain outbreaks; consequently, beetle outbreaks are much less likely to occur in the same area for many decades following severe fire (Bebi et al. 2003; Kulakowski et al. 2013). Lower severity burns in areas with suitable host species and sizes can weaken trees, making them more susceptible to bark beetles where present. Levels of postburn bark beetle-caused mortality varies with tree injury, postfire environment, beetle predation, and other factors (Jenkins et al. 2014). Bark beetles routinely cause additional tree mortality after fire, but outbreaks into adjacent unburned areas are uncommon (Davis et al. 2012; Powell et al. 2012).

Fire-caused tree injury level influences individual tree physiology and susceptibility to bark beetles. Tree injury level influences bark beetle attraction, with moderately-injured (measured by crown scorch and cambium kill levels) trees being more susceptible to attack than unburned or less-injured trees (Hood and Bentz 2007; Powell and Raffa 2011; Powell et al. 2012; Kulakowski and Jarvis 2013). As bark beetles need live trees to reproduce, severely burned trees are unsuitable hosts. Low-severity fire can induce tree defenses within a year, increasing resistance to bark beetles (Hood et al. 2015); however, fire-injured trees may be more susceptible to beetle attacks during this time (Powell and Raffa 2011). Thus, frequent, low-severity fire in dry montane forests may foster tree-level defenses and forest structure that confers resistance to subsequent bark beetle outbreaks, but there is a window of increased susceptibility to beetles initially after fire before induced defenses form (Hood et al. 2015, 2016). Additional research is needed to determine if this pattern extends to other forest types.

8.4.2 Fire-Fire interactions

Fire-fire linkages occur when previous fires change the likelihood, size, or severity of a subsequent burn (Prichard et al. 2017). While there is much current and needed future research on the patterns, mechanisms, and outcomes of short-interval fires, there have been some emerging themes since the 1980s in studies examining satellite atlases of fire activity in the RCKS. Collectively, there is evidence of negative links between past fires and subsequent fire likelihood, size, and severity (typically measured using a satellite index of change) for 5–20 years depending on forest type and the relative strength of other drivers such as weather and climate (Prichard et al. 2017). For example, lightning ignitions in previously burned areas of the Northern RCKS were less likely to develop into fires >20 ha compared to ignitions beyond boundaries of recent fires (Parks et al. 2016). Similarly, past fires can limit the spread of subsequent fires for 6–18 years, although variability is high across forest zones, latitude, and elevation in the RCKS (Teske et al. 2012; Parks et al. 2015). When fires do burn into recently burned forests, severity of several measures (though most commonly satellite indices capture vegetation mortality) is often lower in the first 10–15 years since the prior fire (Parks et al. 2014; Harvey et al. 2016a; Stevens-Rumann et al. 2016). However, as fuels accumulate after fire, high levels of coarse fuel can lead to subsequent high-severity reburns (e.g., Nelson et al. 2016, 2017). For example, in higher-elevation forests where tree regeneration densities (thus live woody fuel loads) following a fire can be high, fire severity can be greater in a subsequent fire, as postfire vegetation has low fire resistance (Harvey et al. 2016a; Turner et al. 2019). Conversely, in contexts when recovery of live woody fuels or coarse down fuels are slower following a fire (or areas where prefire forests had lower biomass or productivity), likelihood of a subsequent high-severity reburn may be reduced for ≥20 years (Parks et al. 2015; Harvey et al. 2016a; Stevens-Rumann et al. 2016).

Even with evidence of negative links between two fires, two high-severity fires can occur in relatively short succession, and when they do, they can produce compound effects on postfire forest recovery. For example, the 1988 Yellowstone Fires demonstrated tremendous postfire resilience, as most lodgepole pine stands had not burned for 150–300 years and contained an abundant canopy seedbank (Romme et al. 2011). However, >20,000 ha of forest recovering from the 1988 Yellowstone Fires burned again in 2016, representing a FRI <20% of the previous one. In forests where both fires were severe (i.e., stand-replacing crown fires), postfire seedling density was reduced by >80% and carbon stocks by >60% compared to the previous long-interval fire (Turner et al. 2019). As lodgepole pine regeneration occurs rapidly after fire, compound effects from short-interval high-severity fires may leave a lasting legacy. The need to understand reburn ecology across a range of forests and gradients will become more urgent as climate warming and fire potential increase.

8.5 Resistance to Fire and Postfire Recovery

The response of an ecological system to fire is a function of the processes resistance – the persistence of species through fire – and recovery – the establishment of species after fire. Together, resistance and recovery determine ecological resilience to environmental disturbance and stress. We focus here on plant resistance and recovery. Resistance, as used here, refers to the aboveground survival of plants; species that are usually topkilled by fire, such as some tree species and most understory plant species, have low resistance. Recovery encompasses (re)establishment from surviving belowground buds, as well as establishment from on-site or off-site seed sources. Many plant species inhabiting fire-prone environments have one or more adaptive fire resistance or postfire regeneration traits (Chap. 1) that confer resilience to the area's dominant historical fire regime. As explained in Keeley et al. (2011), "no species is 'fire adapted' but rather is adapted to a particular fire regime." The disturbance history that shapes forest structure and composition also influences a species' fire resistance through fuel availability and arrangement. Because the concepts of fire resistance and postfire recovery are relevant to all biota in fire-prone systems, we also present an example of cavity nesting birds, which have been the subject of a considerable body of research in the RCKS (Box 8.1).

Box 8.1: Cavity-Nesting Bird Responses to Wildfire in Dry Mixed-Conifer Forests

Recurring severe wildfires globally for the past 30 years prompted increased interest in understanding avian responses to wildfire (e.g., Saab and Powell 2005; Lindenmayer et al. 2008; Clavero et al. 2011). Within the RCKS over last few decades, several researchers began long-term studies of bird responses to wildfire (e.g., Hutto 1995; Saab et al. 2005; Smucker et al. 2005). Here we present a summary of long-term research conducted on responses by cavity-nesting birds to wildfire in dry mixed-conifer forests of the Interior Western USA.

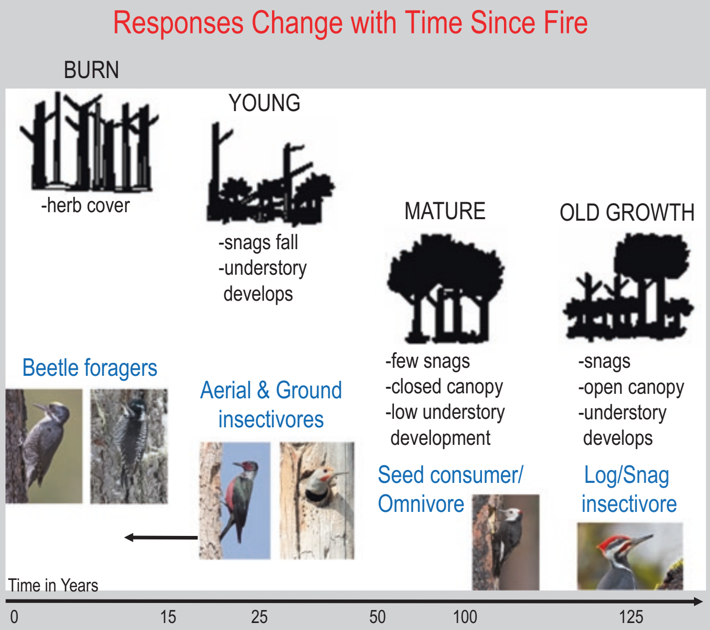
In western North America, woodpeckers and other cavity-nesting birds coevolved with wildfires and bark beetle outbreaks, which are the primary large-scale natural forest disturbances (Saab et al. 2005, 2014). Many woodpecker species directly benefit from the ephemeral habitat created by fire, which results in a resource pulse of snags that provide nesting and foraging substrates. Snags are more easily excavated than live trees for nest cavities, and snags provide substrate for bark beetles and wood-boring (Buprestidae) beetles, key food resources for several woodpecker species. Woodpeckers of the western USA are often focal species for assessing environmental impacts of land management activities, because many rely on dead trees and disturbance-prone landscapes for some portion of their life history. They are of critical ecological importance as keystone species by creating habitat features used by other wildlife species (Martin and Eadie 1999). Several woodpeckers are designated as species of conservation concern by state and federal agencies because they are responsive to fire, beetle outbreaks, and timber management activities. When studying patterns of woodpecker responses to fire, time since disturbance (Box 8.1A) and burn severity are strongly influential. A range of burn severity classes create different habitats for various avian species.

Cavity-nesting bird demographics were studied (1994–2020) in the western USA, with an emphasis on woodpeckers, in relation to wildfires in dry mix-conifer forests. Researchers evaluated measures of responsiveness to fire disturbance, including nest density, nest survival, habitat suitability, and population persistence.

The nest densities and nest survival of seven cavity-nesting bird species were monitored, including five aerial and ground insectivores (American kestrel (*Falco sparverius*); Lewis's woodpecker; western bluebird (*Sialia mexicana*); mountain bluebird (*S. currucoides*), and; northern flicker), and two

(continued)

Box 8.1 (continued)



Box 8.1A Postfire ecological changes through time for foraging assemblages of woodpeckers (graphic modified from Saab and Powell (2005)). Woodpecker photos and credits from left to right: black-backed woodpecker (*Picoides arcticus*) (Tom Kogut); American three-toed woodpecker (*P. dorsalis*) (Tom Kogut); Lewis's woodpecker (*Melanerpes lewis*) (Tom Kogut); northern flicker (*Colaptes auratus*) (Tom Kogut); white-headed woodpecker (*Dryobates albolarvatus*) (Tom Kogut), and; pileated woodpecker (*D. pileatus*) (Tom Kogut)

species of wood-drilling, beetle consumers (hairy woodpecker (*Dryobates villosus*) and black-backed woodpecker), after two wildfires in western Idaho from 1994–2004 (Saab et al. 2004, 2007, 2009, 2011). Nest densities of aerial and ground insectivores generally increased with time since fire (Saab et al. 2007). Vegetation regrowth after fire often results in increases in arthropod populations (McCullough et al. 1998) that likely provide food and subsequent increased nesting densities of open-space foragers (American kestrel, Lewis's woodpecker, and western bluebird). Clearly, increases in nest densities will decline at some point when nesting habitat is saturated and snag falling rates increase (Russell et al. 2006).

In contrast to aerial and ground insectivores, nest densities of wood-probing species that specialize on beetles (black-backed and hairy woodpeckers), peaked 4–5 years postfire. Their primary food resources (bark and wood-boring beetles) were likely diminished during the later postfire period (5 years postfire), perhaps causing nest numbers to decline (Saab et al. 2007).

(continued)

Box 8.1 (continued)

For most species, postfire period and land management activities (partially logged vs. unlogged) had little influence on nest survival. A consistent pattern among studies suggests that recently burned forests may function as source habitats for several woodpeckers (Saab and Vierling 2001; Hollenbeck et al. 2011; Newlon and Saab 2011; Saab et al. 2011; Latif et al. 2016, 2020). Nest survival was highest 1–4 years after wildfire compared to unburned forests and 5–12 years after wildfire. Declining nest survival in the later postfire period and in unburned forests may be a result of increasing predation pressure or declining food abundance (Saab and Vierling 2001; Saab et al. 2004), as small mammalian predators, such as red squirrels (*Tamiasciurus hudsonicus*), recolonize wildfire areas (Fisher and Wilkinson 2005).

Abiotic factors of precipitation and temperature had significant associations with nest survival, a key finding that has important implications for nest survival under climate change (Saab et al. 2011). Daily nest survival rates decreased with increasing precipitation and temperatures in burned forests for some cavity-nesting species. Increasing precipitation decreases activity by flying arthropods, reducing prey availability for aerial insectivores. After wildfire, forests lack canopy closure and snags lack insulation created by limbs and foliage. Such conditions likely cause extremely warm temperatures that may exceed heat tolerance levels of eggs or nestlings (e.g., Conway and Martin 2000).

The focal woodpecker species (black-backed, Lewis's, and white-headed woodpeckers) studied after wildfire represent a range of habitat conditions used by other cavity-nesting birds from the smallest diameter and highest densities of snags, to the largest diameter and lowest densities of snags, and intermediate values (Saab et al. 2009; Hollenbeck et al. 2011; Latif et al. 2013, 2016; Latif et al. 2018). The black-backed woodpecker is a beetle-foraging species that favors stand-replacement fires created by high burn severity, where high densities of moderate diameter snags provide an abundance of foraging and nesting opportunities. Lewis's woodpecker is an aerial insectivore that forages on flying insects, favoring larger diameter snags for nesting and forests burned by high-severity fire, where open areas facilitate ease of foraging maneuvers. In contrast, the white-headed woodpecker is a bark-gleaning and pine seed-foraging species that favors understory burns of low-moderate burn severity, where a mosaic of burned and unburned forest provides nesting and foraging resources. All three species tend to select areas of higher burn severity, measured as ΔNBR, than the average measured at non-nest random locations, evidence that higher severity burns are needed for breeding woodpeckers (Latif et al. 2018; Campos et al. 2020). A GIS tool was developed from this research to derive maps of woodpecker habitat suitability for species of conservation concern to help inform postfire management and forest restoration activities (Saab et al. 2009; Latif et al. 2013, 2016, 2018, 2020; Campos et al. 2020).

8.5.1 Resistance to Fire

For Rocky Mountain tree species, traits such as thick bark and protected buds greatly increase the probability of surviving fire (Brown and Smith 2000; Hood et al. 2018b). Bark is a poor conductor of heat and provides protection to the underlying cambium (Dickinson and Johnson 2001). Species with thick bark include western larch, ponderosa pine, and Douglas-fir, with species such as ponderosa pine that develop thick bark early in development being particularly resistant to surface fire. Species with thicker, longer needles that surround terminal buds, such as ponderosa pine, slow heating to the bud meristems and increase resistance to fire (Michaletz and Johnson 2006). Meristem buds size also affects resistance to heating, with large buds being more thermally resistant to heating than smaller buds (Hood et al. 2018b). Western larch is considered the most fire-tolerant tree species in the RCKS due to its thick bark, spur branches that protect buds, high crown, and deciduous habit. Ponderosa pine and western larch are the only species in the RCKS where it is common to see needles scorched and killed during a fire, but buds surviving. Bud survival allows the crowns to recover over time, conferring additional resistance to fire.

Root and branch habit also influence tree resistance. Species with deeper roots are more resistant, as soil is a poor heat conductor (Dickinson and Johnson 2001). Heat duration is typically low in surface and crown fires, and lethal temperatures are not reached deep in the soil. Smoldering ground fires are an exception, where the slow combustion of organic duff can cause long-duration heating and root and basal cambium death (Hood 2010). A species' branching habit affects heat transfer and how easily flames can travel through the crown (Minore 1979). For example, firs and spruces have short needles with tight branching that typically extends to the forest floor, forming continuous live fuel from the ground through the crown. These lower branches are more susceptible to flames that can consume or scorch needles compared to species that self-prune and have higher crown base heights.

It is important to consider individual trees in their forest context to understand species' responses to a given fire regime (Schoennagel et al. 2004). In fire-maintained ponderosa pine and Douglas-fir forests, low-density forest structure with little midstory development fosters surface fires with lower flame lengths such that overstory tree crowns have less scorching (Arno 1980). Low-elevation and low-density forests with relatively continuous cover of understory forbs and grasses have enough fuels to support frequent, low-intensity fires. These conditions can allow larger trees of thicker-barked species to survive fire, while killing thinner-barked tree species and many smaller seedlings and saplings (Kolb et al. 2007; Fulé et al. 2012). In mesic montane and subalpine forests tree species are generally easily killed by fire due to thin bark and low branches (Schoennagel et al. 2004). In these forests, the heterogeneous fuel conditions foster more patchy burns ranging from low to high intensity (Keane et al. 2020). While high-intensity fires may kill most trees in a given patch, trees survive in unburned and low-intensity patches. Fires in subalpine forests such as lodgepole pine and spruce-fir are often wind-driven, high-intensity fires because there is little understory development to support spread of low-intensity fires (Schoennagel et al. 2012). Species such as limber pine are easily killed by fire, but often survive by growing on localized “safe” sites such as rocky outcrops or where sparse surface fuels facilitate low-intensity burns (Brown and Schoettle 2008). Although these are broad characterizations of how forest structure and composition influence fire intensity, they provide a general description of how trees can survive fire. Table 8.1 provides a ranking of fire resistance for the more common tree species in the RCKS based on both species’ traits and forest characteristics. Baker (2009, Appendix A) described tree resistance to fire for additional species in the RCKS.

8.5.2 Postfire Recovery

The plant assemblages regenerating after fire are influenced by many factors (Brown and Smith 2000). A principal factor is the adaptive postfire regeneration mechanism(s) of plant species growing in and around the burned area (Rowe 1983). For many Rocky Mountain plant species, their postfire presence is primarily due to their ability to regenerate vegetatively, or sprout, from surviving buds (Lyon and Stickney 1976; Turner et al. 1997; Fornwalt 2009). Sprouting species are typically topkilled by fire but subsequently regrow from buds on roots, rhizomes, or other organs located at or below the soil surface. RCKS plant species also establish after fire from seeds originating from canopy (tree species) or soil (tree and understory species) seedbanks present prior to burning, or that disperse postfire from living plants occurring on- or off-site (Lyon and Stickney 1976; Turner et al. 1997; Fornwalt 2009). Below we discuss these three mechanisms of postfire plant recovery by highlighting some common examples from across the RCKS. We also discuss other factors, such as fire severity and climate, that serve as important controls on postfire plant recovery.

Most tree species in the RCKS do not sprout following fire (Table 8.2). Deciduous species, such as aspen and Gambel oak (Fig. 8.1), are exceptions. Much like other regions where these resprouting species are present, they can reestablish in great abundance and density, especially after high-severity fires. Sprouting species can advantageously dominate sites immediately postfire and often exert a competitive advantage over those establishing from seeds in the first few postfire years. These species can maintain dominance on burned landscapes for decades to centuries (Guiterman et al. 2018) and are often promoted by compound disturbances (e.g., wildfire following insect outbreaks or blowdown; Kulakowski et al. 2013).

For species that regenerate through establishment of new individuals, available seed sources are critical. For example, to compensate for its low resistance to fire, lodgepole pine releases seeds from persistent, serotinous cones that open during fire (Lotan and Critchfield 1990). The degree of serotiny is highly variable in space and

Table 8.1 Fire resistance traits and habits by relative fire resistance ranking (high to low) of common Rocky Mountain tree species based on Hood et al. (2018a) and the Fire Effects Information System (FEIS)

Species	Bark thickness of overstory trees	Bark thickness of saplings	Root habit	Crown and branch habit	Understory and midstory stand structure[a]	Fire resistance
Western larch	Very thick	Thick	Deep	High; very open	Open	Very high
Ponderosa pine	Very thick	Thick	Deep	Moderately high; open	Open	Very high
Douglas-fir	Very thick	Thick	Varies, usually deep	Moderately low; dense	Moderate to dense	High
White fir	Very thick	Thin	Varies	Moderately low; dense	Dense	High
Grand fir	Medium	Thin	Varies	Low; dense	Dense	Medium
Western white pine	Thin	Very thin	Medium	High; dense	Dense	Medium
Western redcedar	Thin	Very thin	Shallow	Moderately low; dense	Dense	Medium
Rocky Mountain juniper	Medium	Thin	Deep	Low; moderately dense to open	Open	Low
Whitebark pine	Thin	Very thin	Deep	High; open	Open	Low
Lodgepole pine	Very thin	Very thin	Deep	Moderately high; open	Open to moderate	Low
Limber pine	Thin	Thin	Deep	Low; open	Open	Low
Rocky Mountain bristlecone pine	Thin	Thin	Unclear	Low; open	Open	Low
Great Basin bristlecone pine	Thin	Thin	Shallow	Low, open	Open	Low
Western hemlock	Medium	Thin	Shallow	Low; dense	Dense	Low
Engelmann spruce	Thin	Very thin	Shallow	Low; dense	Dense	Very low
Blue spruce	Thin	Thin	Shallow	Low; dense	Dense	Very low
Subalpine fir	Very thin	Very thin	Shallow	Low; dense	Moderate to dense	Very low
Gambel oak[b]	Thin	Very thin	Shallow	Low; open	Dense (?)	Very low
Aspen[b]	Very thin	Very thin	Shallow to medium	High; open	Open to moderate	Very low

(continued)

Table 8.1 (continued)

Resistance can vary with tree size and age; this table describes species traits of established saplings and mature trees

[a] Descriptions are general, fire-maintained characteristics, but conditions are highly variable and tree resistance may differ depending on stand conditions

[b] Gambel oak and aspen are easily topkilled by fire and thus have low resistance, but readily resprout from belowground meristems

Table 8.2 Regeneration characteristics of common Rocky Mountain tree species ranked from high to low fire resistance as described in Table 8.1. Based on Minore (1979), McCaughey et al. (1986), Burns and Honkala (1990), and Fire Effects Information System (FEIS) species reviews

Species	Age to maturity (~years)	Seed production	Seed dispersal	Seed longevity	Seed germination conditions	Seedling survival conditions
Western larch	25; heavier crops after 40–50	Annually; large crops every 5 years	Wind-dispersed; 50% seeds disperse >45 m; 20% seeds disperse >110 m	1 year in soil	Best on mineral soil	Best in high light
Ponderosa pine	10–20	Large crops every 2–8 years	Wind-dispersed; 50% seeds disperse >25 m; 20% seeds disperse >60 m	1 year in soil	Best on mineral soil or ash	Best in high light
Douglas-fir	12–15	Most years; large crops every 2–11 years	Wind-dispersed; most disperse within 100 m of parent trees	1–2 years in soil	Best on mineral soil or organic seedbeds with high light	Best in partial shade
White fir	40	Medium to large crops every 2–4 years	Wind-dispersed; 50% seeds disperse >40 m; 20% seeds disperse >90 m	1 year in soil	Best on mineral soil	Best in high light, but tolerates shade
Grand fir	20–50	Heavy cone-producing years followed by several light years	Wind-dispersed; generally fall within 100 m of parents	1 year in soil	Best on ash or mineral soil	Drought is a major cause of seedling mortality

(continued)

Table 8.2 (continued)

Species	Age to maturity (~years)	Seed production	Seed dispersal	Seed longevity	Seed germination conditions	Seedling survival conditions
Western white pine	7–20	Large crops every 3–4 years	Wind-dispersed; mostly fall within 120 m of parent trees, but have been recorded at over 800 m	Decreases dramatically after 2 years in soil	Best on mineral soil, but will also germinate in duff	On dry sites seedling survival is favored by partial shade, while on moist sites full sunlight favors survival
Western red cedar	20–30	Most years; large crops every 3–4 years	Wind-dispersed; mostly fall within 120 m of parent trees	Declines rapidly in soil	Best on mineral soil	Best in partial shade
Rocky Mountain juniper	10–20; heavier crops after 50	Most years; large crops every 2–5 years	Dispersed by wildlife, primarily birds	Several years in soil	Best on moist soil under partial shade	Best in rocky crevices or other pockets with elevated moisture; partial shade can enhance survivorship
Whitebark pine	20–30	Large crops every 3–4 years	Dispersed by wildlife, primarily Clark's nutcracker; wildlife can transport seeds up to 30 km	Several years in soil	Best in severe burns and mineral soil; seed germination can be delayed for multiple years; best germination may occur 2 years after large seed crop	Best on moderately to severely burned moist sites; gophers and other wildlife can cause mortality
Lodgepole pine	5–15	Large crops every 1–3 years	Wind-dispersed; 50% seeds disperse >20 m; 20% seeds disperse >45 m	Years to decades in canopy; declines rapidly in soil	Best on mineral soil and in full sunlight	High temperatures and drought may kill seedlings

(continued)

Table 8.2 (continued)

Species	Age to maturity (~years)	Seed production	Seed dispersal	Seed longevity	Seed germination conditions	Seedling survival conditions
Limber pine	20–40	Large crops every 2–4 years	Dispersed by wildlife, primarily Clark's nutcracker	Unclear	Unclear; germination sites may be a product of wildlife preferences	Seedlings very drought tolerant
Rocky Mountain bristlecone pine	10–40	Annually, large crops every couple of years	Unclear; wind dispersal likely <200 m	Unclear, likely 1–2 years in soil	Best on mineral soil	Best in high light
Great Basin bristlecone pine	Unclear	Most years	Wind-dispersed; wildlife may also play a major role	Unclear	Unclear	Best in high light; survival generally low
Western hemlock	25–30	Annually; large crops every 3–4 years	Wind-dispersed;50% seeds disperse >90 m; 20% seeds disperse >120 m	1 year in soil	Germinates well on most natural seedbeds	Seedlings very shade tolerant but sensitive to heat, cold, drought, wind
Engelmann spruce	15–40	Large crops every 2–5 years	Wind-dispersed; 50% seeds disperse >25 m; 20% seeds disperse >60 m	Unclear	Best on moist mineral soil with partial shade	Best under conditions of shade, cool temperatures, and adequate soil moisture
Blue spruce	20; heavier crops after 50	Large crops every 2–3 years	Wind-dispersed; mostly fall with 100 m of parent trees	Unclear	Seeds largely germinate on mineral soil, but can also germinate on other substrates	Probably enhanced by moisture and shade

(continued)

Table 8.2 (continued)

Species	Age to maturity (~years)	Seed production	Seed dispersal	Seed longevity	Seed germination conditions	Seedling survival conditions
Subalpine fir	20; later under closed forest conditions	Large crops every 3–5 years; light crops in intervening years	Wind-dispersed; mostly fall within 80 m of parents	1 year in soil	Best on mineral soil seedbeds but can also germinate on other substrates including litter, duff, and decaying wood	At higher elevations, greater on duff seedbeds; at lower elevations, greater on mineral soil seedbeds
Gambel oak	3–5	Annually	Dispersed by wildlife	Unclear	Unclear	Unclear
Aspen	2–3; heavier crops after 10–20	Large seed crops every 3–5 years	Wind-dispersed; can disperse 500 m, and several km in heavy winds	Up to a few weeks in soil	Best on moist mineral soil	Best in high light

time (Tinker et al. 1994; Schoennagel et al. 2003). In the GYE, for example, the proportion of lodgepole pine trees possessing serotinous cones ranged from 0% to >50% (Tinker et al. 1994). Serotiny prevalence generally decreases with elevation and is thought to be a response to more predictable FRIs at lower elevations (Tinker et al. 1994). The proportion of prefire trees bearing serotinous cones is a strong predictor of postfire lodgepole pine seedling density (Schoennagel et al. 2003; Harvey et al. 2014a;); where serotiny is high, lodgepole pine establishment is high, regardless of distance to living trees (Harvey et al. 2016c). Due to the narrow time window in which serotinous cones drop seed, most lodgepole pine seedlings establish shortly following wildfires (Turner et al. 2016; Stevens-Rumann et al. 2018; Rodman et al. 2020b).

For other tree species that regenerate postfire from seed, seeds must generally be dispersed from living individuals, as the soil seedbank tends not to be a major seed source (Table 8.2). Thus, for these species, seed dispersal distances interact with tree mortality patterns to exert a critical control on postfire recovery (Coop et al. 2010; Kemp et al. 2016). Dispersal distances vary among species and are often dependent on dispersal mechanism (Table 8.2). For example, whitebark pine and limber pine have symbiotic relationships with seed caching wildlife species, which promote effective long-distance dispersal into severely burned areas (Coop and Schoettle 2009; Leirfallom et al. 2015). Dispersal distances of wind-dispersed seeds are dependent on tree height, seed size, seed weight, and seed appendages (e.g., wings). For wind-dispersed species with relatively large, heavy seeds, such as ponderosa pine and Rocky Mountain bristlecone pine, established seedlings become uncommon at distances of approximately 50–200 m from living seed trees (Coop and Schoettle 2009; Chambers et al. 2016; Kemp et al. 2016). Similar patterns have been documented for lodgepole pine in areas where serotiny levels are low (Harvey et al. 2016c). For species with smaller and lighter seeds, such as western larch, Douglas-fir, and many true fir and spruce species, establishment distances may be extended, although the highest densities of regenerating trees are generally still closest to living seed trees (Chambers et al. 2016; Harvey et al. 2016c; Kemp et al. 2016). Aspen tends to disperse seeds even farther than these conifer species due to its light seeds and seed appendages, with postfire aspen seedlings found up to 15 km from the nearest seed source (Turner et al. 2003; Gill et al. 2017). Because of this, and its ability to resprout, the relative abundance of aspen can sometimes increase compared to conifer species following fire (McKenzie and Tinker 2012). As living trees provide seed sources for many years or decades postfire, tree establishment is often continual, especially for shade-tolerant species (Stevens-Rumann et al. 2018).

Fire "avoiders", such as Engelmann spruce and subalpine fir, have little or no adaptations to either resist fire or reestablish in postfire environments immediately following fire (Agee 1993). As such, spruce-fir stand development can follow a number of pathways following fire, often with distance to seed source, moisture conditions, and the prevalence of other tree species as key factors. Xeric sites tend to be colonized first by lodgepole pine, five-needle pine, and/or aspen species, as their relatively high shade tolerance allows them to better establish and grow on these sites than spruce and fir. Mesic sites can be colonized by spruce and fir, accelerating successional development toward spruce-fir dominance (Whipple and Dix 1979).

In contrast to tree species, sprouting is arguably the most common mechanism through which understory plant species in RCKS forests establish following fire (Lyon and Stickney 1976; Anderson and Romme 1991; Fornwalt 2009). For example, the majority of understory species in burned lodgepole pine forests of the Northern RCKS established by sprouting, ensuring that prefire species were well represented in the postfire community (Lyon and Stickney 1976; Anderson and Romme 1991). Shrub species in particular tend to sprout following fire, although it can take several years to attain their prefire size if they are slow growing. Widely distributed shrub species that readily sprout following fire include alderleaf mountain mahogany (*Cercocarpus montanus*), Scouler's willow (*Salix scouleriana*), and russett buffaloberry (*Shepherdia canadensis*), primarily sprouting from the root crown, and common snowberry (*Symphoricarpos albus*), primarily sprouting from rhizomes (Fornwalt and Kaufmann 2014; Ferguson and Byrne 2016) (Fig. 8.2). Many graminoid and forb species also sprout after fire. Ross' sedge (*Carex rossii*) and Geyer's sedge (*Carex geyeri*) are examples of broadly-distributed graminoids that can reestablish from sprouts after burning (Turner et al. 1997; Fornwalt and Kaufmann 2014). Common yarrow (*Achillea millefolium*), heartleaf arnica (*Arnica

Fig. 8.2 Examples of different mechanisms that allow plants to recover following fire. Many conifer species such as (**a**) western larch and (**b**) Douglas-fir (small seedling beneath Gambel oak) regenerate from seeds dispersed into the burned area, which can make them less competitive than resprouting species in the first few years following fire. Many species are top-killed and resprout following fire, including (**b**) Gambel oak, (**c**) aspen, (**d**) russet buffaloberry, and (**e**) alderleaf mountain mahogany. Lodgepole pine (**f**) has serotinous cones that open with the heat of fire, often creating dense patches of regenerating trees. (Photo b - J. Wooten; all others by chapter authors)

cordifolia), and silvery lupine (*Lupinus argenteus*) are common forbs that can regenerate following fire by sprouting (Lyon and Stickney 1976; Turner et al. 1997).

Establishment from seeds stored in the soil seedbank is less common than sprouting, but nonetheless it is an important postfire regeneration mechanism for understory plants (Lyon and Stickney 1976; Anderson and Romme 1991; Fornwalt 2009). Only about a third of the Northern Rocky Mountain shrub species examined by Ferguson and Byrne (2016) readily regenerate from soil-stored seeds postfire. One example is snowbrush ceanothus (*Ceanothus velutinus*), which has long-lived seeds that germinate after heat scarifies the seed coat; this species can dominate some early postfire understory communities even if it was rare immediately prior to fire (Lyon and Stickney 1976). Seeds of the forbs scrambled eggs (*Corydalis aurea*), American dragonhead (*Dracocephalum parviflorum*), and streambank wild hollyhock (*Iliamna rivularis*) also germinate readily after fire from the soil seedbank (Brown and DeByle 1989; Anderson and Romme 1991; Fornwalt and Kaufmann 2014).

Establishment from dispersed seeds is also an important postfire regeneration mechanism for Rocky Mountain understory plants, although it too is less prevalent than sprouting, at least in early postfire years (Stickney 1986; Anderson and Romme

1991; Fornwalt 2009). However, it becomes increasingly important as time since fire passes (Abella and Fornwalt 2015; Romme et al. 2016). The aptly-named fireweed (*Chamerion angustifolium*) is an example of a species that can establish in burned areas from seeds that are dispersed long distances by wind. Indeed, dramatic postfire expansions of this forb have been reported across the RCKS (e.g., Lyon and Stickney 1976; Turner et al. 1997; Rhoades et al. 2018). Prickly lettuce (*Lactuca serriola*), a common non-native forb, can likewise become more abundant after fire from wind-dispersed seeds (Turner et al. 1997; Ferguson and Craig 2010; Fornwalt et al. 2010). Other species that frequently establish in burned areas from wind-dispersed seeds include the forbs Canadian horseweed (*Conyza canadensis*), white hawkweed (*Hieracium albiflorum*), and common dandelion (*Taraxacum officinale*), another non-native (Stickney 1986; Fornwalt and Kaufmann 2014).

Many understory plant species have more than one mechanism for colonizing after fire, which helps ensure their presence in burned areas (Stickney 1986; Anderson and Romme 1991; Fornwalt 2009). For example, Scouler's willow and fireweed establish readily from both sprouts and wind-dispersed seeds (Lyon and Stickney 1976; Anderson and Romme 1991; Turner et al. 1997; Ferguson and Byrne 2016), while snowbrush ceanothus establishes from both sprouts and soil-stored seeds (Lyon and Stickney 1976; Ferguson and Byrne 2016), which may partially explain the frequent dominance of these species in postfire landscapes.

Several other factors determine if and when plant species successfully colonize a recently burned landscape, particularly for species relying on seed for reestablishment. First, seed abundance is important. For several Rocky Mountain tree species, seed production is episodic, with large seed crops produced in mast years (Table 8.2). Ponderosa pine, for example, masts every 2–8 years (Rodman et al. 2020a), while Engelmann spruce masts every 2–5 years (Buechling et al. 2016). Second, variation in postfire climate may alter the windows of seed germination and establishment, even if seed is available. For example, trees in recently burned dry mixed-conifer forests across the RCKS established episodically, and these patterns were highly correlated with cooler, wetter climatic periods (Davis et al. 2019; Rodman et al. 2020b). On the other climatic and temporal extreme, paleo records illustrate that postfire shifts from conifer-dominated to alpine-dominated systems in the subalpine zone were limited by cold (Calder et al. 2019). In this case, tree establishment required warmer temperatures following wildfire to allow for more snow-free periods; when this did not occur, alpine meadows persisted for centuries in once-forested areas (Calder et al. 2019). Additionally, postfire microclimatic conditions may further limit seed germination and establishment windows, especially in areas where they were dramatically altered due to high-severity fire. Such a scenario unfolded in burned ponderosa pine forests in the Southern RCKS, where colonization rates of understory plant species adapted to cool, mesic climates were lower in high-severity sites than in low-severity sites (Stevens et al. 2019).

8.6 How Will Fire Regimes Change in the Future?

Recent wildfire seasons in the RCKS highlight the potential for dramatic future changes to fires regimes. For example, multiple 2020 wildfires in northern Colorado subalpine forests burned for several months and late into the fall. During this time period, numerous red flag days of high winds and low humidities provided opportunities for these fires to have exponential growth with runs of many kilometers in one day (https://inciweb.nwcg.gov/). Future fire trends are uncertain and will depend on multiple drivers, including how climate trends manifest and changes in fuel availability, and ignition sources. The latest climate models consistently predict that warming will continue to drive rapid, large increases in atmospheric vapor pressure deficit, reduced snow packs, and declining soil moisture (Cook et al. 2020). Future climate trends could cause wildfire frequency, size and severity to continue to grow as well (Littell et al. 2018); some models predict as much as a five-fold increase in annual area burned by 2039 compared to a 1961–2004 baseline (Kitzberger et al. 2017).

Whether and where fire regimes will respond to climate change is poorly resolved. Original models of twenty-first century fire activity in the RCKS were driven purely by climate, assuming static vegetation and fuel loads (Westerling et al. 2011). Not surprisingly, such models predict massive increases in burning. For example, in the GYE of the Northern RCKS, increasing aridity caused predicted FRIs to decline from the historical average of 120 years to <30 years by midcentury (Westerling et al. 2011). In the real world, however, fire is unlikely to increase indefinitely; changes to vegetation and reduced fuels will eventually limit subsequent fire (Liang et al. 2017; Hurteau et al. 2019). Even today, some low-elevation dry montane forests (e.g., in the southern RCKS) may lack sufficient fuels to support large increases in fire with warming and drying (Littell et al. 2018). Conversely, where fires were historically limited by cool, wet conditions, fuels are abundant (Nelson et al. 2016) and may not limit future fires. In Grand Teton National Park where vegetation- and fuel-fire feedbacks were represented explicitly, models predict a 1700% increase in burned area by 2100, and fuels were never limiting (Hansen et al. 2020).

Future changes in lightning- and human-caused ignitions are another uncertainty. Lightning strikes in the USA may increase by as much as 50% during the twenty-first century (Romps et al. 2014), which could accelerate increased burning. If population growth continues, human-caused ignitions could also increase (Schoennagel et al. 2017).

8.6.1 Changing Fire Regime Implications for Resistance and Recovery

Changing fire regimes may alter plant resistance to and recovery from fire through several mechanisms. Fire-adapted traits (Sect. 8.5; Tables 8.1 and 8.2) could be less effective at promoting resistance or recovery under novel fire regimes (Johnstone et al. 2016; Stevens et al. 2020). For example, changes in fire frequency may interact with age to maturity to determine what tree species will be able to produce seed following fire, while changes in fire size may alter seed dispersal dynamics (Davis et al. 2018). Here we discuss the main mechanisms through which changes in fire regimes and climate will affect plant resistance and recovery.

The likelihood of areas reburning at short intervals increases with annual area burned and higher fire frequencies associated with climate change; resistance and recovery will depend on life history traits of the dominant species and fire severity (Prichard et al. 2017). Many species in forests with historically frequent, low- or mixed-severity fire regimes have fire-resistant traits (Stevens et al. 2020). More frequent surface fire in mixed-conifer forests may promote fire-resistant species over others. In the Central RCKS, simulated increases in fire frequency accelerated declines in predicted area occupied by the less fire-resistant species lodgepole pine, subalpine fir, and Douglas-fir due to climate change, but maintained the area occupied by the more resistant species ponderosa pine (Campbell and Shinneman 2017). More frequent low-severity fire may favor the establishment of faster-growing ponderosa pine over Douglas-fir, as it develops thicker bark at a younger age (Rodman et al. 2020b).

In some cases, short-interval fire can alter species composition and structure to improve resilience to future fires, especially in montane forests with historically frequent low- or mixed-severity fire regimes. For example, a short-interval reburn (8 year) in Montana killed dense postfire lodgepole pine regeneration, leaving a more open stand structure dominated by large-diameter ponderosa pine (Larson et al. 2013). Elsewhere in the Northern RCKS, areas reburned after 1–18 years had lower postfire tree regeneration densities and woody surface fuel loads than areas burned only once, reducing the likelihood of future high-severity fire (Stevens-Rumann et al. 2016). However, areas that burned twice at high severity had low seedling densities and may transition to non-forest vegetation types, highlighting how outcomes vary with severity of reburns (Stevens-Rumann et al. 2016). Similarly, in the Southern RCKS, short-interval fires, especially at high severity, reinforced transitions from conifer forest to shrublands dominated by resprouting species (Coop et al. 2016; Keyser et al. 2020).

The effects of short fire intervals will differ in subalpine RCKS forests, where historically fire regimes are infrequent and stand-replacing; shorter FRIs will likely more consistently impede forest recovery relative to montane forests. For example, time required to tree maturation and seed production may be insufficient (i.e., “immaturity risk”; Keeley et al. 1999), thereby inhibiting regeneration (Buma et al. 2013). Lodgepole pine may have an advantage over other common subalpine species (e.g., Engelmann spruce, subalpine fir, whitebark pine) because it matures younger (as young as five years), although the production of a large canopy seedbank can take many years and regeneration could be reduced if fires occur at short intervals. For example, sparse lodgepole pine regeneration following short-interval high-severity fire has already been observed in Yellowstone National Park (Sect. 8.4.2), and this phenomenon is likely to become more common under future fire and climate conditions (Hansen et al. 2018; Turner et al. 2019).

Large fires, with more area burned at high severity, and confounded with shorter fire intervals will affect ecosystem recovery mainly by increasing distance to seed source (Harvey et al. 2016b) and reducing fire refugia containing seed sources (Krawchuk et al. 2020). As larger fires reduce live seed sources on the landscape, obligate seeders that disperse into burned areas following fire (e.g., ponderosa pine, Douglas-fir, Engelmann spruce, subalpine fir; Sect. 8.5.2) may decline in abundance, while species that regenerate well following high-severity fire (e.g., lodgepole pine, aspen, Gambel oak, whitebark pine) may increase (Davis et al. 2018; Coop et al. 2020). Some wind dispersers such as aspen may establish postfire at higher elevations as climate conditions change (Hansen et al. 2016). Additionally, understory plant species may increase in abundance and/or diversity in the interior of large high-severity patches as light or other resources increase (Coop et al. 2010; Fornwalt and Kaufmann 2014). If burns under moderate fire weather reduce severity of subsequent fires (Parks et al. 2014), early seral and fire-resistant species like ponderosa pine, Douglas-fir, or western larch may increase at the expense of more fire-vulnerable species such as true firs and Engelmann spruce, especially in lower or mid-elevation mixed-conifer forests.

Warmer, drier postfire future climate conditions may increasingly limit postfire recovery of some species, particularly in lower-elevation forests. Postfire recruitment of ponderosa pine and Douglas-fir tends to be constrained to cool, wet years (Davis et al. 2019; Rodman et al. 2020b), likely contributing to the recent lack of postfire regeneration observed in some drier sites across their range (Stevens-Rumann et al. 2018; Rodman et al. 2020a). Projections based on future climate conditions suggest a substantial decline in postfire ponderosa pine and Douglas-fir regeneration by midcentury (Kemp et al. 2019; Davis et al. 2020; Rodman et al. 2020a), and experiments simulating warmer climate conditions also suggest reduced survival and growth of planted seedlings with higher temperatures (Rother et al. 2015). Rising temperatures and moisture deficits across the RCKS may also cause further reductions in postfire subalpine conifer recruitment beyond what has already been documented (Sect. 8.3.1). Experiments using elevation as a proxy for future climate in Yellowstone National Park indicate postfire lodgepole pine seedling establishment could decrease by up to 92% by 2050 (Hansen and Turner 2019). Other studies found that increased temperatures led to lower recruitment of lodgepole pine and Engelmann spruce establishment across an elevation gradient (Kueppers et al. 2017; Conlisk et al. 2018). A recent modeling study in central Idaho suggested that there may be a decline in area occupied by lodgepole pine, Douglas-fir, and subalpine fir due to the combined effects of climate change and increased fire frequency (Campbell and Shinneman 2017). Fire in subalpine areas may provide an opportunity for recruitment of montane or lower elevation species at higher elevations, within constraints of dispersal distances (Campbell and Shinneman 2017). Aspen may increase in areas previously dominated by conifers because it is less sensitive to many climatically-sensitive disturbances (e.g., fire, insect outbreaks; Gill et al. 2017). Warmer, drier conditions will also affect how adult conifers respond to fire. For example, drought-stressed conifers are less likely to survive fires (van Mantgem et al. 2013). Furthermore, fire-injured trees may be more sensitive to postfire drought, as well as to other stressors such as bark beetles and pathogens (Hood et al. 2018b). Changes in postfire climate also have the potential to alter understory species composition. In Colorado, understory plant species composition shifted to warm, dry adapted species for ≥10 years after moderate- to high-severity fire (Stevens et al. 2019); fire removal of canopy cover creates warmer, drier conditions near the forest floor (Wolf et al. 2021).

8.6.2 Managing for the Future

Natural resource professionals are faced with uncertainty in how to manage forests for a future climate. Historical fire regimes and forest structures that occurred under cooler, wetter climatic conditions might be losing their relevance as we move into a warmer, drier future, raising questions about the utility of managing forests to be within the historical range of variation. Rather, land managers may wish to consider transitioning forests to ones that intentionally accommodate change and enable them to adaptively respond to new conditions (Millar et al. 2007; Nagel et al. 2017). Current fuel reduction and restoration strategies, including reducing surface fuels, decreasing canopy density, and keeping large fire-resistant tree species, are important (Agee and Skinner 2005). Landscape-scale restoration that fosters spatial heterogeneity in forest structure and composition, including managing for open patches is also essential (Hessburg et al. 2015, 2019). However, treatments based on contemporary thresholds of forest structural characteristics (e.g., basal area, tree density) and current climatic conditions (e.g., percentile weather conditions) may be less effective as climate warms, and more aggressive management approaches may be warranted.

Changing fire regimes are and will continue to be a concern for land management professionals (Jolly et al. 2015; Abatzoglou and Williams 2016). In montane forests, warmer temperatures earlier in the spring and later in the fall would allow fuels to be drier longer, increasing the period of high ignition risk (Westerling et al. 2006). Warmer temperatures would also facilitate more severe burning in these forests. In higher-elevation subalpine forests, earlier snowmelt would allow fuels to desiccate more quickly, while later snowfall would delay snowpack development, extending the fire season. Longer fire seasons could lengthen fire events, reducing air quality and necessitating longer term home evacuations and human displacement. Longer fire seasons and greater fire severity could increase fire suppression costs, as well as rehabilitation and restoration costs aimed at minimizing negative postfire impacts to forest ecosystems and the important services they provide.

Land managers are increasingly working toward returning fire to the RCKS landscape. Most focus has been on frequent-fire forest types that have missed several FRIs. Often, mechanical treatment is required prior to safe reintroduction of fire by reducing tree density and fire-intolerant trees. Restoring the complex mosaic of single and clustered trees and openings is desired to mimic historical spatial patterns and reduce fire hazards (Ziegler et al. 2017). Prescribed or managed wildfire is much easier to achieve after initial structural restoration. In some cases, decades of surface fuel accumulation around the bases of older, larger trees must be reduced to avoid high tree mortality (Hood 2010). Restoration of fire regimes in forest types that historically burned at mixed or high fire severity is less straightforward. Since these forest types typically have longer FRIs, the impacts of fire exclusion are less apparent than in frequent fire forests, but many have missed one or more fires based on historical FRIs. Fires ignite each year in these forest types, but climatic conditions generally are unconducive to fire spread and suppression is successful. Suppression prevents large areas from burning, also precludes the creation or maintenance of a structural mosaic of developmental stages, including large treeless meadows. Challenges to fire reintroduction include heavy surface fuels, crown architecture, low resistance of some species to fire, and narrow climatic conditions that allow fires to carry but not escape. Here again, mechanical treatments that break up the landscape into different successional stages may facilitate reintroduction of fire.

Governmental policies, aversion to risk, lack of financial resources, social perception, and the WUI (Theobald and Romme 2007; Radeloff et al. 2018) prevent the widespread use of both managed wildfire and prescribed fire and will likely continue to be barriers to their use in the future (Stephens and Ruth 2005; Stephens et al. 2016; Schultz et al. 2018). Negative social perceptions and threats to property and safety perpetuate a focus on fire suppression, rather than allowing managed wildfire to occur during moderated weather. Prescribed burns are complex operations requiring careful planning and qualified staff. Variable weather conditions in the RCKS make it difficult to find the right combination of fuel moisture, wind speed and direction, temperature, relative humidity, and air movement needed to achieve burn objectives and safety guidelines. Competition for resources (e.g., staff, equipment) among land management agencies is common when these “burn windows” occur. Air quality can be an additional barrier to prescribed burning, especially near urban areas that already exceed air quality standards or areas that experience inversions. In many areas of the RCKS, mixed ownership of federal, state, and private land, and forest types spanning political boundaries not corresponding with topographic features that limit fire spread, present additional challenges to fire management.

There are myriad additional challenges to restoring fire-dependent forests and increasing resiliency. Mechanical tree density reductions in frequent fire forests involve removing small diameter trees that established after fire suppression. Markets for small trees are limited, making these projects expensive. In more productive forest types where trees grow faster, large, but relatively young trees may be perceived as “old-growth” leading to reluctance by the public or biologists to remove them. Sometimes, mechanical treatments of adjacent forest types (e.g., lodgepole pine forests near dry mixed-conifer forests) is needed to enhance the safety of prescribed burns (Stephens et al. 2020). Non-native invasive plants are another challenge to restoring fire-adapted forests (Chaps. 1 and 12). For example, non-native species cover sharply increased immediately after cutting and prescribed burning for fuel reduction in a Northern RCKS ponderosa pine/Douglas-fir forest, then dropped to low, but persistently higher levels than in untreated controls (Jang et al. 2020) . This suggests that some restoration or fuel reduction treatments could exacerbate noxious weeds. Heavy surface fuel loads (e.g., dead standing and downed trees) conducive to intense fire created by recent bark beetle outbreaks present another challenge to fire management for restoration (Sieg et al. 2017). In many cases, young regeneration established after a beetle outbreak are too small to survive a fire with heavy fuel loads (Battaglia et al. 2009). These challenges will require innovations in technology, large-scale collaboration, and embracing the reality of fire as a major disturbance in the RCKS to find solutions that foster forest resilience to disturbances and climate change.

Wildland fire exerts a large influence on many forests in the RCKS, driving species composition and forest structure over vast landscapes. While RCKS ecosystems have evolved with fire, the past 100+ years have caused large deviations in historical fire regimes, especially in lower elevation forests. In addition, anthropogenic climate change is now causing further, more widespread changes by altering disturbance regimes and interactions and recovery processes. There is an opportunity for fuel reduction and restoration treatments to mitigate the likelihood of undesirable ecological and social effects following fire in some areas. However, ongoing climate change will almost certainly increase high-severity fires and lead to larger fires that will further alter disturbance regimes. These stressors will cause changes that will test the resilience of many Rocky Mountain forests in the future.

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci USA 113:11770–11775

Abella SR, Fornwalt PJ (2015) Ten years of vegetation assembly after a North American mega fire. Glob Chang Biol 21:789–802

Agee JK (1993) Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC

Agee JK, Skinner CN (2005) Basic principles of forest fuel reduction treatments. For Ecol Manag 211:83–96

Alexander RR (1987) Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service Agric Handb No 659, Washington, DC

Alexander RR, Sheppard WD (1990) Engelmann spruce. In: Burns RM, Honkala BH (eds) Silvics of North America: Volume 1. Conifers. Agriculture Handbook No 654. USDA Forest Service, Washington, DC

Alexander RR, Shearer RC, Sheppard WD (1990) Subalpine fir. In: Burns RM, Honkala BH (eds) Silvics of North America: Volume 1. Conifers; 2. Hardwoods. Agriculture Handbook No 654. USDA Forest Service, Washington, DC

Anderson MD (2003) *Pinus contorta* var. *latifolia*. In: Fire effects information system, [Online] USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fsfedus/database/feis/ [2015, October 8]

Anderson JE, Romme WH (1991) Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. Int J Wildland Fire 1:119–124

Andrus RA, Veblen TT, Harvey BJ, Hart SJ (2016) Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. Ecol Appl 26:700–711

Andrus RA, Harvey BJ, Rodman KC, Hart SJ, Veblen TT (2018) Moisture availability limits subalpine tree establishment. Ecology 99:567–575

Aplet GH, Laven RD, Smith FW (1988) Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology 69:312–319

Arno SF (1980) Forest fire history in the Northern Rockies. J For 78:460–465

Arno SF, Reinhardt E, Scott JH (1993) Forest structure and landscape patterns in the subalpine lodgepole pine type: A procedure for quantifying past and present conditions. Gen. Tech. Rep. INT-294. USDA Forest Service, Intermountain Research Station, Ogden

Arno SF, Harrington MG, Fiedler CE, Carlson CE (1995a) Restoring fire-dependent ponderosa pine forests in western Montana. Restor Manag Notes 13:32–36

Arno SF, Scott JH, Hartwell MG (1995b) Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. Res. Pap. INT-RP-481. USDA Forest Service, Intermountain Research Station, Ogden

Arno SF, Parsons DJ, Keane RE (2000) Mixed-severity fire regimes in the northern Rocky Mountains: consequences of fire exclusion and options for the future. In: McCool SF, DN Cole, WT Borrie, J O'Loughlin (eds). Wilderness science in a time of change conference, Volume 5: Wilderness ecosystems, threat, and management. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, pp 225–232

Baker WL (2009) Fire ecology in Rocky Mountain landscapes. Island Press, Washington, DC

Baker WL, Veblen TT (1990) Spruce beetles and fires in the nineteenth-century subalpine forests of western Colorado, USA. Arct Alp Res 22:65–80

Balch JK, Bradley BA, Abatzoglou JT, Nagy RC, Fusco EJ, Mahood AL (2017) Human-started wildfires expand the fire niche across the United States. Proc Natl Acad Sci USA 114:2946–2951

Barrett S (1994) Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. Int J Wildland Fire 4:65–76

Barrett SW, Arno SF, Key CH (1991) Fire regimes of western larch – lodgepole pine forests in Glacier National Park, Montana. Can J For Res 21:1711–1720

Battaglia M, Smith FW, Shepperd WD (2009) Predicting mortality of ponderosa pine regeneration after prescribed fire in the Black Hills, South Dakota, USA. Int J Wildland Fire 18:176–190

Battaglia MA, Gannon B, Brown PM, Fornwalt PJ, Cheng AS, Huckaby LS (2018) Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA. For Ecol Manag 422:147–160

Bebi P, Kulakowski D, Veblen TT (2003) Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology 84:362–371

Binkley D, Alsanousi A, Romme WH (2014) Age structure of aspen forests on the Uncompahgre Plateau, Colorado. Can J For Res 44:836–841

Brown PM (2006) Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. Ecology 87:2500–2510

Brown PM, Cook B (2006) Early settlement forest structure in Black Hills ponderosa pine forests. For Ecol Manag 223:284–290

Brown JK, DeByle NV (1989) Effects of prescribed fire on biomass and plant succession in western aspen. Res. Pap. INT- 412. USDA Forest Service, Intermountain Research Station, Ogden

Brown PM, Schoettle AW (2008) Fire and stand history in two limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) stands in Colorado. Int J Wildland Fire 17:339–347

Brown PM, Sieg CH (1999) Historical variability in fire at the ponderosa pine/northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota, vol 6.

Brown JK, Smith JK (eds) (2000) Wildland fire in ecosystems: effects of fire on flora. USDA Forest Service Gen Tech Rep RMRS-GTR-42, vol 2. USDA Forest Service, Ogden

Brown PM, Wu R (2005) Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86:3030–3038

Brown PM, Heyerdahl EK, Kitchen SG, Weber MH (2008) Climate effects on historical fires (1630-1900) in Utah. Int J Wildland Fire 17:28–39

Brown PM, Gannon B, Battaglia MA, Fornwalt PJ, Huckaby LS, Cheng AS, Baggett LS (2019) Identifying old trees to inform ecological restoration in montane forests of the central Rocky Mountains, USA. Tree-Ring Res 75:34–48

Brown SR, Baysinger A, Brown PM, Cheek JL, Diez JM, Gentry CM, Grant TA III, St. Jacques J-M, Jordan DA, Leef ML, Rourke MK, Speer JH, Spradlin CE, Stevens JT, Stone JR, Van Winkle B, Zeibig-Kichas NE (2020) Fire History Across Forest Types in the Southern Beartooth Mountains, Wyoming. Tree-Ring Res 76:27–39

Brunelle A, Rehfeldt GE, Bentz B, Munson AS (2008) Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. For Ecol Manag 255:836–846

Buechling A, Baker WL (2004) A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. Can J For Res 34:1259–1273

Buechling A, Martin PH, Canham CD, Shepperd WD, Battaglia MA (2016) Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. J Ecol 104:1051–1062

Buma B (2015) Disturbance interactions: Characterization, prediction, and the potential for cascading effects. Ecosphere 6:art70

Buma B, Brown CD, Donato DC, Fontaine JB, Johnstone JF (2013) The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience 63:866–876

Burns RM, Honkala BH (1990) Silvics of North America: 1. Conifers; 2. Hardwoods. USDA Forest Service Agriculture Handbook No 654, vol 2, Washington, DC

Calder WJ, Stefanova I, Shuman B (2019) Climate–fire–vegetation interactions and the rise of novel landscape patterns in subalpine ecosystems, Colorado. J Ecol 107:1689–1703

Campbell JL, Shinneman DJ (2017) Potential influence of wildfire in modulating climate-induced forest redistribution in a central Rocky Mountain landscape. Ecol Process 6:7

Campos BR, Latif QS, Burnett RD, Saab VA (2020) Predictive habitat suitability models for nesting woodpeckers following wildfire in the Sierra Nevada and Southern Cascades of California. The Condor 122:duz062

Carlson AR, Sibold JS, Negrón JF (2020) Canopy structure and below-canopy temperatures interact to shape seedling response to disturbance in a Rocky Mountain subalpine forest. For Ecol Manag 472:118234

Carter VA, Brunelle A, Minckley TA, Shaw JD, DeRose RJ, Brewer S (2017) Climate variability and fire effects on quaking aspen in the central Rocky Mountains, USA. J Biogeogr 44:1280–1293

Chambers ME, Fornwalt PJ, Malone SL, Battaglia MA (2016) Patterns of conifer regeneration following high severity wildfire in ponderosa pine–dominated forests of the Colorado Front Range. For Ecol Manag 378:57–67

Clavero M, Brotons L, Herrando S (2011) Bird community specialization, bird conservation and disturbance: the role of wildfires. J Anim Ecol 80:128–136

Conlisk E, Castanha C, Germino MJ, Veblen TT, Smith JM, Moyes AB, Kueppers LM (2018) Seed origin and warming constrain lodgepole pine recruitment, slowing the pace of population range shifts. Glob Chang Biol 24:197–211

Conway CJ, Martin TE (2000) Effects of ambient temperature on avian incubation behavior. Behav Ecol 11:178–188

Cook BI, Mankin JS, Marvel K, Williams AP, Smerdon JE, Anchukaitis KJ (2020) Twenty-first Century Drought Projections in the CMIP6 Forcing Scenarios. Earth's Future 8:e2019EF001461

Coop JD, Schoettle AW (2009) Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. For Ecol Manag 257:893–903

Coop JD, Schoettle AW (2011) Fire and high-elevation, five-needle pine (*Pinus aristata* & *P. flexilis*) ecosystems in the southern Rocky Mountains: What do we know? In: Keane RE, Tomback, DF, Murray MP, Smith CM (eds) The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, Montana. USDA Forest Service RMRS-P-63, Fort Collins, Colorado, pp 164–173

Coop JD, Massatti RT, Schoettle AW (2010) Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. J Veg Sci 21:472–487

Coop JD, Parks SA, McClernan SR, Holsinger LM (2016) Influences of prior wildfires on vegetation response to subsequent fire in a reburned southwestern landscape. Ecol Appl 26:346–354

Coop JD, Parks SA, Stevens-Rumann CS, Crausbay SD, Higuera PE, Hurteau MD, Tepley A, Whitman E, Assal T, Collins BM, Davis KT, Dobrowski S, Falk DA, Fornwalt PJ, Fulé PZ, Harvey BJ, Kane VR, Littlefield CE, Margolis EQ, North M, Parisien M-A, Prichard S, Rodman KC (2020) Wildfire-driven forest conversion in Western North American landscapes. Bioscience 70:659-673

Crotteau J, Keyes C, Hood S, Larson A (2020) Vegetation dynamics following compound disturbance in a dry pine forest: Fuel treatment then bark-beetle outbreak. Ecol Appl 30:e02023

Davis RS, Hood S, Bentz BJ (2012) Fire-injured ponderosa pine provide a pulsed resource for bark beetles. Can J For Res 42:2022–2036

Davis KT, Higuera PE, Sala A (2018) Anticipating fire-mediated impacts of climate change using a demographic framework. Funct Ecol 32:1729–1745

Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT, Parks SA, Sala A, Maneta MP (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci USA 116:6193–6198

Davis KT, Higuera PE, Dobrowski SZ, Parks SA, Abatzoglou JT, Rother MT, Veblen TT (2020) Fire-catalyzed vegetation shifts in ponderosa pine and Douglas-fir forests of the western United States. Environ Res Lett 15:1040b1048

DeRose RJ, Long JN (2009) Wildfire and spruce beetle outbreak: simulation of interacting disturbances in the central Rocky Mountains. Ecoscience 16:28–38

Dickinson Y (2014) Landscape restoration of a forest with a historically mixed-severity fire regime: what was the historical landscape pattern of forest and openings? For Ecol Manag 331:264–271

Dickinson M, Johnson E (2001) Fire effects on trees. In: Johnson E, Miyanishi K (eds) Forest fires: behavior and ecological eeffects. Academic, New York, pp 477–525

Donato DC, Simard M, Romme WH, Harvey BJ, Turner MG (2013) Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. For Ecol Manag 303:160–174

Falk DA, Heyerdahl EK, Brown PM, Farris C, Fulé PZ, McKenzie D, Swetnam TW, Taylor AH, Van Horne ML (2011) Multi-scale controls of historical forest-fire regimes: New insights from fire-scar networks. Front Ecol Environ 9:446–454

Ferguson DE, Byrne JC (2016) Shrub succession on eight mixed-severity wildfires in western Montana, northeastern Oregon, and northern Idaho. Res. Pap. RMRS-RP-106. USDA Forest Service, Fort Collins, 81 p

Ferguson D, Craig C (2010) Response of six non-native plant species to wildfires in the northern Rocky Mountains, USA. Res. Pap. RMRS-RP-78. USDA Forest Service, Fort Collins, 12 p

Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negrón JF, Nowak JT (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For Ecol Manag 238:24–53

Fisher JT, Wilkinson L (2005) The response of mammals to forest fire and timber harvest in the North American boreal forest. Mamm Rev 35:51–81

Flower A, Gavin D, Heyerdahl E, Parsons R, Cohn G (2014) Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: A multi-century dendrochronological record. For Ecol Manag 324:16–27

Fornwalt PJ (2009) Disturbance impacts on understory plant communities of the Colorado Front Range. Dissertation, Colorado State University, Fort Collins

Fornwalt PJ, Kaufmann MR (2014) Understorey plant community dynamics following a large, mixed severity wildfire in a *Pinus ponderosa–Pseudotsuga menziesii* forest, Colorado, USA. J Veg Sci 25:805–818

Fornwalt PJ, Kaufmann MR, Stohlgren TJ (2010) Impacts of mixed severity wildfire on exotic plants in a Colorado ponderosa pine–Douglas-fir forest. Biol Invasions 12:2683–2695

Fornwalt PJ, Huckaby LS, Alton SK, Kaufmann MR, Brown PM, Cheng AS (2016) Did the 2002 Hayman Fire, Colorado, USA, burn with uncharacteristic severity? Fire Ecol 12:117–132

Fulé PZ, Crouse JE, Roccaforte JP, Kalies EL (2012) Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? For Ecol Manag 269:68–81

Gavin DG, Hu FS, Walker IR, Westover K (2009) The northern inland temperate rainforest of British Columbia: Old forests with a young history? Northwest Sci 83:70–78

Gill NS, Sangermano F, Buma B, Kulakowski D (2017) *Populus tremuloides* seedling establishment: An underexplored vector for forest type conversion after multiple disturbances. For Ecol Manag 404:156–164

Graham RT, Asherin LA, Jain TB, Baggett LS, Battaglia MA (2019) Differing ponderosa pine forest structures, their growth and yield, and mountain pine beetle impacts: growing stock levels in the Black Hills. Gen Tech Rep RMRS-393. USDA Forest Service, Fort Collins, 393 p

Guiterman CH, Margolis EQ, Allen CD, Falk DA, Swetnam TW (2018) Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of northern New Mexico. Ecosystems 21:943–959

Hansen WD, Turner MG (2019) Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. Ecol Monogr 89:e01340

Hansen WD, Romme WH, Ba A, Turner MG (2016) Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. For Ecol Manag 362:218–230

Hansen WD, Braziunas KH, Rammer W, Seidl R, Turner MG (2018) It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99:966–977

Hansen WD, Abendroth D, Rammer W, Seidl R, Turner MG (2020) Can wildland fire management alter 21st-century subalpine fire and forests in Grand Teton National Park, Wyoming, USA? Ecol Appl 30:e02030

Hart S, Preston D (2020) Fire weather drives daily area burned and observations of fire behavior in mountain pine beetle affected landscapes. Environ Res Lett 15:054007

Hart SJ, Schoennagel T, Veblen TT, Chapman TB (2015) Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc Natl Acad Sci USA 112:4375–4380

Harvey BJ, Donato DC, Romme WH, Turner MG (2013) Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. Ecology 94:2475–2486

Harvey BJ, Donato DC, Romme WH, Turner MG (2014a) Fire severity and tree regeneration following bark beetle outbreaks: The role of outbreak stage and burning conditions. Ecol Appl 24:1608–1625

Harvey BJ, Donato DC, Turner MG (2014b) Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc Natl Acad Sci USA 111:15120–15125

Harvey BJ, Donato DC, Turner MG (2016a) Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. Ecology 97:2272–2282

Harvey BJ, Donato DC, Turner MG (2016b) Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). Landsc Ecol 31:2367–2383

Harvey BJ, Donato DC, Turner MG (2016c) High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob Ecol Biogeogr 25:655–669

Hessburg PF, Agee JK, Franklin JF (2005) Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. For Ecol Manag 211:117-139

Hessburg PF, Churchill DJ, Larson AJ, Haugo RD, Miller C, Spies TA, North MP, Povak NA, Belote RT, Singleton PH (2015) Restoring fire-prone Inland Pacific landscapes: Seven core principles. Landsc Ecol 30:1805–1835

Hessburg PF, Miller CL, Parks SA, Povak NA, Taylor AH, Higuera PE, Prichard SJ, North MP, Collins BM, Hurteau MD, Larson AJ, Allen CD, Stephens SL, Rivera-Huerta H, Stevens-Rumann CS, Daniels LD, Gedalof Z, Gray RW, Kane VR, Churchill DJ, Hagmann RK, Spies TA, Cansler CA, Belote RT, Veblen TT, Battaglia MA, Hoffman C, Skinner CN, Safford HD, Salter RB (2019) Climate, environment, and disturbance history govern resilience of Western North American Forests. Front Ecol Evol 7:article 239

Heyerdahl EK, Miller RF, Parsons RA (2006) History of fire and Douglas-fir establishment in a savanna and sagebrush–grassland mosaic, southwestern Montana, USA. For Ecol Manag 230:107–118

Heyerdahl EK, Morgan P, Riser JP (2008) Multi-season climate synchronized historical fires in dry forests (1650-1900), northern Rockies, USA. Ecology 89:705–716

Hicke JA, Johnson MC, Hayes JL, Preisler HK (2012) Effects of bark beetle-caused tree mortality on wildfire. For Ecol Manag 271:81–90

Hoffman CM, Hull Sieg C, McMillin JD, Fulé PZ (2012) Fuel loadings 5 years after a bark beetle outbreak in south-western USA ponderosa pine forests. Int J Wildland Fire 21:306–312

Hollenbeck JP, Saab VA, Frenzel RW (2011) Habitat suitability and nest survival of white-headed woodpeckers in unburned forests of Oregon. J Wildl Manag 75:1061–1071

Hood SM (2010) Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. Gen Tech Rep RMRS-238. USDA Forest Service, Fort Collins. 71 p

Hood SM, Bentz B (2007) Predicting post-fire Douglas-fir beetle attacks and tree mortality in the Northern Rocky Mountains. Can J For Res 37:1058–1069

Hood S, Sala A, Heyerdahl EK, Boutin M (2015) Low-severity fire increases tree defense against bark beetle attacks. Ecology 96:1846–1855

Hood S, Baker S, Sala A (2016) Fortifying the forest: Thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. Ecol Appl 26:1984–2000

Hood S, Abrahamson I, Cansler CA (2018a) Fire resistance and regeneration characteristics of Northern Rockies tree species. In: Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Available: https://www.fs.fed.us/database/feis/pdfs/other/FireResistRegen.html.

Hood S, Varner M, van Mantgem P, Cansler CA (2018b) Fire and tree death: Understanding and improving modeling of fire-induced tree mortality. Environ Res Lett 13:113004

Hurteau MD, Liang S, Westerling AL, Wiedinmyer C (2019) Vegetation-fire feedback reduces projected area burned under climate change. Sci Rep 9:2838

Hutto RL (1995) Composition of bird communities following stand-replacement fires in northern Rocky Mountain (USA) conifer forests. Conserv Biol 9:1041–1058

Jain TB, Battaglia MA, Han H-S, Graham RT, Keyes CR, Fried JS, Sandquist J (2012) A comprehensive guide to fuels management practices for dry mixed conifer forests of the Northwestern United States. Gen Tech Rep RMRS-GTR-292. USDA Forest Service, Fort Collins. 331 p

Jang W, Crotteau J, Ortega YK, Hood SM, Keyes CR, Pearson DE, Lutes D, Sala A (2020) Native and non-native understory vegetation responses to restoration treatments in a dry conifer forest over 23 years. For Ecol Manag 481:118684

Jenkins MJ, Runyon JB, Fettig CJ, Page WG, Bentz BJ (2014) Interactions among the mountain pine beetle, fires, and fuels. For Sci 60:489–501

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nat Commun 6:7537

Kane JM, Varner JM, Metz MR, van Mantgem PJ (2017) Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western US Forests. For Ecol Manag 405:188–199

Kaufmann MR, Ryan KC, Fulé PZ, Romme WH (2004) Restoration of ponderosa pine forests in the interior western U.S. after logging, grazing, and fire suppression. In: Stanturf JA, Madsen P (eds) Restoration of Boreal and Temperate Forests. CRC Press, Boca Raton, pp 481–500

Keane B, Bower A, Hood S (2020) A burning paradox: Whitebark is easy to kill but also dependent on fire. Nutcracker Notes 38:7–8, 34

Keeley JE, Ne'eman G, Fotheringham C (1999) Immaturity risk in a fire-dependent pine. J Mediterr Ecol 1:41–48

Kemp KB, Higuera PE, Morgan P (2016) Fire legacies impact conifer regeneration across environmental gradients in the US northern Rockies. Landsc Ecol 31:619–636

Kemp KB, Higuera PE, Morgan P, Abatzoglou JT (2019) Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA. Ecosphere 10:e02568

Keyser AR, Krofcheck DJ, Remy CC, Allen CD, Hurteau MD (2020) Simulated increases in fire activity reinforce shrub conversion in a Southwestern US Forest. Ecosystems 23:1702–1713

Kimmerer RW, Lake FK (2001) The role of indigenous burning in land management. J For 99:36–41

Kitzberger T, Falk DA, Westerling AL, Swetnam TW (2017) Direct and indirect climate controls predict heterogeneous early-mid 21st century wildfire burned area across western and boreal North America. PloS One 12:e0188486

Klutsch JG, Battaglia MA, West DR, Costello SL, Negron JF (2011) Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. West J Appl For 26:101–109

Kolb TE, Agee JK, Fulé PZ, McDowell NG, Pearson K, Sala A, Waring RH (2007) Perpetuating old ponderosa pine. For Ecol Manag 249:141–157

Krawchuk MA, Meigs GW, Cartwright JM, Coop JD, Davis R, Holz A, Kolden C, Meddens AJ (2020) Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. Front Ecol Environ 18:235–244

Kueppers LM, Conlisk E, Castanha C, Moyes AB, Germino MJ, de Valpine P, Torn MS, Mitton JB (2017) Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Glob Chang Biol 23:2383–2395

Kulakowski D, Jarvis D (2011) The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: a look at the past century. For Ecol Manag 262:1686–1696

Kulakowski D, Jarvis D (2013) Low-severity fires increase susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. For Ecol Manag 289:544–550

Kulakowski D, Veblen TT (2007) Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88:759–769

Kulakowski D, Matthews C, Jarvis D, Veblen TT (2013) Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). J Veg Sci 24:168–176

Larson ER, Van De Gevel SL, Grissino-Mayer HD (2009) Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. Ecoscience 16:282–298

Larson AJ, Belote RT, Cansler CA, Parks SA, Dietz MS (2013) Latent resilience in ponderosa pine forest: Effects of resumed frequent fire. Ecol Appl 23:1243–1249

Latif QS, Saab VA, Dudley JG, Hollenbeck JP (2013) Ensemble modeling to predict habitat suitability for a large-scale disturbance specialist. Ecol Evol 3:4348–4364

Latif QS, Sanderlin JS, Saab VA, Block WM, Dudley JG (2016) Avian relationships with wildfire at two dry forest locations with different historical fire regimes. Ecosphere 7:e01346

Latif QS, Saab VA, Haas JR, Dudley JG (2018) FIRE-BIRD: a GIS-based toolset for applying habitat suitability models to inform land management planning. Gen Tech Rep RMRS-GTR-391. USDA Forest Service, Fort Collins, p 391

Latif QS, Saab VA, Dudley JG, Markus A, Mellen-McLean K (2020) Development and evaluation of habitat suitability models for nesting white-headed woodpecker (*Dryobates albolarvatus*) in burned forest. PloS One 15:e0233043

Leirfallom SB, Keane RE, Tomback DF, Dobrowski SZ (2015) The effects of seed source health on whitebark pine (*Pinus albicaulis*) regeneration density after wildfire. Can J For Res 45:1597–1606

Lentile LB, Smith FW, Shepperd WD (2005) Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Can J For Res 35:2875–2885

Liang S, Hurteau MD, Westerling AL (2017) Response of Sierra Nevada forests to projected climate-wildfire interactions. Glob Chang Biol 23:2016–2030

Lindenmayer DB, Wood JT, Cunningham RB, MacGregor C, Crane M, Michael D, Montague-Drake R, Brown D, Muntz R, Gill AM (2008) Testing hypotheses associated with bird responses to wildfire. Ecol Appl 18:1967–1983

Littell JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecol Appl 19:1003–1021

Littell JS, McKenzie D, Wan HY, Cushman SA (2018) Climate change and future wildfire in the western United States: An ecological approach to nonstationarity. Earth's Future 6:1097–1111

Lotan JE, Critchfield WB (1990) Lodgepole pine. In: Burns RM, Honkala BH (eds) Silvics of North America: Volume 1. Conifers. Agriculture Handbook No 654. USDA Forest Service, Washington, DC

Lyon LJ, Stickney PF (1976) Early vegetal succession following large northern Rocky Mountain wildfires. In: Proceedings of the Montana tall timbers fire ecology conference and fire and land management symposium, 1976. Tall Timbers Research Station, pp 355–375

Madany MH, West NE (1983) Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64:661–667

Malone MP, Roeder RB, Lang WL (1991) Montana: A History of Two Centuries. University of Washington Press, Seattle

Martin K, Eadie JM (1999) Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. For Ecol Manag 115:243–257

McCaughey WW, Schmidt WC, Shearer RC. 1986. Seed-dispersal characteristics of conifers in the Inland Mountain West. In: Shearer RC, compiler. Conifer tree seed in the Inland Mountain West Symposium. General Technical Report INT-GTR-203. USDA Forest Service, Intermountain Research Station, Missoula, Montana, USA. pp 50–62

McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. Annu Rev Entomol 43:107–127

McKenzie DA, Tinker DB (2012) Fire-induced shifts in overstory tree species composition and associated understory plant composition in Glacier National Park, Montana. Plant Ecol 213:207–224

McKinney ST (2019) Systematic review and meta-analysis of fire regime research in ponderosa pine (*Pinus ponderosa*) ecosystems, Colorado, USA. Fire Ecol 15:38

Meddens AJH, Hicke JA, Ferguson CA (2012) Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecol Appl 22:1876–1891

Meigs GW, Campbell JL, Zald HSJ, Bailey JD, Shaw DC, Kennedy RE (2015) Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6:art118

Michaletz ST, Johnson EA (2006) Foliage influences forced convection heat transfer in conifer branches and buds. New Phytol 170:87–98

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: Managing in the face of uncertainty. Ecol Appl 17:2145–2151

Miller C, Aplet GH (2016) Progress in wilderness fire science: embracing complexity. J For 114:373–383

Millspaugh SH, Whitlock C (1995) A 750-year fire history based on lake sediment records in central Yellowstone National Park, USA. Holocene 5:283–292

Minore D (1979) Comparative autecological characteristics of northwestern tree species—a literature review. Gen Tech Rep PNW-GTR-087. USDA Forest Service, Portland. 77 p

Morgan P, Bunting SC, Keane RE, Arno SF (1981) Fire ecology of whitebark pine forests of the Northern Rocky Mountains, USA. In: Schmidt WC, Holtmeier F (eds) Proceedings of the International workshop on subalpine stone pines and their environment: the status of our knowledge. Gen. Tech. Rep. INT-GTR-309. USDA, Forest Service, Intermountain Research Station, Odgen, UT. pp 136–141

Moriarty K, Cheng AS, Hoffman CM, Cottrell SP, Alexander ME (2019) Firefighter observations of “surprising” fire behavior in mountain pine beetle-attacked lodgepole pine forests. Fire 2:34

Morris JL, DeRose RJ, Brussel T, Brewer S, Brunelle A, Long JN (2019) Stable or seral? Fire-driven alternative states in aspen forests of western North America. Biol Lett 15:20190011

Mueggler WF (1989) Age distribution and reproduction of Intermountain aspen stands. West J Appl For 4:41–45

Murray MP, Bunting SC, Morgan P (1998) Fire history of an isolated subalpine mountain range of the Intermountain Region, United States. J Biogeogr 25:1071–1080

Naficy CE (2017) A cross-scale assessment of historical fire severity patterns, landscape dynamics, and methodological challenges in mixed-severity fire regimes of the northern US Rockies. Dissertation. University of Colorado, Boulder

Naficy C, Sala A, Keeling EG, Graham J, DeLuca TH (2010) Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecol Appl 20:1851–1864

Naficy CE, Keeling EG, Landres P, Hessburg PF, Veblen TT, Sala A (2016) Wilderness in the 21st century: A framework for testing assumptions about ecological intervention in wilderness using a case study of fire ecology in the Rocky Mountains. J For 114:384–395

Nagel LM, Palik BJ, Battaglia MA, D’Amato AW, Guldin JM, Swanston CW, Janowiak MK, Powers MP, Joyce LA, Millar CI (2017) Adaptive silviculture for climate change: A national experiment in manager-scientist partnerships to apply an adaptation framework. J For 115:167–178

NatureServe (2018) International ecological classification standard: terrestrial ecological classifications. Terrestrial ecological systems of CONUS and Puerto Rico on the LANDFIRE Legend. NatureServe Central Databases. Version 2.0, Arlington, Virginia

Negrón JF, Huckaby L (2020) Reconstructing historical outbreaks of mountain pine beetle in lodgepole pine forests in the Colorado Front Range. For Ecol Manag 473:118270

Negrón JF, Popp JB (2004) Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. For Ecol Manag 191:17–27

Nelson KN, Turner MG, Romme WH, Tinker DB (2016) Landscape variation in tree regeneration and snag fall drive fuel loads in 24-year old post-fire lodgepole pine forests. Ecol Appl 26:2424–2438

Nelson KN, Turner MG, Romme WH, Tinker DB (2017) Simulated fire behaviour in young, post-fire lodgepole pine forests. Int J Wildland Fire 26:852–865

Newlon KR, Saab VA (2011) Nest-site selection and nest survival of Lewis’s Woodpecker in aspen riparian woodlands. Condor 113:183–193

O'Fallon BD, Fehren-Schmitz L (2011) Native Americans experienced a strong population bottleneck coincident with European contact. Proc Natl Acad Sci 108:20444–20448

Oliver WW, Ryker RA (1990) Ponderosa Pine. In: Burns RM, Honkala BH (eds) Silvics of North America: Volume 1. Conifers. Agriculture Handbook No 654. USDA Forest Service, Washington, DC

Page WG, Alexander ME, Jenkins MJ (2013) Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. For Chron 89:783–794

Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric For Entomol 8:167–189

Parks S, Abatzoglou J (2020) Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985–2017. Geophys Res Lett 47:e2020GL089858

Parks SA, Holsinger LM, Miller C, Nelson CR (2015) Wildland fire as a self-regulating mechanism: The role of previous burns and weather in limiting fire progression. Ecol Appl 25:1478–1492

Parks SA, Miller C, Holsinger LM, Baggett LS, Bird BJ (2016) Wildland fire limits subsequent fire occurrence. Int J Wildland Fire 25:182–190

Parks SA, Miller C, Nelson CR, Holden ZA (2014) Previous fires moderate burn severity of subsequent wildland fires in two large western US wilderness areas. Ecosystems 17:29–42

Peet RK (2000) Forests of the Rocky Mountains. In: Barbour MG, Billings WD (eds) North American Terrestrial Vegetation, 2nd edn. Cambridge University Press, New York, pp 63–102

Powell E, Raffa K (2011) Fire injury reduces inducible defenses of lodgepole pine against mountain pine beetle. J Chem Ecol 37:1184–1192

Powell EN, Townsend PA, Raffa KF (2012) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. Ecol Monogr 82:69–84

Prichard SJ, Stevens-Rumann CS, Hessburg PF (2017) Tamm Review: Shifting global fire regimes: Lessons from reburns and research needs. For Ecol Manag 396:217–233

Pyne SJ (1982) Fire in America: A Cultural History of Wildland and Rural Fire. Princeton University Press, Princeton

Radeloff VC, Helmers DP, Kramer HA, Mockrin MH, Alexandre PM, Bar-Massada A, Butsic V, Hawbaker TJ, Martinuzzi S, Syphard AD (2018) Rapid growth of the US wildland-urban interface raises wildfire risk. Proc Natl Acad Sci 115:3314–3319

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience 58:501–517

Rhoades CC, Pelz KA, Fornwalt PJ, Wolk BH, Cheng AS (2018) Overlapping bark beetle outbreaks, salvage logging and wildfire restructure a lodgepole pine ecosystem. Forests 9:101

Rocca ME, Brown PM, MacDonald LH, Carrico CM (2014) Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For Ecol Manag 327:290–305

Rodman KC, Veblen TT, Battaglia MA, Chambers ME, Fornwalt PJ, Holden ZA, Kolb TE, Ouzts JR, Rother MT (2020a) A changing climate is snuffing out post-fire recovery in montane forests. Glob Ecol Biogeogr 29:2039–2051

Rodman KC, Veblen TT, Chapman TB, Rother MT, Wion AP, Redmond MD (2020b) Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. Ecol Appl 30:e02001

Rogers PC, Landhäusser SM, Pinno BD, Ryel RJ (2014) A functional framework for improved management of western North American aspen (*Populus tremuloides* Michx.). For Sci 60:345–359

Romme W, Walsh J (2003) A comparison of fire regimes and stand dynamics in whitebark pine (*Pinus albicaulis*) communities in the Greater Yellowstone Ecosystem. The University of Wyoming National Park Service Research Center Annual Report 27:art17

Romme WH (1982) Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol Monogr 52:199–221

Romme WH, Allen CD, Bailey JD, Baker WL, Bestelmeyer BT, Brown PM, Eisenhart KS, Floyd ML, Huffman DW, Jacobs BF (2009) Historical and modern disturbance regimes, stand structures, and landscape dynamics in pinon–juniper vegetation of the western United States. Rangel Ecol Manag 62:203–222

Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG (2011) Twenty years after the 1988 Yellowstone fires: Lessons about disturbance and ecosystems. Ecosystems 14:1196–1215

Romme WH, Whitby TG, Tinker DB, Turner MG (2016) Deterministic and stochastic processes lead to divergence in plant communities 25 years after the 1988 Yellowstone fires. Ecol Monogr 86:327–351

Romps DM, Seeley JT, Vollaro D, Molinari J (2014) Projected increase in lightning strikes in the United States due to global warming. Science 346:851–854

Rother MT, Veblen TT, Furman LG (2015) A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Can J For Res 45:1607–1616

Rowe JS (1983) Concepts of fire effects on plant individuals and species. In: Wein R, MacLean D (eds) The role of fire in northern circumpolar ecosystems. SCOPE 18. Wiley, New York, pp 135–154

Russell RE, Saab VA, Dudley JG, Rotella JJ (2006) Snag longevity in relation to wildfire and postfire salvage logging. For Ecol Manag 232:179–187

Saab VA, Dudley J, Thompson WL (2004) Factors influencing occupancy of nest cavities in recently burned forests. Condor 106:20–36

Saab VA, Latif QS, Rowland MM, Johnson TN, Chalfoun AD, Buskirk SW, Heyward JE, Dresser MA (2014) Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. For Sci 60:539–559

Saab VA, Powell HD (2005) Fire and avian ecology in North America: process influencing pattern. In: Saab V, Powell H (eds) Fire and avian ecology in North America. Stud Avian Biol 30:1–13

Saab VA, Powell HDW, Kotliar NB, Newlon KR (2005) Variation in fire regimes of the Rocky Mountains: Implications for avian communities and fire management. In: Saab V, Powell H (eds) Fire and Avian Ecology in North America. Stud Avian Biol 30:76–96

Saab VA, Russell RE, Dudley JG (2007) Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109:97–108

Saab VA, Russell RE, Dudley JG (2009) Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. For Ecol Manag 257:151–159

Saab VA, Russell RE, Rotella J, Dudley JG (2011) Modeling nest survival of cavity-nesting birds in relation to postfire salvage logging. J Wildl Manag 75:794–804

Saab VA, Vierling KT (2001) Reproductive success of Lewis's Woodpecker in burned pine and cottonwood riparian forests. Condor 103:491–501

Schoennagel T, Balch JK, Brenkert-Smith H, Dennison PE, Harvey BJ, Krawchuk MA, Mietkiewicz N, Morgan P, Moritz MA, Rasker R, Turner MG, Whitlock C (2017) Adapt to more wildfire in western North American forests as climate changes. Proc Natl Acad Sci 114:4582–4590

Schoennagel T, Sherriff RL, Veblen TT (2011) Fire history and tree recruitment in the Colorado Front Range upper montane zone: Implications for forest restoration. Ecol Appl 21:2210–2222

Schoennagel T, Turner MG, Romme WH (2003) The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84:2967–2978

Schoennagel T, Veblen TT, Negron JF, Smith JM (2012) Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PloS One 7:e30002

Schoennagel T, Veblen TT, Romme WH (2004) The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience 54:661–676

Schoennagel T, Veblen TT, Romme WH, Sibold JS, Cook ER (2005) ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain subalpine forests. Ecol Appl 15:2000–2014

Schultz CA, Huber-Stearns H, McCaffrey S, Quirke D, Ricco G, Moseley C (2018) Prescribed fire policy barriers and opportunities: A diversity of challenges and strategies across the

West. Ecosystem Workforce Program Working Paper Number 86; Public Lands Policy Group Practitioner Paper Number 2. 36 p

Shepperd WD, Battaglia MA (2002) Ecology, siliviculture, and management of Black Hills ponderosa pine. Gen Tech Rep RMRS-GTR-97. USDA Forest Service, Fort Collins

Sherriff RL, Platt RV, Veblen TT, Schoennagel TL, Gartner MH (2014) Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. PloS One 9:e106971

Sherriff RL, Veblen TT (2006) Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. J Veg Sci 17:705–718

Sherriff RL, Veblen TT (2007) A spatially-explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. Ecosystems 10:311–323

Sherriff RL, Veblen TT (2008) Variability in fire–climate relationships in ponderosa pine forests in the Colorado Front Range. Int J Wildland Fire 17:50–59

Shinneman DJ, Baker WL (1997) Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conserv Biol 11:1276–1288

Shinneman DJ, Baker WL, Rogers PC, Kulakowski D (2013) Fire regimes of quaking aspen in the Mountain West. For Ecol Manag 299:22–34

Sibold JS, Veblen TT, González ME (2006) Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. J Biogeogr 33:631–647

Sieg CH, Linn RR, Pimont F, Hoffman CM, McMillan JD, Winterkamp J, Baggett LS (2017) Fires following bark beetles: Factors controlling severity and disturbance interactions in ponderosa pine. Fire Ecol 13:1

Simard M, Romme WH, Griffin JM, Turner MG (2011) Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol Monogr 81:3–24

Smucker KM, Hutto RL, Steele BM (2005) Changes in bird abundance after wildfire: Importance of fire severity and time since fire. Ecol Appl 15:1535–1549

Stephens SL, Battaglia MA, Churchill DJ, Collins BM, Coppoletta M, Hoffman CM, Lydersen JM, North MP, Parsons RA, Ritter SM, Stevens JT (2020) Forest restoration and fuels reduction: Convergent or divergent? Bioscience 71:85–1018

Stephens SL, Collins BM, Biber E, Fulé PZ (2016) US federal fire and forest policy: Emphasizing resilience in dry forests. Ecosphere 7:e01584

Stephens SL, Ruth LW (2005) Federal forest-fire policy in the United States. Ecol Appl 15:532–542

Stevens-Rumann C, Morgan P, Hoffman C (2015) Bark beetles and wildfires: How does forest recovery change with repeated disturbances in mixed conifer forests? Ecosphere 6:1–17

Stevens-Rumann CS, Prichard SJ, Strand EK, Morgan P (2016) Prior wildfires influence burn severity of subsequent large fires. Can J For Res 46:1375–1385

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT (2018) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243–252

Stevens JT, Kling MM, Schwilk DW, Varner JM, Kane JM (2020) Biogeography of fire regimes in western U.S. conifer forests: a trait-based approach. Glob Ecol Biogeogr 29:944-955

Stevens JT, Miller JE, Fornwalt PJ (2019) Fire severity and changing composition of forest understory plant communities. J Veg Sci 30:1099–1109

Stickney P (1986) First decade plant succession following the Sundance forest fire, northern Idaho. Gen Tech Rep INT-GTR-197. USDA Forest Service, Ogden

Strauss D, Bednar L, Mees R (1989) Do one percent of the forest fires cause ninety-nine percent of the damage? For Sci 35:319–328

Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. J Clim 11:3128–3147

Talucci AC, Krawchuk MA (2019) Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10:e02744

Tepley AJ, Veblen TT (2015) Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. Ecol Monogr 85:583–603

Teske CC, Seielstad CA, Queen LP (2012) Characterizing fire-on-fire interactions in three large wilderness areas. Fire Ecol 8:82-106

Teste FP, Lieffers VJ, Landhäusser SM (2011) Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecol Appl 21:150–162

Theobald DM, Romme WH (2007) Expansion of the US wildland urban interface. Landscape Urban Plan 83:340–354

Tinker DB, Romme WH, Hargrove WW, Gardner RH, Turner MG (1994) Landscape-scale heterogeneity in lodgepole pine serotiny. Can J For Res 24:897–903

Tomback DF, Achuff P, Schoettle AW, Schwandt JW, Mastrogiuseppe RJ (2011) The magnificent high-elevation five-needle white pines: Ecological roles and future outlook. In: Keane RE, Tomback DF, Murray MP, Smith, CM (eds) The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, Montana. USDA Forest Service RMRS-P-63. Fort Collins, Colorado, pp 2–28

Turner MG, Braziunas KH, Hansen WD, Harvey BJ (2019) Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc Natl Acad Sci 116:11319–11328

Turner MG, Romme WH (1994) Landscape dynamics in crown fire ecosystems. Landsc Ecol 9:59–77

Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol Monogr 67:411–433

Turner MG, Romme WH, Reed RA, Tuskan GA (2003) Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landsc Ecol 18:127–140

Turner MG, Whitby TG, Tinker DB, Romme WH (2016) Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97:1260–1273

Urza AK, Sibold JS (2017) Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest. J Veg Sci 28:43–56

van Mantgem P, Nesmith JCB, Keifer M, Knapp EE, Flint A, Flint L (2013) Climatic stress increases forest fire severity across the western United States. Ecol Lett 16:1151–1156

van Wagtendonk JW (2007) The history and evolution of wildland fire use. Fire Ecol 3:3–17

Veblen TT, Kitzberger T, Donnegan J (2000) Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecol Appl 10:1178–1195

Veblen TT, Lorenz DC (1986) Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Phys Geogr 7:1–24

Westerling AL (2016) Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. Philos Trans R Soc Bull 371:20150178

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943

Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proc Natl Acad Sci 108:13165

Whipple SA, Dix RL (1979) Age structure and successional dynamics of a Colorado subalpine forest. Am Midl Nat 101:142–158

Wolf KD, Higuera PE, Davis KT, Dobrowski SZ (2021) Wildfire impacts on forest microclimate vary with biophysical context. Ecosphere 12:e03467

Yazzie V (2007) The tribal perspective of old growth in frequent-fire forests—its history. Ecol Soc 12:21

Ziegler JP, Hoffman C, Battaglia M, Mell W (2017) Spatially explicit measurements of forest structure and fire behavior following restoration treatments in dry forests. For Ecol Manag 386:1–12