Chapter 8: Effects of Climate Change on Ecological Disturbances

Danielle M. Malesky, Barbara J. Bentz, Gary R. Brown, Andrea R. Brunelle, John M. Buffington, Linda M. Chappell, R. Justin DeRose, John C. Guyon II, Carl L. Jorgensen, Rachel A. Loehman, Laura L. Lowrey, Ann M. Lynch, Marek Matyjasik, Joel D. McMillin, Javier E. Mercado, Jesse L. Morris, Jose F. Negrón, Wayne G. Padgett, Robert A. Progar, and Carol B. Randall

Introduction

This chapter describes disturbance regimes in the Intermountain Adaptation Partnership (IAP) region, and potential shifts in these regimes as a consequence of observed and projected climate change. The term "disturbance regime" describes the general temporal and spatial characteristics of a disturbance agent (e.g., insects, disease, fire, weather, human activity, invasive species) and the effects of that agent on the landscape (tables 8.1, 8.2). More specifically, a disturbance regime is the cumulative effect of multiple disturbance events over space and time (Keane 2013). The shifting mosaic of diverse ecological patterns and structures, in turn, affects future patterns of disturbance, in a reciprocal, linked relationship that shapes the fundamental character of landscapes and ecosystems. Disturbance creates and maintains biodiversity in the form of shifting, heterogeneous mosaics of diverse communities and habitats across a landscape (McKinney and Lockwood 1999), and biodiversity is generally highest when disturbance is neither too rare nor too frequent on the landscape (Grime 1973).

Changing climate is altering the characteristics of disturbance agents, events, and regimes, with additional effects expected in the future (Dale et al. 2001). As described in other chapters in this report, climate change can alter the timing, magnitude, frequency, and duration of disturbance events, as well as the interactions of disturbances on a landscape. Interactions among disturbance regimes, such as the co-occurrence in space and time of bark beetle outbreaks and wildfires, can result in highly visible, rapidly occurring, and persistent changes in landscape composition and structure. Understanding how multiple disturbance interactions may result in novel and emergent landscape conditions is critical for addressing climate change effects and designing land management strategies that are appropriate for future climates (Keane et al. 2015).

We have summarized the following climate-sensitive disturbance agents present in the IAP region: wildland fires, insects, forest tree diseases, invasive plants, and geologic hazards. We discuss ways in which climate change will potentially affect each disturbance agent, and we include a discussion on how these disturbance agents may differ among the IAP subregions. Last, we discuss how disturbance agents may interact. Understanding how, when, where, and why climate change alters disturbance characteristics can help resource managers to anticipate future management challenges and identify where landscapes may shift into new and sometimes novel states.

Paleo-Ecological Overview

The effects of global environmental change are projected to alter the frequency and extent of landscape disturbances in the western United States, including wildfire and insect outbreaks (Flannigan et al. 2009; Raffa et al. 2008). In the IAP region, some conifer-dominated forests face an uncertain future from concomitant climate warming and intensifying disturbance regimes (Rehfeldt et al. 2006; Westerling et al. 2006). Recent studies suggest that unusually severe disturbances can promote transitions of high-elevation conifer-dominated forests to grasslands (Odion et al. 2010; Savage and Mast 2005). Retrospective ecological records derived from lake sediments and tree rings can help to establish baseline understanding about how ecosystem dynamics and disturbance regimes have responded and may respond during transitional climate periods involving changes in moisture and temperature.

The IAP region is topographically complex, with steep environmental gradients and vegetation ranging from sagebrush-steppe at low elevations to alpine tundra at the highest elevations. Between these extremes are forested zones that include pinyon-juniper woodlands, ponderosa pine parklands, montane forests of Douglas-fir (*Pseudotsuga menziesii*), and spruce-fir forests in the subalpine zone (Arno and Hammerly 1984).

The IAP region encompasses two distinct geologic provinces—the Great Basin and the Colorado Plateau— and many important physiographic, hydrological, and ecological linkages. The spatial pattern and seasonality of precipitation maximums throughout the region are heterogeneous and

Table 8.1—Area of forest land, by forest type group and primary disturbance class in the USFS Intermountain Region (2005-2014). This includes data from all forested Forest Inventory and Analysis (FIA) plots (n = 7,572) (2005–2014).

Forest-type group	Disturbance class											
	None	Insect	Disease	Fire	Wild animals	Domestic animals	Weather	Vegetation	Other	Human	Geological	All land[a]
	Thousand acres											
Pinyon-juniper	18,360	431	542	145	42	169	116	6	18	19	27	19,877
Douglas-fir	3,554	563	181	211	3	105	6	-	12	-	10	4,647
Ponderosa pine	1,185	17	44	117	-[b]	5	-	-	-	5	-	1,376
Fir-spruce-mountain hemlock	4,316	777	121	96	-	28	39	9	-	-	98	5,487
Lodgepole pine	1,818	566	100	129	-	26	6	-	-	-	-	2,647
Western larch	-	-	-	4	-	6	-	-	-	-	-	10
Other western softwoods	867	130	9	34	-	30	12	-	-	-	9	1,093
California mixed conifer	31	-	20	-	-	-	-	-	-	-	-	52
Elm-ash-cottonwood	97	-	3	3	-	1	-	-	-	-	-	106
Aspen-birch	2,244	157	240	157	4	18	19	-	-	5	10	2,857
Other hardwoods	3	-	-	-	-	-	-	-	-	-	-	3
Woodland hardwoods	3,235	27	23	170	3	24	38	-	7	-	1	3,531
Nonstocked	1,761	61	26	944	5	61	-	-	-	18	1	2,881
Total	37,476	2,732	1,316	2,015	58	476	237	15	37	47	159	44,572

[a] Columns and rows may not add to their totals due to rounding.
[b] Table cells without observations are indicated by "–".

Table 8.2—Area of forest land, by National Forest and primary disturbance class in the USFS Intermountain Region (2005–2014). This includes data from all forested Forest Inventory and Analysis (FIA) plots (n = 7,572) (2005–2014).

National forest	Disturbance class											All land[a]
	None	Insect	Disease	Fire	Wild animals	Domestic animals	Weather	Vegetation	Other	Human	Geological	
	------Thousand acres------											
Ashley	723	160	75	45	-[b]	-	-	-	-	-	-	1,004
Boise	1,424	80	34	182	5	7	-	-	-	5	-	1,739
Bridger-Teton	1,650	515	14	101	-	-	-	-	-	-	-	2,282
Dixie	1,255	88	23	92	6	4	18	-	-	-	-	1,489
Fishlake	1,009	15	16	34	-	1	-	-	-	-	-	1,077
Manti-La Sal	875	84	61	28	6	-	6	-	-	-	18	1,081
Payette	1,548	33	24	350	-	14	-	-	-	-	6	1,977
Salmon-Challis	1,850	662	79	362	-	104	12	9	6	-	17	3,103
Sawtooth	809	136	30	49	-	15	-	-	-	-	34	1,076
Caribou-Targhee	1,871	59	52	-	-	27	14	-	6	5	12	2,048
Humboldt-Toiyabe	3,047	113	137	119	-	24	24	-	-	5	15	3,487
Uinta-Wasatch-Cache	1,322	214	95	25	-	-	19	-	7	-	11	1,694
Total	17,388	2,164	645	1,392	18	199	94	9	19	16	115	22,063

[a] Columns and rows may not add to their totals due to rounding.
[b] Table cells without observations are indicated by "–".

temporally dynamic (Mock 1996; Mock and Brunelle-Daines 1999). Generally, in the southern portion of the IAP region, precipitation occurs during the summer via the North American Monsoon and during winter from Pacific frontal storms (Adams and Comrie 1997; Mitchell 1976). El Niño-Southern Oscillation (ENSO) is the primary driver of winter precipitation delivery, and ENSO varies in intensity and frequency over decadal to millennial timescales (Moy et al. 2002; Ropelewski and Halpert 1986). ENSO phase is an important control on fire regimes in the IAP region, with increased burning associated with the La Niña phase in the areas of the IAP region south of the 40 to 42° ENSO dipole transition zone (Brown et al. 2008; Schoennagel et al. 2005; Wise 2010).

Over millennial timescales, vegetation and disturbance regimes are shaped by climatic changes mediated by variations in incoming solar radiation (insolation), which result from subtle shifts in Earth-sun geometry. During the Holocene Thermal Maximum (HTM), which occurred 6,000 to 9,000 years BP, summers were warmer and winters were colder (Berger and Loutre 1991). Reconstructions of past environmental conditions help us to understand how past climates shaped plant communities and affected disturbance regimes. More specifically, lake sediment cores, which rely on the analysis of ecological proxy data, such as pollen and charcoal particles, facilitate reconstructions of forest composition and the frequency of past fire episodes. Chronologies for lake sediment records are produced through the analysis of radiometric isotopes, such as 210Pb/137Cs and 14C. In the IAP region, many paleo-environmental reconstructions have been done in subalpine environments, where perennial wetlands are more common than at lower-elevation sites.

The HTM is commonly emphasized in paleo-environmental reconstruction because of potential analogs for a warming 21st century. A summer temperature reconstruction from the Snake Range in western Nevada suggests that HTM warmth may have peaked 5,000 to 6,000 years BP (Reinemann et al. 2009). A calcite-based precipitation reconstruction from western Colorado, near the eastern margin of the IAP region, indicates that high-elevation HTM climate was dominated by high rainfall relative to snow, though this trend essentially reversed later in the period, when high-elevation sites were dominated by snowfall (Anderson 2011).

Despite long-term changes in seasonal temperature and precipitation regimes, upper-elevation sites in the IAP region have been dominated by Engelmann spruce (*Picea engelmannii*) for at least the last 9,000 years, with increasing abundances of subalpine fir (*Abies lasiocarpa*) and aspen (*Populus* spp.) beginning around 3,000 years BP (Morris et al. 2013). Fire regimes for this region are dynamic; the Aquarius Plateau recorded more frequent fires during the HTM period relative to recent millennia (Morris et al. 2013). On the other hand, sites located farther north (~40° N) near the ENSO dipole transition zone show essentially the opposite pattern, with reduced area burned during the HTM and increasing area burned toward present. In the

IAP region, the quantity of moisture delivery during winter is modulated by ENSO. Because the fire season is strongly linked with snow cover (e.g., Westerling et al. 2006), shifts in the rates of biomass burning are apparent at sites located in the north and south of the ENSO dipole during the Holocene due to long-term dynamics of ENSO (Moy et al. 2002).
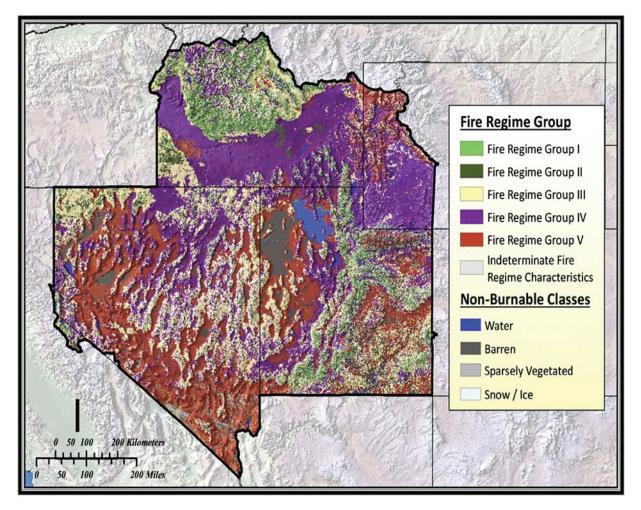
Wildland Fire

Wildland fire is defined in the 2009 Guidance for Implementation of Federal Wildland Fire Management Policy glossary as: "A general term describing any non-structure fire that occurs in the wildlands." Wildland fire includes both wildfires and prescribed fires. In contrast, wildfire is defined as: "An unplanned ignition of a wildland fire (such as a fire caused by lightning, volcanoes, unauthorized or accidental human-caused fires) and escaped prescribed fires" (USDA and DOI 2009). The terms "fire," "wildfire," and "wildland fire" are used throughout this document.

Wildland fire is an important overarching process that has significantly shaped the landscapes of the IAP region, dictating plant community structure and the direction and pace of ecosystem processes (Kitchen 2010). Historically, wildland fires maintained sagebrush-grass-forb-dominated landscapes in lower to mid-elevations, and lodgepole pine (*Pinus contorta* var. *latifolia*) and aspen-mixed conifer communities at mid- to high elevations. It maintained open understories in ponderosa pine (*Pinus ponderosa*) communities and created openings for other subalpine forest species to regenerate.

It is critical that we understand fire behavior, its ecological effects, and how human impacts on fuels and our environment have affected and continue to shape the roles that fire plays in our ecosystems. What are the relationships with wildland fire and vegetation cover types? How does climate change affect those relationships? How do fire and climate change affect carbon sequestration, and what is the importance of carbon sequestration in the IAP region? How do we manage risks associated with wildland fire, and how are the socioeconomics associated with wildland fire changing? These questions are important to consider for resource planning in the context of climate change.

Fire Regimes

The role of fire in ecosystems and its interactions with dominant vegetation is called a fire regime. Fire regimes can be defined by fire frequency (mean number of fires per time period), extent, intensity (measure of the heat energy released), severity (net ecological effect), and seasonal timing (Agee 1993). Fire regimes characterize the spatial and temporal patterns of fires and the impacts on ecosystems on the landscapes where they occur (Bradstock et al. 2002; Brown and Smith 2000; Keeley et al. 2009; Morgan et al. 2001). Understanding fire regimes is critical for understanding the

Figure 8.1—Distribution of LANDFIRE Fire Regime Groups in the Intermountain Adaptation Partnership region (Fire Regime Groups IVa and IVb have not been distinguished) (data described in Rollins [2009] and at https://www.landfire.gov/NationalProductDescriptions12.php).

role that climate change has on fire patterns (Brown et al. 2008; Grissino-Mayer and Swetnam 2000; Pechony and Shindell 2010; Schoennagel et al. 2004).

Fire regime groups, intended to characterize the presumed historical fire regimes, have been developed at a national scale (Hann et al. 2004) (see figure 8.1 for fire regimes in the IAP region). These groups are based on interactions among dynamic vegetation, fire spread, and fire effects, all in a spatial context. The natural (historical) fire regime groups are classified based on average number of years between fires (fire frequency), combined with the severity (amount of replacement) of the fire on the dominant overstory vegetation. Table 8.3 has been adjusted for the IAP region based on knowledge of local scientists and represents mean fire return intervals and severity groups that are more applicable to our geographic area (Kitchen 2015).

Low-severity, high-frequency fires representing **Fire Regime Group I** were once more typical in ponderosa pine forests at low elevations than they are today (fig. 8.2); fire suppression has reduced fire frequency in these forests (Stein 1988). Fires historically burned frequently enough to maintain low fuel loads and an open stand structure, producing a landscape in which fire-caused mortality of mature trees was relatively low (Agee 1998; Jenkins et al. 2011; Moritz et al. 2011). Adaptive traits, such as thick bark, also allowed mature ponderosa pines to survive many repeated fires over time.

Gambel oak (*Quercus gambelii*) communities were historically characterized by high-frequency, stand-replacing fires associated with **Fire Regime Group II** (fig. 8.3). Although insufficient historical data are available to adequately compare pre-Euro-American fire return intervals in Gambel oak communities to those of post-Euro-American settlement, there are accounts that Native Americans frequently burned these landscapes. The removal of Native Americans, as well as the introduction of domestic livestock grazing, led to a decrease in the number of ignitions and the spatial distribution of wildland fires in these ecosystems (Wadleigh et al. 1998). Today, many of these areas have a fire return interval of 35 to 200 years and would be classified as **Fire Regime Group IV**.

Table 8.3—Revised fire regime groups following LANDFIRE, with examples of cover types included in each group (numbers in parentheses developed by Hann et al. 2004).

Group	Mean fire return interval	Severity	Example cover types
I	<35 years (often <25 years)	Low (surface fires most common). Generally low-severity fires replacing <75% of the dominant overstory vegetation; can include mixed-severity fires that replace up to 75% of the overstory	Ponderosa pine; dry mixed conifer; aspen with mixed conifer
II	<35 years (often less than 25 years)	Mixed to high (high-severity fires replacing greater than 75% of the dominant overstory vegetation)	Gambel oak-maple; grasslands
III	35-80 (200) years	Mixed	Douglas-fir; western larch, lodgepole pine, and Douglas-fir; curl-leaf mountain mahogany; seral juniper and pinyon-juniper shrublands; riparian deciduous woodland; mesic mixed-conifer-aspen
IVa	35-80 (200) years	High	Lodgepole pine; Douglas-fir; mountain big sagebrush; Gambel oak-maple, curl-leaf mountain-mahogany, persistent aspen, mesic mixed conifer-aspen
IVb	81-200 (35) years	High	Wyoming big sagebrush; low and black sagebrush; lodgepole pine; persistent aspen; oak-maple; curl-leaf mountain-mahogany.
V	200+ years	Mixed to high (generally replacement-severity; can include any severity type in this frequency range)	Spruce-fir forests; salt desert shrub; persistent pinyon-juniper; juniper woodlands

Figure 8.2—Ponderosa pine forest on the east side of Boulder Mountain in Dixie National Forest, Utah. This forest type represents Fire Regime Group I, with high-frequency ground fires that maintain low understory fuels (photo: Wayne Padgett, U.S. Forest Service).

Figure 8.3—Regenerating Gambel oak along the Wasatch Front east of Farmington, Utah. This forest type represents Fire Regime Group II**,** with high-frequency, stand-replacing fires (photo: W. Padgett, U.S. Forest Service).

Generally, areas with mixed-severity fire with a return interval of 35 to 80 years, such as cool moist Douglas-fir and lodgepole pine types, are classified as **Fire Regime Group III**. Historically, patterns of fire intensity and frequency in cool moist Douglas-fir and lodgepole pine habitat types were driven by topography, weather, stand structure, and fuel loading. As a result, a range of fire behavior characteristics are represented in Fire Regime Group III, from light surface fire to stand-replacement fire, depending on conditions, thus creating a mixed-severity fire regime.

Historically, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) was maintained by high-severity, stand-replacing fires of **Fire Regime Group IVa** (Miller et al. 2001). Today, the fire return interval in these communities is often much longer than it was historically, with associated juniper (*Juniperus* spp.) expansion replacing both sagebrush and their diverse herbaceous understory (Miller et al. 2001) (fig. 8.4).

Fire Regime Group IVb is representative of a variety of cover types in the IAP region, from Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities found at lower elevations to lodgepole pine forests in mountainous portions of the region. Lodgepole pine communities undergo large, stand-replacing fires (Romme 1982), and many, but not all, lodgepole pine trees can regenerate prolifically when heating from fires releases seed from serotinous cones (fig. 8.5) (Schoennagel et al. 2003).

Figure 8.4—Utah juniper establishment in a mountain big sagebrush-bunchgrass community in the Stansbury Mountains of central Utah (photo: W. Padgett, U.S. Forest Service).

Figure 8.5—Regeneration after fire in a lodgepole pine forest. Lodgepole pine forests are in Fire Regime Group IV, characterized by stand-replacing, high-severity fires with a 35- to 200-year fire return interval (photo: J. Peaco, National Park Service).

Figure 8.6—A recently burned spruce-fir forest on the north slope of the Uinta Mountains in northern Utah. This forest type represents Fire Regime Group V, with stand-replacing fires with a long (200 or more years) fire return interval (photo: Wayne Padgett, U.S. Forest Service).

High-severity fires that occur at intervals of 200 or more years representing **Fire Regime Group V** are typical in subalpine forests (fig. 8.6) and those of 1,000 or more years are typical of salt desert shrublands (fig. 8.7). In subalpine forests, fires tend to cause high mortality of mature trees because long intervals between fires result in dense, multistoried forest structures that are susceptible to crown fires (Agee 1998). There is little evidence that fires burned historically in salt desert shrublands, and they may have never burned until the introduction of invasive species, such as cheatgrass (*Bromus tectorum)*, to their understory (West 1994).

Wildland Fire Behavior

Fire behavior can be defined as the manner in which fuel ignites, flame develops, and fire spreads, as determined by the interactions of weather, fuels, and topography. A change in any one factor will alter the behavior of fires. Humans also play a significant role in the occurrence of fire in the conterminous United States (Hawbaker et al. 2013).

Figure 8.7—A salt desert shrubland near the La Sal Mountains in southeastern Utah. This cover type represents Fire Regime Group V, with stand-replacing fires with a long (200 or more years) fire return interval (photo: Wayne Padgett, U.S. Forest Service).

Climate and Weather

The terms "climate" and "weather" are often used interchangeably, and both affect wildland fires in direct and indirect ways. The difference between these is a matter of time; weather is what happens on a day-to-day basis, whereas climate is a measure of how weather and the atmosphere "behave" over a longer period of time (NASA 2005). Climate determines broad vegetation cover types that occur in any given area of the IAP region. Weather affects the seasonal and annual variability in fuel production in a particular landscape and expected fire behavior for that day. For example, unusually wet weather in the spring can increase fine fuel production.

The Plateaus subregion and southern portion of the Great Basin and Semi Desert subregion (fig. 1.1) are characterized by mild winters with long, hot, and typical monsoonal summer weather patterns. These monsoons are less pronounced and the temperatures are somewhat cooler, in the northern portion of the Great Basin and Semi Desert and the Uinta and Wasatch Front subregions. The Middle Rockies and Southern Greater Yellowstone subregions to the north have a maritime-influenced temperate climate with warm, dry summers and cool to cold and moist winters. These climates dictate the vegetation cover types dominating each subregion.

Weather as a driver of fire behavior is certainly the most dynamic of the three environmental conditions affecting fire behavior (weather, fuels, and topography). Wind, temperature, relative humidity, and precipitation, all features of weather, affect fire behavior. During the fire season, the amount and timing of precipitation largely determine availability of fine fuels, and short periods of dry weather are sufficient to precondition these systems to burn (Gedalof et al. 2005; Westerling and Swetnam 2003). Large fires are most strongly correlated with low precipitation, high temperatures, and summer drought (July through September) in the year of the fire (Littell et al. 2009).

Fuels

Fire regimes are also influenced by fuel structure, composition, continuity, and moisture content. These characteristics vary across vegetation and depend on the amount and configuration of live and dead fuel present at a site, environmental conditions that favor combustion, and ignition sources (Agee 1993; Krawchuk et al. 2009). Drier fuels can be ignited more easily, and a continuous layer of fuels can aid in the spread of fire. In some cases, high fuel moisture ultimately controls the extent and severity of fire (fig. 8.8).

Where rates of vegetation production outpace decomposition, sufficient biomass accumulates and is available to support fires, although higher-elevation regions with abundant fuels do not always have sufficiently dry conditions to sustain a fire. However, prolonged dry weather conditions (about 40 days without precipitation) can sufficiently dry live fuels and larger dead fuels to carry large, intense fires once they are ignited (Schoennagel et al. 2004). Wildland fuels lose moisture and become flammable in warm and dry summers typical throughout the IAP region; during this time there are ample sources of ignition from lightning strikes and humans. Therefore, the active wildfire season (period conducive to active burning) is in the summer, typically from late June through October, with shorter seasons at higher-elevation sites where snowpack can persist into July.

Fuels are generally less dynamic over time than the other drivers of fire behavior. Seasonal changes in annual and perennial grasses are a major driver of fuel conditions in grassland and shrublands, but in forests, changes in fuels, such as down woody fuels, are relatively slow; changes depend on the dead woody fuel size classes and decomposition rates, which vary by species.

Figure 8.8—Quaking aspen (*Populus tremuloides*) communities with high fuel moisture (in background). These stands helped to stop a fire on the north slope of the Uinta Mountains in northern Utah in fall 2002 (photo: Wayne Padgett, U.S. Forest Service).

Topography

There are strong interactions among topography, fuels, and weather. Aspect, elevation, and topographic features have affect moisture profiles across the landscape that directly affect vegetation and fuels. Slope steepness, aspect, valleys, ridges, chutes, and saddles all affect fire behavior differently. Rate of fire spread increases with slope steepness. Topographic features that channel fire tend to increase fire intensity, or the amount of energy release per unit time, whereas those that disperse energy tend to reduce fire intensity.

Human Effects on Historical Fire Regimes

Fires historically played a significant role in a variety of forest and nonforest types in the IAP region (Bartos and Campbell 1998; Gruell 1999; Heyerdahl et al. 2011; Miller and Tausch 2001). Wildland fire, as well as other disturbances such as insect outbreaks, disease, drought, invasive species, and storms, is part of the ecological history of both forest and nonforest ecosystems, influencing vegetation age and structure, plant species composition, productivity, carbon storage, water yield, nutrient retention, and wildlife habitat (Ryan and Vose 2012).

When comparing the historical to the current role of wildland fire on various ecosystems, we see significant change because of human influences (Kitchen 2015). Humans have affected fuels and ignition patterns in a variety of ways, including livestock grazing, introduction of invasive annual grasses, fire ignitions, fire suppression and exclusion, and landscape fragmentation, all of which affect the quantity and structure of fuels (Allen et al. 2002; Falk et al. 2011; Ogle and DuMond 1997; Pausas and Keeley 2014). Human activities have created either a "fire deficit" through fire suppression and exclusion, or a "fire surplus" through the addition of highly flammable invasive species to landscapes (Parks et al. 2015). Parks et al. (2015) noted that primarily nonforested portions of the western United States had a surplus of fires between 1984 and 2012 because of the abundance of cheatgrass (*Bromus tectorum*) in the Great Basin and red brome (*B. rubens*) in the Mojave Desert; the

forested portions of the region experienced a deficit of fires because of fire exclusion.

Fire Deficit

Fire exclusion has increased the potential for crown fires in forests that historically had low-severity fire regimes (Agee 1998; Peterson et al. 2005) and in some forests with mixed-severity regimes (Taylor and Skinner 2003). Historically, ground or surface fires were frequent in ponderosa pine communities and maintained open understories. Fire exclusion since the 1920s has increased surface fuel loads, tree densities, and ladder fuels, especially in low-elevation, dry conifer forests (Schoennagel et al. 2004) (fig. 8.9). As a result, fires in these forests may be larger and more intense, and may cause higher rates of tree mortality than historical fires. In higher-elevation forests where fires were historically infrequent, fire exclusion has had minimal effects on fire regimes (Romme and Despain 1989; Schoennagel et al. 2004). The fire deficit has also resulted in the increase in pinyon pines and junipers (e.g., Utah juniper [*Juniperus osteosperma*] throughout the West) (fig. 8.10).

Increased Fire Frequency

Fire intervals for many sagebrush ecosystems of low to moderate productivity are perhaps 10 to 20 times shorter today than what is estimated for the pre-20th-century era (Peters and Bunting 1994; Whisenant 1990) because of the spread and dominance of invasive annual grasses, including cheatgrass (fig. 8.11). Cheatgrass invasion is not dependent upon livestock grazing. However, once cheatgrass was first introduced to the sagebrush-dominated rangelands in the early 1900s, it spread quickly into areas that had been grazed in the late 1800s (Young et al. 1987). Once a site is invaded by cheatgrass, it will not easily return to native perennial grass and forb dominance with exclusion of livestock grazing (Young and Clements 2007).

Livestock Grazing

Moderate levels of livestock grazing can be used to reduce fine fuel loading and subsequent fire severity in
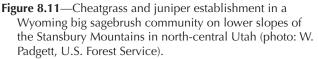
Figure 8.9—High fuel loading in a ponderosa pine forest in Dixie National Forest in southern Utah as a result of decades of fire exclusion (photo: W. Padgett, U.S. Forest Service).

a)

b)

Figure 8.10—Big Creek Canyon on the west side of the Stansbury Mountains in north-central Utah in (a) 1901 and (b) 2004, showing an increase in Utah juniper in the mountain big sagebrush-Wyoming big sagebrush ecotone as a result of fire exclusion (left photo: G. K. Gilbert, U.S. Geological Survey; right photo: W. Padgett, U.S. Forest Service).

Figure 8.11—Cheatgrass and juniper establishment in a Wyoming big sagebrush community on lower slopes of the Stansbury Mountains in north-central Utah (photo: W. Padgett, U.S. Forest Service).

sagebrush-steppe plant communities and potentially other rangelands (Davies et al. 2010). However, grazing has been shown to change community composition over time, thereby influencing fuel characteristics (Chambers 2008). In some rangeland ecosystems, overgrazing and fire exclusion have caused the expansion of pinyon pine and juniper, with an associated increase in woody fuels in many sagebrush ecosystems (fig. 8.12); fire severity and size have increased as a result (Chambers 2008; Marlon et al. 2009).

Landscape Fragmentation

Practices such as timber harvest, road construction, and oil and gas development fragment the patterns of fuel loads on the landscape. In addition, sagebrush communities in the Intermountain West have been fragmented by conversion to agricultural uses and brush control projects (Kitchen and McArthur 2007). Fragmentation affects the spatial distribution and variation of fuel loads, which can in turn affect the susceptibility of a landscape to fire (Gould et al. 2008). Fragmented fuels can inhibit the spread of fire and ultimately contribute to the accumulation of fuels on the landscape (Sexton 2006).

Ignitions

On average, between 2002 and 2012, humans caused 24 percent of the fires in the U.S. Department of Agriculture Forest Service (USFS) Intermountain Region (fig. 8.14). A combination of human- and lightening-caused fires burned an average of 310,000 acres annually during that period, ranging from a low of 44,046 acres (2004) to 1,194,537 acres (2007) (FIRESTAT 2015) (fig. 8.13).
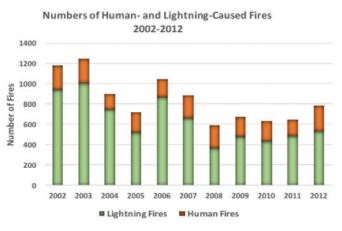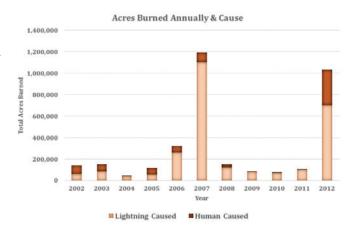

Figure 8.12—Number of human- and lightning-caused fires annually in the U.S. Forest Service Intermountain Region, 2002–2012 (data from FIRESTAT [2015]).

Climate Change and Wildland Fire

Climate controls the magnitude, duration, and frequency of weather events, which, in turn, drive fire behavior. In a warming climate, we are experiencing earlier snowmelt (Mote et al. 2005) and longer fire seasons (Westerling et al. 2006), and these trends are expected to continue. These changes are likely to result in increases in area burned, but fire activity will ultimately be limited by the availability of fuels (Brown et al. 2004; Flannigan et al. 2006; Loehman et al. 2011a; McKenzie et al. 2004; Torn and Fried 1992). Grissino-Mayer and Swetnam (2000) note that climate change may not result in simple linear responses in fire regimes. In some places in the IAP region, climate-driven changes in vegetation may lead to fuel limitations and lower fire area burned (McKenzie and Littell 2017).

Despite general agreement that warming temperatures will lead to increased area burned at broad scales in the western United States (McKenzie et al. 2004; Westerling et al. 2006), finer scale patterns are less certain. Projections

Figure 8.13—Wildfire area burned in the U.S. Forest Service Intermountain Region, 2002–2012 (data from FIRESTAT [2015]).
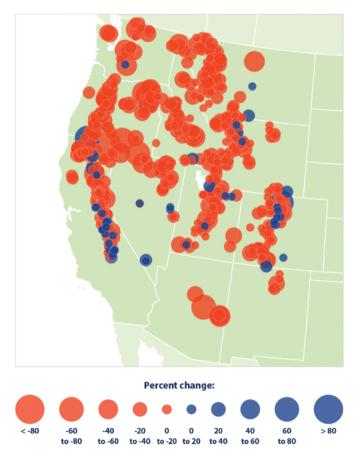
may be especially pronounced in mid- to high-elevation forested systems where fuels are abundant and snowpack can be limiting to fire (Westerling et al. 2006).

Climate Change and Fire Size and Severity

Changes in climate, especially drought and excessive heat, are linked to increased tree mortality, shifts in species distributions, and decreased productivity (Allen et al. 2010; van Mantgem et al. 2009; Williams et al. 2013). However, the most visible and significant short-term effects of climatic changes on forest ecosystems are caused by altered disturbance regimes, including insects and fire (Hicke et al. 2016). Large and long-duration forest fires have increased fourfold over the past 30 years in the West, and the length of the fire season has also increased (Westerling and Bryant 2008; Westerling et al. 2006). In addition, area burned increased between 1960 and 2015 (NIFC 2015) (fig. 8.15).
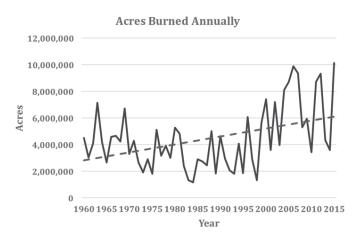
Analysis of fire data since 1916 for the 11 contiguous western States shows that for a temperature increase of 4 °F, annual area burned will be 2 to 3 times higher (McKenzie et al. 2004). The occurrence of very large wildfires is also projected to increase (Barbero et al. 2015; Stavros et al. 2014), as longer fire seasons combine with regionally dry fuels to promote larger fires. Fire severity over the long term will be dependent on vegetation changes and fuel conditions; if productivity is reduced and fuel loads are lower, fire severity may decrease in some systems (Parks et al. 2016).
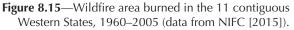
Wildland Fire and Carbon Balance

In all vegetated ecosystems, there is a balance between the ability of the ecosystems to store (sequester) carbon and the release of carbon to the atmosphere with fire. Globally, forests and their soils contain the Earth's largest terrestrial carbon stocks. In the United States, forests and their soils represent 89 percent of the national terrestrial carbon sink (North and Hurteau 2011; Pacala et al. 2007; Pan et al. 2011). Forests in the western United States are estimated to account for 20 to 40 percent of the total annual carbon sequestration in the country (Pacala et al. 2001; Schimel and Braswell 2005). Carbon typically accumulates in forests (in woody biomass) and forest soils for decades to centuries until a disturbance event releases this stored carbon into the atmosphere (Goward et al. 2008).

Carbon Release

Wildland fires in forest ecosystems are one of the primary means for regulating carbon storage (sink) and emissions (Kasischke et al. 2000). Carbon is released to the atmosphere through wildland fires, but quantifying or projecting wildland fire emissions is difficult because their amount and character vary greatly from fire to fire, depending on biomass densities, quantity and condition of consumed fuels, combustion efficiency, and weather (Loehman et al. 2014; Sommers et al. 2014). The release

Percent change:

| < -80 | -60 to -80 | -40 to -60 | -20 to -40 | 0 to -20 | 0 to 20 | 20 to 40 | 40 to 60 | 60 to 80 | > 80 |

Figure 8.14—April 1 snow water equivalent in the western United States, 1955–2015 (from USEPA [2016]).

of future climate are somewhat uncertain at the regional and local scales that influence fire occurrence and behavior. For example, projections for future precipitation are characterized by both uncertainty and high variation (IPCC 2007; Littell et al. 2011). Although lightning and high wind events may increase in the future, thus increasing the potential for fire activity, confidence in these projections is low (Seneviratne et al. 2012).

Climate Change and Snowpack

Large and consistent decreases in snowpack have been observed throughout the western United States between 1955 and 2015 (fig. 8.14) (USEPA 2016). Although some individual stations in the 11 contiguous western States saw increases in snowpack, April 1st snow water equivalent declined at more than 90 percent of the sites measured. The average change across all sites amounts to a 23 percent decline. Declining snowpacks, when combined with other ongoing changes in temperature and drought, contributed to warmer, drier conditions that have fueled wildfires in parts of the western United States (Kitzberger et al. 2007; Westerling et al. 2006). Earlier onset of snowmelt reduces fuel moisture during the fire season, making a larger portion of the landscape flammable for longer periods of time (McKenzie et al. 2004; Miller et al. 2011a). This shift

Acres Burned Annually

Figure 8.15—Wildfire area burned in the 11 contiguous Western States, 1960–2005 (data from NIFC [2015]).

of carbon from fires in forest ecosystems depends on climate and disturbance regime (Keith et al. 2009). Emissions measured from an individual fire event may not be characteristic of large-scale emissions potential, because of complex ecological patterns and spatial heterogeneity of burn severity within fire perimeters. Predisturbance productivity and conditions further affect the carbon emitted (Bigler et al. 2005; Dale et al. 2001; Falk et al. 2007).

High-severity fires typical of mid- to high-elevation forests in the IAP region may consume a large amount of aboveground biomass, resulting in an instantaneous pulse of carbon (i.e., the area affected becomes a carbon source to the atmosphere). However, these fires typically occur infrequently, and eventually carbon is recaptured by forest regrowth. Low-severity fires such as those that occur in low-elevation, dry forest types typically release less carbon per fire event (although total emissions depend on area burned) at more frequent intervals than with stand-replacing regimes. Low-severity fires favor long-lived and fire-resistant (or fire-tolerant) forest species that typically survive multiple fire events (Ritchie et al. 2007).

Carbon loss from wildland fire is balanced by carbon capture from forest regrowth over multiple decades, unless a lasting shift in dominant plant life form occurs or fire return intervals change (Kashian et al. 2006; Wiedinmyer and Neff 2007). This shift in balance has occurred in many of the low-elevation sagebrush communities that have been converted to cheatgrass (McArthur et al. 2009; Rau et al. 2011; Whisenant 1990). Wyoming big sagebrush communities, prior to Euro-American settlement, were composed of sagebrush and perennial grasses that were clumped in distribution and carried fire only under extreme weather conditions (low humidity and high windspeed). The invasion of cheatgrass into these communities increased fuel continuity, greatly increasing the frequency and extent of fire occurrences (West 1999; Young et al. 1972). Fire return intervals have decreased from between 50 and 100 years to less than 10 years because of cheatgrass invasion (Miller et al. 2011b; Whisenant 1990).
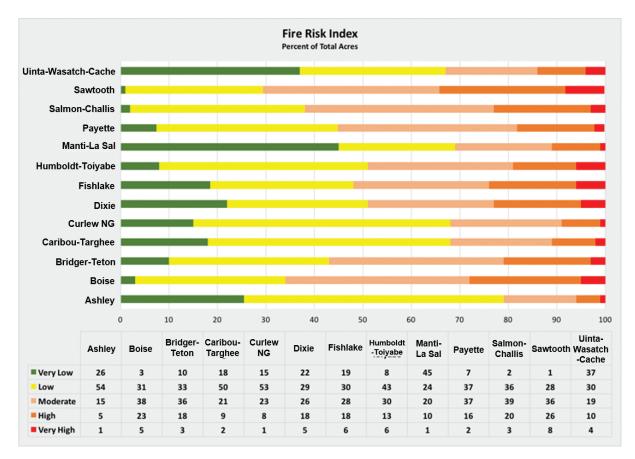
Carbon Sequestration

The potential for forests and rangelands to mitigate climate change depends on human activities such as land use and land management, and environmental factors such as vegetation composition, structure, and distribution; disturbance processes; and climate (Derner and Schuman 2007; Loehman et al. 2014). Although much has been written about the ability of forests to sequester carbon, less is written about the corresponding ability of rangelands, which also contribute to this ecosystem service. There are approximately 770 million acres of rangelands in the United States (Havstad et al. 2009); of these, half are on public lands in the West (Follet et al. 2001). If carbon saturation is reached, rangelands and pasturelands have the potential to remove 198 million tons of carbon dioxide from the atmosphere each year for 30 years (Follet et al. 2001). However, rangelands dominated by cheatgrass have much less capacity to store carbon than do rangelands dominated by native perennials, and high-frequency fire in cheatgrass-dominated communities provides a frequent source of carbon to the atmosphere (Rau et al. 2011).

Risk Management and Wildland Fire Decisionmaking

Risk is a part of working with wildland fire. Risk is a two-dimensional measure that includes both the probability and magnitude of potential outcomes (Wildland Fire Leadership Council 2014). In recent years, wildland fire risk evaluations and decisionmaking have focused on determining the values affected positively and negatively by fire, and the probability or likelihood of the event occurring, and then identifying the possible mitigation or suppression actions needed. To meet these challenges, the National Cohesive Strategy Science Panel (Wildland Fire Leadership Council 2014) proposed the use of comparative risk assessment tools as a rigorous basis for analyzing response alternatives. Comparative risk assessment is a long-standing and mature scientific approach to qualifying risk that allows managers and stakeholders to explore the tradeoffs between alternative courses of action (Wildland Fire Leadership Council 2014).

Several datasets and assessment tools are available to assess risk and prioritize management actions. First, data have been generated for the National Cohesive Wildland Fire Management Strategy (Wildland Fire Leadership Council 2014). Second, there is a West-wide wildfire risk assessment (Oregon Department of Forestry 2013). Third, "A Wildfire Risk Assessment Framework for Land and Resource Management*"* (Scott et al. 2013) guides managers in creating their own risk assessment at the level of detail to match their situation. Finally, the USFS has developed a wildland fire risk potential map for the lower 48 States to highlight areas that have a higher probability of experiencing high-intensity fire (Dillon et al. 2015) (see figure 8.16 for fire risk potential for National Forests in the IAP region).

Figure 8.16—Data on wildland fire risk potential for each national forest in the Intermountain Adaptation Partnership region (data from Dillon et al. 2015). Areas with higher wildland fire risk values have a higher probability of experiencing high-intensity fire. Rounding errors result in totals different from 100 on some national forests.

Changing Socioeconomics of Fire

New residential construction continues to grow outside of communities into areas with higher risk of fire, expanding the wildland-urban interface (WUI). The presence of more homes in the WUI results in increased strain on fire responders and wildland fire management organizations. Fire suppression costs have increased steadily over the past 20 years. The annual cost of suppression reached $1 billion for the first time in 2000 and only barely dropped below that threshold twice in the following 14 years (Jeffrey 2015). The combination of increasing human populations and increasing fire area burned with warming climate is likely to lead to increased fire risk in the WUI and increased fire suppression costs. The path to avoiding the worst possible impacts of wildland fire may be for the public and governments at all levels to become more comfortable with prescribed fire, managed wildfire, and smoke, achieved in part with improved outreach and understanding of the ecological role of fire (USDA and DOI 2014).

Insects

Insect species, in general, have relatively short life cycles, high reproductive capacity, and a high degree of mobility, and thus the physiological responses to warming temperatures can produce large and rapid effects on species population dynamics (Stange and Ayres 2010). Climatic and atmospheric changes can impact biotic disturbances of forests via three general mechanisms: effects on the physiology of insects (direct); effects on tree defenses and tolerance (indirect); and effects on interactions between disturbance agents and their own enemies, competitors, and mutualists (indirect) (Weed et al. 2013). These direct and indirect effects of climate change on biotic disturbances are described next, along with species of insects important in the IAP region: Bark beetles, defoliators, and invasive insects.

Direct Effects of Climate on Insects

Warmer temperatures associated with climate projections will tend to impact (and frequently amplify) insect population dynamics directly through effects on survival, generation time, fecundity, and dispersal. High reproductive

potential, rapid evolution, and roles in food webs make insects a good model organism for understanding the effects of a changing climate. Mid- to high-latitudinal insect populations are anticipated to benefit from climate change through more rapid life cycle completion (see the *Expected Effects of Climate Change on Bark Beetle Outbreaks* subsection below) and increased survival. Insect mortality may decrease with warmer winter temperatures, thereby leading to higher-elevation and poleward range expansions (Stange and Ayres 2010).

Indirect Effects of Climate on Host Tree and Insect Interactions

Increased drought severity and frequency are likely to make forests more vulnerable to both direct (reduced growth and mortality) and indirect (insect outbreaks, pathogens, and wildfire) impacts (Dale et al. 2001; Kolb et al. 2016b; Schlesinger et al. 2016; Weed et al. 2013). A forest ecosystem can support an insect outbreak only if the preferred host species is available. Under drought conditions, plants may become more attractive to some insect herbivores, such as defoliators, because of the physiological response that increases concentration of nitrogen compounds and sugars in young plant tissue (McDowell et al. 2016). Most forest insects that cause damage to trees are monophagous (single host). Native insect communities will therefore follow forest communities. Consequently, as forests change (structure, type, and species diversity), so do their associated insect communities.

Bark Beetles

The scolytines (Coleoptera: Curculionidae, Scolytinae), or bark and ambrosia beetles (hereafter bark beetles), represent an ecologically and often economically important group of forest insects. Around 519 species occur north of Mexico in North America (Mercado 2011). Most of these species develop in the inner bark (their name is defined by their feeding niche). The eruptive nature of bark beetles allows populations to build rapidly, causing extensive tree mortality events. Several species, including the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), spruce beetle (*D. rufipennis* Engelm.), and Douglas-fir beetle (*Dendroctonus pseudotsugae*), have caused landscape-scale tree mortality events in the IAP region over the past decades (see following discussion).

The Ecological Role of Native Bark Beetle Disturbances

Both endemic and eruptive bark beetle population levels can affect important ecosystem processes, such as the allocation of water and nutrients within a stand or a watershed, as well as forest structure and composition (Collins et al. 2011; Mikkelson et al. 2013). Typically, endemic populations of bark beetles kill old, suppressed, or otherwise unhealthy host trees suffering some type of stress. Dead

trees provide food and a niche to other organisms, such as cavity-nesting birds and detritivores. When dead trees fall, younger or previously suppressed understory trees can respond to an increased availability of resources, including light, water, and nutrients. Nutrients and carbon return to the atmosphere and to the soil, where they are recycled by other plants; over time, there is no significant carbon stock change between bark beetle-disturbed or undisturbed stands (Hansen et al. 2015). Although the short-term effects of bark beetle-caused tree mortality bring change to the age structure of affected forests, the long-term effects can modify tree species composition in a forest (Amman 1977), altering diversity, and potentially resilience, in the face of a changing climate (Peterson et al. 1998). Native bark beetles are an important component of healthy and dynamic forest ecosystems. However, large mortality events are often considered undesirable when they conflict with human resource objectives and ecosystem services.

Population Dynamics of Eruptive Bark Beetles

During any given time, native bark beetles occur at different population levels within the range of their hosts. At low or endemic population levels, these insects usually lack the capacity to overwhelm the defenses of healthy trees; populations survive in susceptible trees experiencing abiotic or biotic stress factors. Stress factors, such as intertree competition (Fettig et al. 2007), pathogens (Goheen and Hansen 1993; Tkacz and Schmitz 1986), drought (Chapman et al. 2012; Hart et al. 2014), and moderate fire damage (Elkin and Reid 2004; Powell et al. 2012), can allow endemic beetle populations to successfully kill trees.

Given suitable stand conditions and susceptible landscapes, endemic populations of eruptive bark beetles can achieve exponential growth, affecting hosts at the landscape level in relatively short periods of time (Lundquist and Reich 2014; Safranyik et al. 2010). Large-scale epidemics can occur following inciting factors such as drought events, when large numbers of trees of suitable size become susceptible (Negrón 1998). Factors fostering epidemic population growth include: (1) an abundance of suitable hosts, (2) a predisposing condition, (3) a potent host attraction signal, (4) a strong intraspecific recruitment signal, (5) reduced competition and depredation during attack and establishment, (6) high nutrient availability, and (7) suitable temperatures for survival and life cycle completion.

Eruptive Bark Beetles in the IAP Region

Climate affects bark beetles directly and indirectly. Many bark beetle life history traits influencing population success are temperature dependent (Bentz and Jönsson 2015), and warming temperatures associated with climate change have directly fostered bark beetle-caused tree mortality in some areas of western North America (Safranyik et al. 2010; Weed et al. 2015a). Specific risk and hazard ratings that

incorporate stand- or tree-level metrics are available for several bark beetle species. Risk and hazard rating systems are a critical piece in assessing susceptibility to bark beetle-caused mortality. Indirect effects of climate change include impacts on host tree vigor and susceptibility to bark beetle attack (Chapman et al. 2012; Hart et al. 2014).

Although bark beetle mortality events occur every year in the IAP region, large-scale events for any one agent usually occur infrequently. Bark beetles causing landscape-level tree mortality include species in the genera *Dendroctonus*, *Ips*, *Scolytus*, and *Dryocoetes*. In the IAP region, several species have caused major tree mortality events in the past (table 8.4). The most recent large mortality event associated with mountain pine beetle occurred from 2001 to 2014 across the region, with a peak mortality of 4.5 million trees reported in 2010 (fig. 8.17a). Since the early 1990s, spruce beetle populations have been at outbreak levels at various locations throughout the region, with the greatest tree mortality reported in 2013 (fig. 8.17b). Douglas-fir beetle (fig. 8.17c) attacked Douglas-fir at outbreak levels for more than a decade, from 2000 until 2016, across the region. Two other species that recently have shown population increases in the region are pinyon ips and Jeffrey pine beetle (*Dendroctonus jeffreyi*). Pinyon engraver beetle, also known as pinyon *Ips,* had a spike in population in 2004 (2.9 million trees reportedly killed), when surveys concentrated on the pinyon habitat to document this mortality event (fig. 8.17d).

Expected Effects of Climate Change on Bark Beetle Outbreaks

Indirect Effects on Host Tree Susceptibility and Community Associates

Climate change will have indirect effects on bark beetle population outbreaks within the IAP region. Depending on future carbon dioxide emissions, annual precipitation is predicted to vary greatly across the IAP, ranging from a decrease of about 10 percent to an increase of nearly 30 percent, with a mean projected increase of 5 percent (RCP 4.5) and 8 percent (RCP 8.5) across the region (Chapter 3). With an associated increase in temperature, these precipitation changes suggest a decline in the snow-to-rain ratio for many forested areas in the region, with more precipitation falling as rain than snow (Gillies et al. 2012; Regonda et al. 2005). Interannual changes in snowpack can have significant effects on hydrological processes and ecosystem services (Chapter 13), in addition to effects on trees. Although insects are typically not directly influenced by precipitation, except during adult flight, changes in the timing and type of precipitation will have indirect effects on bark beetles through an influence on the suitability and spatial distribution of host trees. Tree physiological processes can be greatly affected by changes in the type and timing of precipitation.

Carbon-based compounds can be the main defense against bark beetles, and these defenses can be weakened when water availability is altered (Chapman et al. 2012; Gaylord et al. 2013; Hart et al. 2014). Water availability, however, has nonlinear impacts on carbon-based plant compounds (Kolb et al. 2016a). Mild or moderate drought that does not close stomata can increase carbon-based defenses as carbon produced during photosynthesis is shunted away from growth (Herms and Mattson 1992). But intense water stress can cause stomata to close to avoid excessive water loss. This causes a reduction in carbon-based defense compounds (i.e., terpenoids) through carbon starvation and hydraulic failure (McDowell et al. 2011).

Intense drought can also result in an induced production of certain volatile compounds, such as alcohols, that work as olfactory attractants to some bark beetles (Kelsey et al. 2014). Although trees in intense drought conditions may be more attractive and susceptible to bark beetles, low levels of nitrogen, carbohydrates, and phloem moisture could negatively affect developing brood by indirectly affecting the growth of blue-stain fungi (reviewed in Kolb et al. 2016a). Drought intensity and timing will therefore be important factors in predicting effects on bark beetle population success in the future. Moderate tree water stress can reduce bark beetle impact, and more severe water stress can be favorable for bark beetles and result in increased bark beetle-caused tree mortality. Species that are currently considered incapable of attacking live, healthy trees in some areas, including some *Ips* species, could become primary tree killers as their favored habitat increases.

Climate change may influence the frequency and intensity of inciting factors that can trigger bark beetle population outbreaks. An increase in tree fall from wind events could provide a reservoir of favorable habitat of stressed or damaged trees used by some bark beetle species (e.g., spruce beetle), allowing them to surpass the endemic-epidemic threshold (Jenkins et al. 2014). In addition, community associates important to bark beetle population success, including fungi, natural enemies, and competitors, could also be influenced by climatic changes, with both positive and negative indirect effects on bark beetle population outbreaks (Addison et al. 2013; Kalinkat et al. 2015).
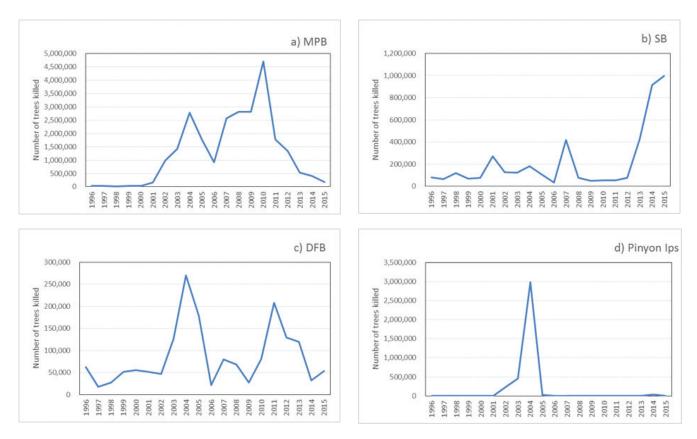
Direct Effects on Overwinter Survival

Within the IAP region, projected changes in temperature by the 2040–2060 period range between 2 and 8 °F (Chapter 3). Generally, increasing minimum temperatures will result in increased winter survival for most species, and could result in range expansion, both northward and upward in elevation. All insect species within the IAP region will be affected. For example, *Ips lecontei* populations became more active at higher elevations during the early 2000s, when both winter and summer temperatures increased (Williams et al. 2008). Across mountain pine beetle habitats in the western United States from 1960 to 2011, minimum temperatures increased 6.5 °F. This increase in minimum temperature resulted in a decrease in winter larval mortality and a subsequent increase in beetle-caused tree mortality

Table 8.4—Major bark beetle species affecting trees in the IAP region. Inciting factors associated with climate change effects are listed with supporting literature.

Bark beetle	Subregions affected[a]	Host tree	Inciting factors for outbreaks	Supporting literature
Douglas-fir beetle (*Dendroctonus pseudotsugae*)	All	Douglas-fir	Drought intensity and timing Defoliation events Little known on direct effects of temperature Fire Stand conditions	Cunningham et al. 2005; Furniss 1965; Hadley and Veblen 1993; Hood et al. 2007; McDowell et al. 2011; Negrón et al. 2014
Mountain pine beetle (*D. ponderosae*)	All	Limber pine, ponderosa pine, lodgepole pine, whitebark pine, sugar pine and western white pine	Drought intensity and timing Temperature warming can reduce development to univoltine at highest elevations Stand conditions	Bentz and Powell 2014; Bentz et al. 2010, 2014, 2016; Fettig et al. 2007
Spruce beetle (*D. rufipennis*)	1, 2, 3, 4, 6	Engelmann spruce, blue spruce, lodgepole pine (rarely; recent regional occurrences)	Wind events Temperature warming can reduce development to univoltine at highest elevations	Bentz et al. 2010, 2016; Holsten et al. 1999
Western pine beetle (*D. brevicomis*)	1, 4, 5, 6	Ponderosa pine	Drought intensity and timing Warming temperatures can increase development to multivoltine Fire Stand conditions	Fettig et al. 2008; Furniss and Johnson 2002; Miller and Keen 1960; Miller and Patterson 1927; Negrón et al. 2009
Jeffrey pine beetle (*D. jeffreyi*)	5	Jeffrey pine	Little known on direct effects of temperature Fire Stand conditions	Bradley and Tueller 2001; Maloney et al. 2008
Fir engraver (*Scolytus ventralis*)	All	Grand fir, white fir, subalpine fir (occasionally)	Drought timing and intensity Defoliation events Temperature warming can reduce development to univoltine at highest elevations Fire Stand conditions	Bentz et al. 2010, 2016; Ferrell 1986; Fettig et al. 2008; Maloney et al. 2008; Schwilk et al. 2006
Western balsam bark beetle (*Dryocoetes confusus*)	All	Subalpine fir, grand fir and white fir (occasionally)	Drought intensity and timing Root diseases, fungal pathogens Wind events Temperature warming can reduce development to univoltine at highest elevations Stand conditions	Bentz et al. 2010, 2016; McMillin et al. 2003
Pine engraver beetle (*Ips pini*)	All	Lodgepole pine, ponderosa pine, Jeffrey pine	Drought intensity and timing Wind events Warming temperatures can increase multivoltiism Stand conditions	Kegley et al. 1997; Negrón et al. 2009

Table 8.4—*Continued*.

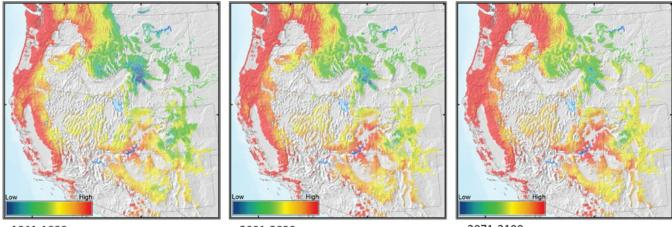| Bark beetle	Subregions affected[a]	Host tree	Inciting factors for outbreaks	Supporting literature
Spruce engraver beetle (*I. pilifrons*)	All	Spruce	Little known on direct effects of temperature Wind events	Forest Health Protection 2011
Pinyon Ips (*I. confusus*)	3, 4, 5, 6	Singleleaf pinyon pine, two-needle pinyon pine	Drought intensity and timing Dense stands Mistletoe infections	Gaylord et al. 2015; Kleinman et al. 2012; Negrón and Wilson 2003; Shaw et al. 2005
Roundheaded pine beetle (*D. adjunctus*)	4, 5	Ponderosa pine	Little known on direct effects of temperature Drought effects on growth	Negrón et al. 2000

[a]Subregions include: (1) Middle Rockies, (2) Southern Greater Yellowstone, (3) Uintas and Wasatch Front, (4) Plateaus, (5) Great Basin and Semi Desert, (6) Intermountain Semi Desert.

Figure 8.17—Number of trees killed by (a) mountain pine beetle (MPB), (b) spruce beetle (SB), (c) Douglas-fir beetle (DFB), and (d) pinyon ips in the U.S. Forest Service Intermountain Region, 1996–2015. Data are from Aerial Detection Surveys 1996–2015, Intermountain Region, Forest Health Protection.

in some areas. Areas that were historically the coldest showed the greatest increase in tree mortality with warming temperatures (Weed et al. 2015b). Similarly, within the IAP region, winter warming in recent years resulted in increased beetle-caused tree mortality in the subregions that were previously the coldest: the Middle Rockies and Southern Greater Yellowstone subregions (Weed et al. 2015b). Future projections also suggest an increase in mountain pine beetle

cold-temperature survival across most IAP subregions, although elevations greater than about 7,800 feet in the Southern Greater Yellowstone subregion remain cold enough for continued low predicted winter survival (Bentz et al. 2010) (fig. 8.18).

Survival will also be complicated by other factors. Bark beetles time their development to reduce cold-caused mortality using several strategies that include developmental

Figure 8.18—Predicted probability of cold survival for mountain pine beetle in pine forests of the western United States during three climate normal periods: 1961–1990, 2001–2030, and 2071–2100. Model results are shown only for areas estimated to be 20th-century spruce habitat (sensu Little [1971]). See Bentz et al. (2010) for a description of the mountain pine beetle model and temperature projections used to drive the model.

thresholds, diapause, and cold hardening (Bentz and Jönsson 2015). Specific thresholds and induction temperatures vary among the species. Therefore, effects of changing temperature will depend on the beetle species, as well as the seasonal timing, amount, and variability of thermal input, as dictated by geographic location.
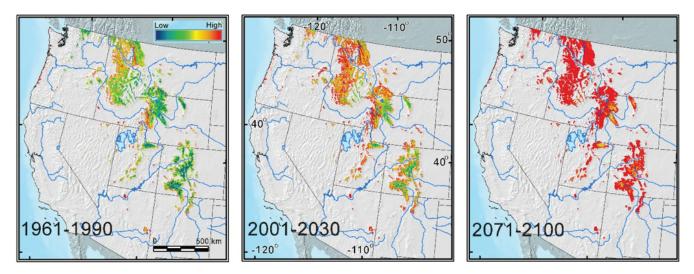
Although winter warming will generally be beneficial for bark beetles, extreme within-year variability in winter warming could be detrimental to insect survival. Bark beetles metabolize supercooling compounds as temperatures decrease and catabolize compounds as temperatures warm (Bentz and Mullins 1999). Large temperature fluctuations could result in excessive metabolic investment in maintaining appropriate levels of antifreeze compounds, leaving individuals with minimal energy stores at the end of winter. In addition, many bark beetle species overwinter at the base of tree boles, garnering protection from predators and excessive cold temperatures when insulated beneath snow. Reduced snow levels associated with winter warming, and the fact that precipitation will be more likely to fall as rain than snow, could add to increased overwinter mortality.

Direct Effects on Generation Time

In addition to winter warming, projected warming at other times of the year will also directly influence bark beetles within the IAP region. But warming temperatures will not provide a direct and linear response in population increases. Changing temperature regimes can either promote or disrupt bark beetle temperature-dependent life history strategies that drive seasonality and length of a generation. Generally, an increase in the number of generations produced in a year increases tree mortality (Bentz et al. 2010). Voltinism is the number of generations that can be produced in a single year. Within the IAP region, bark beetle species are multivoltine (more than two generations in a year), bivoltine (two generations in a year), univoltine (one generation in a year),

or semivoltine (one generation every 2 years), depending on the species, location, and annual thermal input (Bentz et al. 2014; Furniss and Johnson 2002; Hansen et al. 2001; Kegley et al. 1997). As mentioned, generation timing must be appropriately timed with the seasons to avoid excessive winter mortality, in addition to maintaining synchronized adult emergence that facilitates mass attacks on trees (Bentz and Powell 2015). Seasonality strategies, such as developmental thresholds and diapause, are used in this process. Thermal warming in some habitats may allow a reduction in generation time that also maintains seasonality. Other thermal regimes, however, could disrupt diapause and thermal thresholds and hence seasonality (Régnière et al. 2015). Because temperature varies with topography, latitude, and elevation, insect response to warming will also vary across landscapes, with both positive and negative effects on population growth (Bentz et al. 2016).

At the highest elevations within the IAP region, spruce beetle, mountain pine beetle, fir engraver (*Scolytus ventralis*), and western balsam bark beetle (*Dryocoetes confusus*) are generally semivoltine, although in warm years and at lower-elevation sites, populations of these species develop on a univoltine life cycle (Bentz et al. 2014; Hansen 1996; Hansen et al. 2001). Projected warming temperatures through 2100 are predicted to reduce generation time (i.e., from semivoltine to univoltine) at the highest elevations within the IAP region for both mountain pine beetle and spruce beetle (Bentz et al. 2010, 2016) (fig. 8.19). Warming temperatures, however, could also potentially disrupt population success at middle elevations when diapause and development thresholds are disrupted in altered thermal regimes (Bentz et al. 2016; Hansen et al. 2001).

Within the IAP region, western pine beetle (*Dendroctonus brevicomis*) and *Ips* species have developmental thresholds that allow for bivoltinism and multivoltinism (Furniss and Johnson 2002), and warming

Figure 8.19—Predicted probability of spruce beetle developing in a single year in spruce forests in the western United States during three climate normal periods: 1961–1990, 2001–2030, and 2071–2100. Higher probability of 1-year life cycle duration translates to higher probability of population outbreak and increased levels of tree mortality. Model results are shown only for areas estimated to be 20th-century spruce habitat (sensu Little [1971]). See Bentz et al. (2010) for a description of the spruce beetle model and temperature projections used to drive the model.

temperatures could allow these species to have additional generations in a single year. Bivoltinism of other species that are adapted to cooler temperatures at higher elevations, including mountain pine beetle and spruce beetle, has been limited historically due to diapause and thermal threshold constraints (Bentz and Powell 2014; Hansen et al. 2011; but see Mitton and Ferrenberg 2012). Although temperatures at the lowest elevations (less than 4,000 feet) are projected to warm enough in the next 30 years to produce bivoltine mountain pine beetle populations that are timed appropriately for population success, thermal requirements for bivoltinism will remain generally unmet at locations greater than 4,000 feet (Bentz et al. 2016).

By the end of the century, however, under the warmest emissions scenario (RCP 8.5), portions of the Middle Rockies subregion are predicted to support moderate levels of bivoltine mountain pine beetle populations (Bentz et al. 2016). As temperatures warm in the Plateaus subregion of southern Utah, a complex of bark beetle species (e.g., mountain pine beetle, roundheaded pine beetle [*Dendroctonus adjunctus*], western pine beetle, *Ips* spp.) that infest relatively low-elevation ponderosa pine may also have the potential for a reduction in generation time and an increase in the length of biological activity (i.e., flight initiation and cessation) (Gaylord et al. 2008; Williams et al. 2008).

Douglas-fir beetle, Jeffrey pine beetle, red turpentine beetle (*Dendroctonus valens*), and roundheaded pine beetle are all considered univoltine within current IAP region climates. Although we do not know enough about thermally dependent traits for these species to quantify predictions, warming temperatures could result in outcomes similar to those for mountain pine beetle and spruce beetle. Additional partial generations that could be disruptive to population success could occur. Alternatively, if temperatures warm

sufficiently, bivoltine populations that are timed appropriately could enhance population success. Two generations rather than one generation in a single year could result in a doubling of beetle-caused tree mortality in a given year. But some species, such as Douglas-fir beetle and spruce beetle, may not be able to produce two generations in a year due to a required adult winter resting state, or diapause (Bentz and Jönsson 2015). More information is needed on the physiological strategies of these species to better understand the potential for beetle population growth in a changing climate.

Summary

The impact of climate change on bark beetle-caused disturbance patterns will be complex. Temperature-dependent life history strategies that facilitate population success and promote outbreaks have evolved through local adaptation (Bentz et al. 2011). Although bark beetle populations can absorb relatively small changes in temperature and remain successful, as seen in the past decade, changes projected throughout the century for the IAP region may surpass existing phenotypic plasticity in traits. Adaptation to new thermal regimes will be required. Due to local adaptations, population irruptions will be specific for a species and geographic location, although some generalizations can be made. Increasing minimum temperatures are likely to benefit all bark beetle species in cold habitats within the IAP region, probably resulting in increased tree mortality. This effect, however, will be influenced by thermal changes at other times of the year. Warming at other times of the year could reduce generation time and length of adult flight, but also potentially disrupt evolved strategies, resulting in poor population performance and reduced tree mortality. Averaged across the IAP region, precipitation is projected to increase. The timing and type of precipitation (i.e., rain

rather than snow), however, will greatly influence tree defense against bark beetle attacks, and the response is likely to be nonlinear. Alterations in water availability that result in moderate water stress can reduce bark beetle performance, whereas more severe water stress can be favorable for bark beetles and result in increased bark beetle-caused tree mortality.

Evaluating future disturbance patterns of native bark beetles in the context of management will benefit from an understanding of changes in future patterns relative to current and historical patterns. Climate change may result in a shift in the severity, location, and particular species of bark beetle responsible for tree mortality. A mechanistic understanding of the influence of temperature on important bark beetle life history traits, as is available for mountain pine beetle, will be required to predict population success in future climates. Moreover, climate has direct effects on both the host tree and the beetle, and models that integrate our understanding of the influence of climate on host trees and beetle populations are needed.

Defoliators

Introduction

Tree folivores are found in many insect orders, with most of the important defoliating insects in western North America occurring in a variety of Lepidoptera families (butterflies and moths); Hymenoptera, particularly Diprionidae (sawflies); and Hemiptera (aphids and scales). The most important native insect defoliators in the IAP region are western spruce budworm (*Choristoneura occidentalis* [Lepidoptera: Tortricidae]), Douglas-fir tussock moth (*Orgyia pseudotsugata* [Lepidoptera: Erebidae]), and pine butterfly (*Neophasia menapia* [Lepidoptera: Pieridae]) (table 8.5). The biology, population dynamics, and outbreak regimes of defoliating insects vary considerably because of this taxonomical diversity.

The Ecological Role of Native Defoliator Disturbances

Western Spruce Budworm

Western spruce budworm defoliation affects cone production, understory regeneration, and tree growth and survival. Effects on stand structure include reducing shade-tolerant host abundance, lowering stand densities, increasing mean tree diameter, and creating more open stands with a greater prevalence of nonhost and more fire-adapted tree species, particularly pine (Carlson et al. 1983; Fellin et al. 1983; Ferguson 1985; Johnson and Denton 1975). Budworm defoliation on large trees increases vulnerability to bark beetles, particularly Douglas-fir beetle, which may increase outbreak likelihood of that insect (Lessard and Schmid 1990; Negrón 1998; Schmid and Mata 1996).

Tree-ring studies indicate that western spruce budworm has coexisted with and developed outbreaks in host forests for centuries (Lynch 2012). Historically, western spruce

budworm defoliation and more frequent wildfire resulted in lower stand densities, less susceptibility to western spruce budworm, and greater landscape patchiness. However, fire exclusion favors increased host species abundance and multistoried stands. Fire exclusion has resulted in extensive landscapes of suitable host type throughout the IAP region, and impacts associated with prolonged defoliation on larger landscapes may be more severe (Hadley and Veblen 1993; Johnson and Denton 1975; Swetnam and Lynch 1989, 1993).

Douglas-Fir Tussock Moth

Douglas-fir tussock moth contributes to structuring forest communities and to the stability of forest systems through its effects on tree growth and survival, species composition, forest heterogeneity, and succession (Mason and Wickman 1991; Wickman et al. 1973). After outbreaks, understory vegetation and plant forage biomass increase considerably, and shade-tolerant herbaceous species decline (Klock and Wickman 1978).

Tussock moth outbreaks may cause an increase in bark beetle activity, similar to drought, blowdown, and avalanches. Bark beetle- and tussock moth-related mortality affect different tree size classes, and thus dissimilarly affect post-outbreak stand structure (Negrón et al. 2014). Douglas-fir tussock moth outbreaks can completely defoliate host trees in 1 to 3 years and cause subsequent tree mortality by Douglas-fir beetle and fir engraver attacks. Severe defoliation may significantly suppress tree growth for up to 4 years after an outbreak (Mason et al. 1997). Surviving tree growth and recruitment often increase following an outbreak (Klock and Wickman 1978; Wickman et al. 1973, 1986).

Pine Butterfly

Tree survival is generally high during severe pine butterfly outbreaks (Hopkins 1907; Scott 2012) unless western pine beetle activity increases significantly, killing stressed trees (Evenden 1936, 1940; Helzner and Thier 1993; Hopkins 1907; Scott 2012; Thier 1985). Pine butterfly prefers old foliage and begins feeding at the time of bud break (Evenden 1926, 1936). Although feeding has a severe impact on tree growth (Cole 1966; Dewey et al. 1973; Evenden 1936; Helzner and Thier 1993), production of new foliage usually enables trees to take up nutrients and survive. Pine butterfly may affect wildlife populations. For example, an absence of songbirds and bats has been noted during pine butterfly outbreaks (Scott 2010, 2012; Stretch 1882), although information about explanatory factors and seasonality is lacking.

Population Dynamics of Defoliators

Abundance, condition, and distribution of host foliage in the forest canopy as buds, new foliage, and old foliage of different tree species, as well as complexity of stand structure, influence defoliator regimes. Climate and host

Table 8.5—Major defoliating insect species affecting trees in the IAP region. Inciting factors for outbreaks, including stand susceptibility, are listed with supporting literature.

Defoliator	Subregions affected[a]	Host trees	Factors affecting outbreaks	Supporting literature
Western spruce budworm (*Choristoneura occidentalis*)	All	Douglas-fir, grand fir, subalpine fir, white fir, western larch, Engelmann spruce	Climatic suitability Susceptible host availability Forest structure: multi-storied and high density stands Altered fire regimes (fire intolerant and shade tolerant host species) Parasites and predators	Beckwith and Burnell 1982; Campbell 1993; Carlson et al. 1983; Chen and others 2003; Hadley and Veblen 1993; Johnson and Denton 1975; Fellin and Dewey 1986; Fellin et al. 1983; Maclauchlan and Brooks 2009; Morris and Mott 1963; Mott 1963; Nealis 2008; Shepherd 1992; Volney 1985
Douglas-fir tussock moth (*Orygia pseudotsugata*)	1, 3, 5	Douglas-fir, grand fir, white fir, and subalpine fir	Nuclear polyhedrosis virus (NPV) Other mortality agents Significant variability in triggers Host availability (regional variances) Outbreak control largely unknown Climatic suitability unknown Fire exclusion Forest structure: older (>50 years), multi-storied, dense stands Warm, dry sites Increased susceptibility to bark beetles (see fir engraver beetle and Douglas-fir beetle)	Alfaro et al. 1987; Beckwith 1978; Campbell 1978; Coleman et al. 2014; Dahlsten et al. 1977; Hansen 1996; Huber and Hughes 1984; Ignoffo 1992; Jaques 1985; Killick and Warden 1991; Mason 1976, 1996; Mason and Luck 1978; Mason and Wickman 1991; Mason et al. 1997; Moscardi 1999; Negrón et al. 2014; Shepherd et al. 1988; Stoszek et al. 1981; Thompson and Scott 1979; Thompson et al. 1981; Vezina and Peterman 1985; Weatherby et al. 1992, 1997; Wickman 1963, 1978a,b; Wickman et al. 1973, 1981, 1986; Wright 1978
Pine butterfly (*Neophasia menapia*)	1, 3, 4, 5	Ponderosa pine	Host availability Logging history and fire exclusion Parasitic and predatory controls on pine butterfly populations (i.e., Theronia atalantae) Climatic suitability unknown Abiotic and biotic controls on *T. atalantae* See western pine beetle in table 8.4	Agee 2002; Aldrich 1912; Campbell 1963; Cole 1956; DeMarco 2014; Dewey and Ciesla 1972; Dewey et al. 1973; Di Giovanni et al. 2015; Ehle and Baker 2003; Evenden 1936, 1940; Helzner and Their 1993; Hopkins 1907; Huntzinger 2003; Kerns and Westlind 2013; Lazarus 2012; Orr 1954; Scott 2010, 2012; Stretch 1882; Thier 1985; Weaver 1961; Webb 1906

[a] Subregions include: (1) Middle Rockies, (2) Southern Greater Yellowstone, (3) Uintas and Wasatch Front, (4) Plateaus, (5) Great Basin and Semi Desert, (6) Intermountain Semi Desert

abundance are important factors controlling defoliator regimes. Climate affects host susceptibility (indirect effect) and insect distributions (indirect and direct effects), as well as seasonal and annual variation in insect abundance (indirect and direct effects).

Defoliator Outbreaks in the Intermountain Adaptation Partnership Region

Both western spruce budworm and Douglas-fir tussock moth inhabit Douglas-fir, true fir, and mixed conifer stands in the IAP region. The areas with historical defoliation generally reflect the known distribution of western spruce budworm (Harvey 1985; Lumley and

Sperling 2011) and Douglas-fir tussock moth (Beckwith 1978; Shepherd et al. 1988), although western spruce budworm is known to occur in eastern Nevada (Lumley and Sperling 2011). Ranges and host species preferences for western spruce budworm and Douglas-fir tussock moth populations overlap considerably and are regulated by complex factors that are likely to respond differently to climate change.

Western Spruce Budworm

Extensive western spruce budworm outbreaks occur episodically (Fellin et al. 1983; Lynch 2012), and the IAP region is in the early stages of the third extensive outbreak since the 1920s (Johnson and Denton 1975) (fig. 8.20).
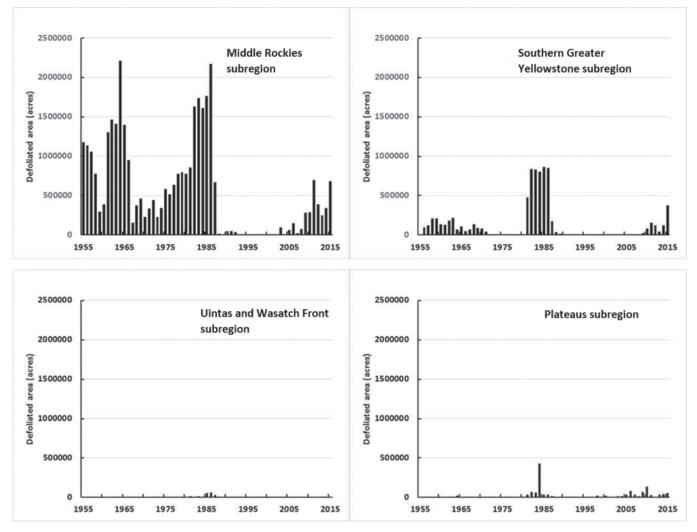
Douglas-Fir Tussock Moth

In the IAP region, Douglas-fir tussock moth outbreaks occur at the landscape scale in the Middle Rockies subregion. They are smaller but more frequent in the Great Basin. The insect has a more restricted range than its

hosts (Beckwith 1978; Mason 1996; Mason and Wickman 1991). The early 1990s outbreak in the Middle Rockies was more extensive and severe than previously recorded outbreaks (Weatherby et al. 1997) (fig. 8.21).
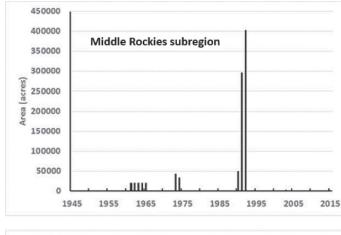
Outbreaks occur regularly in many areas, including the Great Basin (fig. 8.21), and are often synchronous across distant portions of western North America (Mason and Luck 1978; Shepherd et al. 1988; Wickman et al. 1981). Outbreaks develop from increasing local populations over a 1- to 3-year period before reaching outbreak status (Daterman et al. 2004; Shepherd et al. 1985). In most areas, outbreaks occur with a 7- to 10-year cycle. Outbreaks usually last 2 to 4 years and collapse abruptly. Between outbreaks, tussock moth populations are often at undetectable levels (Daterman et al. 2004; Mason 1974; Mason and Luck 1978; Shepherd et al. 1988).
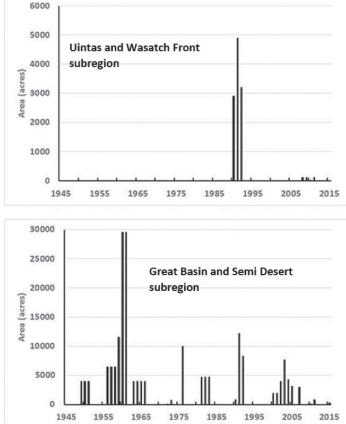
Pine Butterfly

Pine butterfly is the most damaging defoliator of ponderosa pine (Furniss and Carolin 1977). Outbreaks vary

Figure 8.20—Area defoliated by western spruce budworm in four subregions of the Intermountain Adaptation Partnership region, 1955–2015. Johnson and Denton (1975) also documented an extensive but unquantified outbreak in the 1920s in the Greater Yellowstone Area.

Figure 8.21—Area defoliated by Douglas-fir tussock moth in three subregions of the Intermountain Adaptation Partnership region, 1945–2015. A 500-acre area of Fishlake National Forest in south-central Utah was also defoliated in 1999–2000.

considerably in size and intensity, and can be severe in the Middle Rockies subregion (Cole 1956; Evenden 1940; Orr 1954; Scott 2010, 2012). Though outbreaks have serious ecological consequences, pine butterfly ecology is poorly understood.

Non-outbreak cycles often go unnoticed as the insect prefers the tops of large trees, which are poorly visible from

the ground. Light and moderate damage is difficult to detect during aerial surveys because pine butterfly feeds on new foliage only when population densities are high (Helzner and Thier 1993; Orr 1954; Stretch 1882) and is a neat feeder (Evenden 1926; Scott 2012; Stretch 1882). Thus, dead and dying foliage is inconspicuous and damage is obscured by new foliage (Helzner and Thier 1993; Lazarus 2012; Orr 1954; Scott 2012).

Potential Future Effects of Climate Change on Defoliator Outbreaks

Temperature effects on insect biology and population dynamics have not been quantified in natural systems for most defoliating species, though laboratory and field studies provide some information. The seasonality and effects of extreme events are often known to some degree, and general projections can be made for some species about the potential effects of climate change.

Western Spruce Budworm

Climate change will have direct and indirect effects on western spruce budworm outbreaks. Temperature affects budworm developmental rates, dispersion, feeding, fecundity, and survival (Carlson et al. 1983; Kemp et al. 1985; Volney et al. 1983), but these relationships are not well understood. With warming, higher-elevation habitats are likely to support more frequent or severe outbreaks than they have in the past. However, more frequent late-spring frosts or more variability in frost timing would diminish outbreak frequency, extent, and severity by reducing populations. Severe defoliation can trigger Douglas-fir beetle and spruce beetle outbreaks in Douglas-fir and spruce-fir forests, respectively (Johnson and Denton 1975; McGregor et al. 1983; O'Connor et al. 2015). Changing temperature and precipitation regimes will influence the occurrence and spatial distribution of host species, thereby affecting western spruce budworm abundance. Combined effects of climate change and resource management activities, particularly those associated with fire management, are likely to determine forest condition and susceptibility to western spruce budworm.

Weather conditions that negatively affect western spruce budworm population dynamics include warm fall or winter temperatures, which result in (1) overwintering larvae metabolizing at a higher rate and depleting energy reserves (Carlson et al. 1983; Régnière et al. 2012; Thomson 1979; Thomson et al. 1984); (2) frost after budworm emergence from overwintering hibernacula (Carlson et al. 1983; Thomson 1979); (3) rain during larval dispersal or adult flight (Beckwith and Burnell 1982); and (4) unusually cool spring and early summer conditions that slow budworm development (Carlson et al. 1983; Thomson 1979). Factors that slow budworm development increase larval exposure to parasites and predators and may disrupt synchrony between larvae and buds or expanding needles. However, adverse weather events may only temporarily suppress budworm populations if forest stand conditions and subsequent

weather still favor budworm dynamics (Fellin and Dewey 1986; Johnson and Denton 1975).

Weather affects budworm and host biological processes that govern budworm population rates of change (Nealis 2008; Volney 1985), such as (1) the degree of synchrony between springtime emergence and host foliage development; (2) energy reserves available for dispersal and establishment at feeding sites after spring emergence; (3) the quality, quantity, and spatial distribution of foliage; (4) long-distance dispersion of adults; and (5) the lack of adverse weather events during dispersal and development. Budworms emerging from overwintering sites may more often encounter host buds and needles in suitable phenological condition in stands composed of several hosts (Volney et al. 1983). The effect of climate change on the complexities of budworm phenology are difficult to predict but will play a significant role in future population dynamics.

Budworm populations are likely to persist during years or decades of less suitable host phenology and then develop outbreaks when host foliage phenology is favorable. Compared to other *Choristoneura* species in western North America, western spruce budworm is associated with relatively warm interior and lower latitude forests (relative to the boreal zone) (Fellin et al. 1983; Harvey 1985; Kemp et al. 1985; Lumley and Sperling 2011; Stehr 1967). It incurs outbreaks as far south as southern New Mexico, and is well adapted to a wide variety of montane situations, including climates warmer than historical climates in the Middle Rockies. Many species of *Choristoneura* in western North America hybridize readily (Harvey 1985; Lumley and Sperling 2011; Nealis 2005; Volney 1989), so new western spruce budworm strains could develop rapidly in new climatic regimes and host species mixtures (Lumley and Sperling 2011; Volney and Fleming 2007).

Several factors make it unlikely that western spruce budworm will be lost from IAP region montane forests, excepting possible retraction at lower elevations and latitudes through the effects of warm winters on larval metabolism and energy reserves. Western spruce budworm outbreaks occur on many conifer species, and the species inhabits forests that vary widely in moisture and temperature regime. Populations encounter a wide range of foliage phenological patterns, so new host species mixtures and altered spring phenological patterns are likely to still be suitable to some extent. Furthermore, at stand and regional levels, western spruce budworm populations can exhibit considerable variation in the heating required for springtime emergence in both single- and multi-species stands (Volney et al. 1983). Although synchrony with bud development may be important for outbreak development, sufficient individuals emerge over a long enough time period to ensure that populations persist when synchrony is poor (Nealis 2012; Reichenbach and Stairs 1984; Volney et al. 1983).

Douglas-Fir Tussock Moth

The influence of climate in regulating Douglas-fir tussock moth populations is unknown and uncertain (Mason 1976,

1996; Mason and Wickman 1991; Shepherd et al. 1988; Vezina and Peterman 1985; Weatherby et al. 1997; Wickman et al. 1973). The role of climate in determining the distribution, frequency, extent, and severity of Douglas-fir tussock moth outbreaks is likely to be indirect. Douglas-fir tussock moth does not attain outbreak status over its entire range and is absent over large portions of host ranges (Beckwith 1978; Daterman et al. 1977; Mason and Luck 1978). Where present, cyclic populations are primarily regulated by nuclear polyhedrosis virus, a viral entomopathogen (Shepherd et al. 1988; Wickman et al. 1973).

The diversity of acceptable and preferred hosts, as well as an evolutionary history of distant races adapting to various host species, indicates that Douglas-fir tussock moth is adaptable to the changes in tree species composition and distribution that are likely to occur with climate change. Outbreaks in mixed-species stands can alter tree species composition, but fire exclusion practices favor increased host species abundance (Wickman et al. 1986). Mortality may be greater with warming temperatures because of the association between Douglas-fir tussock moth outbreaks and warm dry sites (Mason and Wickman 1991), and the combined effects of drought and defoliation on bark beetle activity. Effects of resource management on fire regimes, species composition, stand density, and canopy structure are likely to be stronger determinants of Douglas-fir tussock moth outbreak regimes than climate.

Pine Butterfly

The biology, ecology, and factors regulating populations of pine butterfly are not sufficiently understood to predict its response to a warmer climate. Indications regarding whether there are climatic limitations to pine butterfly outbreak dynamics are meager and contradictory. Outbreaks are more frequent and severe on ponderosa pine in the IAP region (Fletcher 1905; Furniss and Carolin 1977; Hopkins 1907; Ross 1963; Scott 2012). However, outbreaks can occur in relatively cool, mesic climates throughout its range, on a variety of acceptable hosts (virtually all western pine species plus Douglas-fir) that occupy a wide variety of thermal habitats (Hopkins 1907; Stretch 1882). Pine butterfly outbreaks also occur in semiarid pinyon-juniper forests in Colorado (Scott 2010; Young 1986). Thus, pine butterfly is not limited to a narrow thermal zone.

Pine butterfly exhibits some flexibility in its seasonal life history, indicating that a warmer climate may not directly diminish future outbreak frequency or severity. Egg eclosion and adult emergence vary with elevation, aspect, and weather (Evenden 1926, 1936; Scott 2012), and in some cases there may be two emergence periods (Bell 2012; Shellworth 1922). In some places, sympatric allochronic populations produce two broods, where each brood is produced from a univoltine life cycle but they emerge at different times, and interbreeding between the two broods is limited (Bell 2012). It is unknown why pine butterfly outbreaks occur in some portions of the host type but not others. The implications of variability in seasonal life history for population

dynamics under a warmer climate are unknown, because of the lack of information about the factors regulating pine butterfly outbreak dynamics. However, pine butterfly outbreaks combined with drought can increase western pine beetle populations on susceptible landscapes. Thus, under a warming climate on susceptible landscapes, more frequent or severe drought periods, combined with tree stress caused by significant or repeated defoliation events, are likely to increase western pine beetle populations and their impacts.

Invasive Insects

Overview

Influences of climate change on invasive insects are likely to depend on host abundance and shifts in hosts. Most non-native invasive insect species in the Intermountain West have not fully populated their potential range. Additionally, invasive species impacts on ecosystems may differ with changing climates. Examples of invasive insect invasions currently affecting National Forests of the IAP region may provide some insight into ecosystem changes that may occur under climate change and when introductions of other invasive insects occur. Adaptive management will be key as more is learned about introduced species.

Effects of Climate Change on Invasive Insect Species

Warmer temperatures can accelerate the development rates of invasive insects, as for native insect species, and increase or decrease overwintering brood survival (see section below). Increased brood production may hasten range expansion once established. For example, balsam woolly adelgid (*Adelges piceae*), an invasive insect, has been affecting eastern North American fir (*Abies* spp.) since 1900 and western coastal fir since the 1920s. It was discovered in northern Idaho in 1983 (Livingston et al. 2000). During the early 2000s, balsam woolly adelgid expanded its range across the Middle Rockies and into the Southern Greater Yellowstone subregion, and in 2017, it was found in Utah. It is expected to continue to expand its range south and east, causing widespread mortality of true fir (Hrinkevich et al. 2016; Lowrey 2015a).

Winter temperature is likely to be an important factor determining the future distribution of balsam woolly adelgid (Greenbank 1970). Quiring et al. (2008) found that a mean January temperature of 12 °F explained presence or absence of balsam woolly adelgid infestation of balsam fir (*A. balsamea*) in New Brunswick. Surveys suggest a similar threshold in lower latitudes for subalpine fir in the Middle Rockies subregion (Lowrey 2015a). At present, some areas of the IAP region reach the cold threshold affecting balsam woolly adelgid populations, thus reducing impacts and subsequent mortality in those locations (Lowrey 2015a). As mean winter temperatures increase, however, these formerly unsuitable sites may favor balsam woolly adelgid survival and establishment (Lowrey 2015b). As a result of a warming

climate, balsam woolly adelgid may invade fir stands at all elevations throughout Utah, Colorado, and Wyoming in the coming decades, potentially affecting species viability and ecosystem function.

Larch casebearer (*Coleophora laricella*) was first reported in mixed conifer forests of the Middle Rockies in 1977 (Valcarce 1978). Host abundance, climate suitability, and lack of natural enemies resulted in successful establishment and range expansion of the larch casebearer into the IAP region. Larch casebearer parasitoids were introduced into southern Idaho in 1978 as a biological control program release (Valcarce 1978). Larch casebearer populations are often kept at tolerable levels with introduced biological control agents (parasitic wasps), native predators and parasitoids, and adverse weather conditions (Miller-Pierce et al. 2015). Changing temperature and precipitation regimes could influence range expansion and impacts, with host shifts and parasitoid synchrony affecting population abundance and effectiveness.

In 2006, invasive poplar scale (*Diaspidiotus gigas*) was found on *Populus* species in Sun Valley, Idaho, and in Colorado (Vail, Aspen) (Progar et al. 2011). Infestations are associated with urban aspen forests, but expansion into forest environments and on other poplar species is probable. Host abundance and quality, conducive weather conditions, and native predators affect population viability (Progar et al. 2014). Recently identified nonnative parasitoid wasps could be used in future suppression programs if populations become damaging to nonurban aspen.

Spruce aphid (*Elatobium abietinum*) is a non-indigenous species that has a high likelihood of incurring outbreak status in the IAP region in a warmer climate. This insect has already altered natural disturbance regimes in southwestern spruce-fir forests (Lynch 2009; O'Connor et al. 2015). Spruce aphid was introduced to Pacific Northwestern coastal forests in the early 1900s, and to Southwestern montane forests in the 1970s (Lynch 2014). Temperature regimes in Intermountain high-elevation forests are comparable to those in areas where spruce aphid and the original host are native (Alexander and Shepperd 1990; Mäkinen et al. 2003; Vygodskaya et al. 1995; Weed et al. 2015b). The primary difference between Southwestern and Intermountain climate regimes at high elevations is in precipitation, not temperature (Alexander and Shepperd 1990). Therefore, ecosystems inhabited by Engelmann and blue spruce (*Picea pungens*) in the IAP region will probably support spruce aphid populations with only modest warming in the coming decades.

Numerous other potentially invasive forest insects are in various phases of introduction, establishment, and integration in the United States (Klepzig et al. 2010). Species in several insect families such as wood-boring beetles (Coleoptera: Cerambycidae and Buprestidae), bark beetles and ambrosia beetles (Coleoptera: Curculionidae), and woodwasps (Hymenoptera: Sircidae) have been identified as potentially invasive to North American forests by the U.S. Department of Agriculture Animal Plant Health Inspection

Service, Plant Protection and Quarantine and State regulatory agencies (Hitchcox 2015).

Early detection rapid response is a tactic employed to identify initial introductions and to assist in developing strategies to address them. In 1989, multiple life stages of European gypsy moth (*Lymantria dispar dispar*) were found in Utah. A successful eradication program was conducted with technical and financial assistance provided by the USFS Intermountain Region, Forest Health Protection program. Currently, an annual interagency trapping program monitors for gypsy moth introductions within the States in the IAP region. Isolated single catches of male moths have occurred occasionally, but established populations have not been found. Unlike the European gypsy moth, Asian gypsy moth (*L. dispar asiatica*, *L. dispar japonica*, *L. albescens*, *L. umbrosa*, and *L. postalba*) females are capable of flight, affecting dispersal and subsequent rate of spread if established (Reineke and Zebitz 1998). The Asian gypsy moths have a much larger host range, exceeding 250 species, that includes crops, shrubs, and trees, both coniferous and deciduous. In 2015, Asian gypsy moth introductions occurred in Washington and Oregon, arriving on ships and cargo from Russia and Japan. Global trade, favorable climate, and a large host range heighten the need to monitor for this invasive insect in the IAP region.

Changing climate regimes have the potential to alter insect vector distributions and associated wildlife diseases, with potentially severe consequences for affected species and ecosystems, but those dynamics are poorly understood for the Intermountain West (Runyon et al. 2012). For example, increased temperatures and altered precipitation patterns can increase the range and abundance of vector species (e.g., mosquitoes and ticks) and thus affect the frequency and severity of vectorborne disease outbreaks. Changes in precipitation are likely to affect migrations, water availability, and congregation patterns of wildlife, increasing exposure to disease by affecting host susceptibility to infection (Lafferty 2009; Rosenthal 2009). However, climate change could limit the spread of some diseases by creating environments that are not conducive to the pathogens or their insect vectors (Runyon et al. 2012).

The potential for new invasions will continue because of global trade. Regulatory measures are in place to reduce the risk of invasive introductions through agency regulations, contract requirements, overseas monitoring, inspection of ships and cargo, and public outreach. Although these strategies reduce risk, they do not eliminate it. Koch et al. (2011) estimated that approximately two nonnative forest insect species will become established in the United States annually, with one identified as a significant forest pest every 5 to 6 years. Determining which introduced insect will become a serious pest can be difficult, and some may not appear to cause significant damage until well after establishing. The added influence of changing temperature and precipitation regimes will affect any introduced species, their potential hosts, and their impacts on agricultural, forest, range, and urban ecosystems.

Diseases of Forest Communities

Overview

Forest diseases are found in all forest ecosystems of the IAP region but the overall impacts of forest diseases on various resources are difficult to quantify. Forest diseases tend to be more cryptic and chronic in their effects than other disturbance agents, and thus estimating their occurrence and abundance is difficult. Native pathogens cause most forest diseases, and as such function as part of their ecosystems.

Climate can affect the impact of forest diseases through impacts on the environment, the disease-causing organisms, and their hosts. This section focuses on the disease-causing agents in the IAP region that are known to have significant effects on ecosystems and ecosystem services, and for which there is some information on their response to climate.

Dwarf Mistletoe

Dwarf mistletoes (*Arceuthobium* spp.) are a group of parasitic seed plants that are widespread across the IAP region (table 8.6). The IAP region covers a broad range of forest ecosystems, and consequently is home to several dwarf mistletoes, including: *A. abietinum* on true firs, *A. americanum* on lodgepole pine; *A. campylopodum* on ponderosa and Jeffrey pine (*Pinus jeffreyi*) in the northern and western parts of the region; *A. cyanocarpum* on limber pine (*Pinus flexilis*); *A. divaricatum* on pinyon pine; *A. douglasii* on Douglas-fir; *A. laricis* on western larch (*Larix laricina*); and *A. vaginatum* ssp. *cryptopodum* on ponderosa pine in the southern part of Utah. Mistletoes can occasionally infest other tree species when they are growing interspersed with infected primary hosts.

Mistletoes primarily cause reduced tree growth and forest structural changes, but in some cases also cause tree mortality. Mortality rates are higher if other stresses are present, such as drought and high tree densities (Schultz and Allison 1982; Schultz and Kliejunas 1982), or insect agents such as the California flathead borer (*Phaenops californica*) (Kliejunas 2011). Mistletoes may play a significant role in tree mortality as trees become stressed by drought and other climate-related stressors (Kliejunas 2011).

The distribution and abundance of dwarf mistletoes are closely related to fire regime in many IAP region forest types (Geils et al. 2002). Frequent, low-intensity fire can maintain low levels of mistletoe infestation in forests. Stand-replacing fires tend to eliminate dwarf mistletoes. Management history also plays an important role, and any management practices that promote interfaces between infected overstory trees and susceptible regeneration promote the spread and intensification of dwarf mistletoes.

Table 8.6—Forest Inventory and Analysis (FIA) plots with dwarf mistletoe present in the USFS Intermountain Region. FIA plot data may not adequately capture the presence of this pathogen where its distribution is clumpy.

Forest type	FIA plots with dwarf mistletoe
	Percent
California mixed conifer	18.0
Douglas-fir	30.8
Engelmann spruce	4.7
Engelmann spruce-subalpine fir	16.2
Limber pine	12.7
Lodgepole pine	33.6
Pinyon-juniper woodland	13.0
Ponderosa pine	15.3
White fir	10.3
Whitebark pine	10.0
Other forest types	1.9
All forest types	15.1

Root Disease

Caused by various species of fungi, root disease is a major cause of tree growth reduction and mortality in the IAP region, although most infections are relatively small (McDonald et al. 1987). Root diseases often occur with bark beetle activity (Tkacz and Schmitz 1986). They typically affect canopy closure by creating small gaps and can be persistent on a site, affecting multiple generations of trees. Mortality from root disease can cause a transition to species more tolerant of root disease, or maintain stands of more susceptible species in early-seral stages (Byler and Hagle 2000). Root disease can alter ecosystem services by degrading landscape aesthetics and limiting accessibility of recreational resources.

The three most significant native root diseases in the region are *Armillaria* root disease (*A. oystoyea*), the tomentosus root disease (*Inonotus tomentosus*), and annosum disease (*Heterobasidium occidentale, H. irregulare*). In the southern portion of the IAP region, *Armillaria* root disease tends to occur on cool-dry to cold-dry fir sites, as well as some high-elevation lodgepole pine-dominated sites with subalpine fir or adjacent to subalpine fir sites (McDonald 1998; Tkacz and Baker 1991). In the rest of the IAP region, the disease occurs on wetter sites, being most common in cool to cold locations.

Tomentosus root disease is locally important in the region, primarily affecting spruce species. The disease can cause growth reduction, butt cull, windthrow, and tree mortality. It can lead to creation of small to large gaps in forest canopies and to regeneration problems in isolated locations (Guyon 1997; Tkacz and Baker 1991).

Annosus root disease can affect forests at broader spatial scales. It is caused by *H. occidentale* on fir and Douglas-fir. This root disease is ubiquitous in fir forests in the IAP region, and plays an important role in the subalpine fir mortality that has occurred over hundreds of thousands of acres over the last two decades.

White Pine Blister Rust

White pine blister rust (*Cronartium ribicola*) is a nonnative fungus that was introduced to western North America from Europe around 1910 (Bingham 1983; Tomback and Achuff 2010). The white pine blister rust fungus infects only five-needle pine species. All nine North American white pine species are susceptible in vitro, but Great Basin bristlecone pine (*Pinus longaeva*) remains uninfected in the field. The life cycle of white pine blister rust requires two hosts, with two spore-producing stages on white pine and three separate spore-producing stages, primarily on *Ribes* species, and rarely on *Pedicularis* and *Castilleja* species (Zambino 2010). Pine infection begins when spores produced on *Ribes* leaves in late summer are wind dispersed to nearby pines. The spores germinate on pine needles, and fungal hyphae grow through the stomata into the cell tissues, needles, and stems (Patton and Johnson 1970).

White pine blister rust-caused tree mortality greatly affects stand structure and species composition, but the most serious impact of white pine blister rust are its long-term effects on white pine regeneration capacity. This may be a critical factor if five-needle pines undergo climatic migration. White pine blister rust causes direct mortality of rust-susceptible seedlings and saplings and the loss of cone and seed production following branch dieback and top kill. This type of impact has been best documented in the IAP region on whitebark pine (*Pinus albicaulis*) (McKinney and Tomback 2007).

White pine blister rust is largely thought to be a disease of cool to cold-moist sites, where sporulation and infection are at their highest levels (Van Arsdel et al. 2006). Relatively warm-dry (lower elevations) or cold-dry (upper elevations) climatic conditions may be the reason that white pine blister rust has not proliferated as widely or been as damaging in the IAP region as other, moister regions (Smith and Hoffman 2000). Another reason may be the relative isolation of the region's five-needle pine stands; most occur as either scattered components in forest dominated by other tree species or are limited to high elevations (Charlet 1996; Richardson 2000). Many host populations are also typically isolated from other populations of rust-infected pines (Smith and Hoffman 2000).

All native white pine populations show some heritable resistance to white pine blister rust, but the frequency of resistance is low and variable (Zambino and McDonald 2004). Natural and assisted selection can increase

resistance, but only if resistant trees are also adapted to other aspects of their environment. Under moderate drought conditions, blister rust-resistant limber pine have greater cold tolerance and lower stomatal conductivity than susceptible trees, indicating that resistant limber pine may be better adapted than susceptible trees to a drier climate (Vogan and Schoettle 2015).

Climate-mediated changes in white pine blister rust host regeneration dynamics could restrict or expand host ranges (Helfer 2014). If mosaics of *Ribes* host populations shift into new higher-elevation areas, driven by drought at lower elevations, white pine blister rust may spread into areas where it has not yet occurred and thus alter white pine blister rust range. It is unlikely that any direct responses of the tree to future climates, such as increased growth, will enhance or degrade the ability of the host to ward off infections. Density of pines and *Ribes* could decrease and sun exposure increase if water limitation becomes severe (Allen et al. 2010). More open stands could decrease spore production on many *Ribes* species, because infections and spore production are typically much lower on *Ribes* plants grown in full sun than plants of the same species grown in shade (Zambino 2010).

Foliar Disease

Needle diseases have historically been of limited significance in the IAP region. Needle casts, rusts, and needle blights in pines, Douglas-fir, and fir usually cause loss of needles in the year following a season favorable for infection. Periodic outbreaks can cause severe damage in local areas (Lockman and Hartless 2008), and several wide-ranging outbreaks have been detected in the IAP and neighboring regions in the last 10 years (Worrall et al. 2008). Severe infection years occur only occasionally, and effects are mostly limited to crown thinning and loss of lower branches, with some mortality of young trees. Needle diseases are favored by long, mild, and damp springs, which may be more common with climate change. Their occurrence at epidemic levels depends on favorable weather conditions and presence of an adequate host population. The significance of recent defoliation events and whether they are increasing in frequency or intensity are yet to be determined.

Abiotic Disease

Most abiotic diseases result from the effects of adverse environmental factors (e.g., drought, freeze injury, wind damage, and nutrient deficiency) on tree physiology or structure. Abiotic diseases can affect trees directly or interact with biotic agents, including pathogens and insects. A number of abiotic and environmental factors can affect foliage, individual branches, or entire trees, tree physiology, and overall tree vigor. The most significant abiotic damage is tree mortality.

Forests in the IAP region periodically suffer damage from weather extremes, such as high temperature and drought. Factors such as air pollutants and nutrient extremes occur infrequently or locally. Drought injury, an abiotic factor that can cause disease through loss of foliage and tree mortality, can initiate a decline syndrome by predisposing trees with stressed crowns and roots and low energy reserves to infection by less aggressive biotic agents, such as canker fungi and secondary beetles.

Canker Disease

Canker disease affects tree branches and boles, where the damage is caused by breakage at the site of the cankers, or by death of branches and boles beyond girdling cankers. Many canker diseases are commonly called facultative parasites (Schoeneweiss 1975), which refers to the tendency of these diseases to be facilitated by environmental stress on the host. Some important canker diseases in the IAP region are the complex of several cankers found on aspen, several cankers found on alder and willows in riparian areas, and a few cankers on conifers, such as Atropellis canker of pines and Valsa cankers on fir and spruce. Cankers in aspen are caused by several fungi, including *Hypoxylon mammatum*, *Encoelia pruinosa*, *Ceratocystis fimbriata*, *Cryptosphaeria populina*, and *Valsa sordia* (anamorph: *Cytospora chrysosperma*). Fungi that cause cankers of alder or willow in riparian areas include *Valsa melanodiscus* (anamorph: *Cytospora umbrina*) on alder, and *V. sordida* on willow.

Declines and Complexes

There are several definitions of forest decline phenomena in the literature. Houston (1981) emphasized that decline can result from stress alone, but that in natural forests, "secondary-action organisms" were necessary to complete the decline, differentiating decline from natural attrition. The most commonly accepted modern definition of a decline was postulated by Manion (1991), and involves a cycle containing predisposing, inciting, and contributing factors involved in a downward spiral of forest and tree health.

Aspen dieback and decline have been detected over the last decade across western North America (Fairweather et al. 2008; Frey et al. 2004; Guyon and Hoffman 2011; Worrall et al. 2008). Anderegg et al. (2012) have posited that the recent aspen mortality is caused by drought stress. Aspen mortality is also occurring under heavy browsing pressure by native and domesticated ungulates (Kay 1997). With aspen already stressed by drought and ungulate pressure, forest insects and diseases can play an important role in aspen dieback and decline; they can have a similar role in the dieback seen in riparian willow and alder (Kaczynski and Cooper 2013; Worrall 2009). While mortality caused by forest insects and diseases is part of fully functioning ecosystems, stands dying due to decline-type phenomena can alter not only the forest canopy structure, but the entire forest community, including understory shrubs and herbaceous plants (Anderegg et al. 2012).

Invasive Plants

Overview

An invasive species is a nonnative species whose introduction does or is likely to cause economic or environmental harm or harm to human health (NISC 2016). Human activity moves species from place to place both accidentally and deliberately and does so at rates that are without precedent in the last tens of millions of years (D'Antonio and Vitousek 1992). Invasive plants do not necessarily have higher growth rates, competitive ability, or fecundity than native plants; rather, the frequent absence of natural enemies in the new environment, and increased resource availability and altered disturbance regimes associated with human activities, increases the performance of invaders over that of natives (Daehler 2003; MacDougall and Turkington 2005; Mack 1989).

A nonnative plant species must pass through a variety of environmental filters to survive in a new habitat (Theoharides and Dukes 2007). First, the nonnative plant species must travel across major geographic barriers to its new location (introduction/transport stage). Once in the new location, the nonnative plant species must survive and tolerate environmental conditions at the arrival site and then acquire critical resources while surviving interactions with the plants, animals, and pathogens already occupying the site (establishment stage). Finally, to become invasive, the nonnative plant species must spread, establishing populations in new sites across the landscape (spread stage). The progression from nonnative to invasive often involves a delay or lag phase, followed by a phase of rapid exponential increase that continues until the invasive species reaches the bounds of its new range and its population growth rate slackens (Cousens and Mortimer 1995; Mack 1985). This lag phase may simply be the result of the normal increase in size and distribution of a population. However, other mechanisms can keep newly introduced species at low levels for decades before they become invasive. These mechanisms include environmental change (both biotic and abiotic) after establishment and genetic changes to the founder populations that enable subsequent spread (Mooney and Cleland 2001). During the lag phase it can be difficult to distinguish nonnative plants that will ultimately not survive in the new range from future invaders (Cousens and Mortimer 1995).

Most invasions over the past several centuries have involved species transported directly or indirectly by humans (McKinney and Lockwood 1999). Invasive plants have attracted much attention because of their economic costs as weeds (Pimentel 2002) and because they may reduce native biodiversity (Daehler and Strong 1994; Wilcove et al. 1998), alter ecosystem functions (D'Antonio and Vitousek 1992; Vitousek 1990), change nutrient pools (Duda et al. 2003; Ehrenfeld 2003), and alter fire regimes (Brooks et al. 2004).

Climate change is expected to alter the distribution and spread of invasive plants, but in largely unknown ways. Climate change can fundamentally alter the behavior and spread of invasive species and the harm they cause, as well as the effectiveness of control methods; likewise, climate change may favor and convert nonnative species considered benign today into invasive plants tomorrow (Runyon et al. 2012). Although some aspects of global change, such as climate change, may be reversed by societal actions, this will not be possible for biotic exchange; the mixing of formerly separated biota and the extinctions these introductions may cause are essentially irreversible (Mooney and Cleland 2001). The Working Group on Invasive Species and Climate Change (WGISCC 2014: 1) summarizes the interaction of invasive species and climate change as follows:

> *Combining the threats of invasive species with those posed by climate change can magnify the intensity associated with both issues. Climate change may reduce the resilience of ecosystems to resist biological invasions, while biological invasions can similarly reduce the resiliency of ecosystems and economies to the impacts of climate change. Beyond that, the interactions among drivers of change become significantly more complex due to the interplay of diverse phenomena like severe climatic events, changing precipitation patterns, and coastal erosion exacerbated by invasive species.*

The History of Plant Invasion in the Intermountain Adaptation Partnership Region

The Intermountain West was intensively settled from 1870 to 1890. European settlers brought with them the cereal, legumes, and forage crops of Western Europe, medicinal and ornamental plants that they valued, and other Western European plants which "hitched a ride" on livestock or as crop seed contaminants. Vast areas in the Intermountain West were converted to crops, and tracts of land unsuitable for crops were rapidly converted to pasture. Livestock destroyed much of the native plant communities in areas not plowed. Nonnative plants became more diverse and conspicuous as settlement increased. Of the many nonnative plants introduced in the West, a small percentage became invasive and began to spread. The speed and extent of regional invasion was facilitated by a railroad system established simultaneously with the wave of human immigrants in the late 19th century. As a result of this convergence of dispersal factors, some invasive plants filled their new ranges in as little as 40 years (Mack 1989).

Where undisturbed, the temperate grasslands of the Intermountain West are dominated solely by bunch (caespitose) grasses, including bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), needle-and-thread grass (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*); or these grasses share dominance with drought-tolerant shrubs, principally sagebrush (*Artemisia tridentata*), but also greasewood (*Sarcobatus vermiculatus*), rabbit brush (*Chrysothamnus*

Table 8.7—The number of invasive plant species reported by State in the Intermountain Adaptation Partnership region, according to the Early Detection and Distribution Mapping System (EDDMapS 2016) on February 5, 2016. The EDDMapS is an online database that combines data from other databases, organizations, and volunteer observations to create a national network of invasive species distribution data.

Invasive plant type	State			
	Nevada	Utah	Wyoming	Idaho
Grasses/grasslike	81	86	61	71
Forbs/herbs	194	249	198	271
Shrubs/subshrubs	12	35	17	28
Vines	17	17	15	22
Hardwood trees	15	34	16	27
Conifer trees	0	0	0	1
Aquatic	8	8	7	13
Total	327	440	319	433

nauseosus), and saltbrush (*Atriplex confertifolia*). The prominence of shrubs is greater where precipitation is lower. In the spaces between the grasses and shrubs are annual and perennial herbs and cryptobiotic crust (Daubenmire 1969).

With Euro-American settlement, many nonnative species arrived and became naturalized, but probably less than a dozen became community dominants (e.g., wild oats [*Avena fatua*], cheatgrass, bull thistle [*Cirsium vulgare*], medusahead [*Taeniatherum caput-medusae*], hologeton [*Hologeton glomeratus*], Kentucky bluegrass [*Poa pratensis*], Russian thistle [*Salsola tragus*], and tall tumblemustard [*Sisymbrium altissimum*] [Yensen 1981; Young et al. 1972]). The combination of settlement-related disturbance, introduction of invasive plants, and subsequent shifts in native vegetation significantly altered much of the regional vegetation within 50 years (Daubenmire 1970). Current invasive plants in the IAP region are listed in table 8.7.

Invasive Plants in the Intermountain Adaptation Partnership Region

Implications of Increasing Numbers of Invasive Plants

There is little evidence that interference among nonnative species at levels currently observed significantly impedes further invasions. Rather, groups of nonnative species can facilitate one another's invasion in various ways, increasing the likelihood of survival and ecological impact, and possibly the magnitude of impact; the result is an accelerating accumulation of introduced species and effects (Simberloff and Von Holle 1999). The damage of invasive plants to the ecosystems of the IAP region may increase as more nonnative plants establish, and as climate change results in shifts in the environment, giving certain nonnative plants an advantage and allowing them to become invasive.

Invasive plants can alter the evolutionary pathway of native species through competitive exclusion, niche displacement, hybridization, introgression, predation, and ultimately extinction. Invasive species hybridization with native species can cause a loss in fitness in the native species, which may result in extinction of the native plant (Rhymer and Simberloff 1996). There are many examples of the large populations of invading species outcompeting small populations of native species through hybridization (e.g., invasive *Spartina alterniflora* hybridizing with the common native *Spartina foliosa* and the hybrid then invading new marshes [Anttila et al. 1998; Ayres et al. 2008]). In certain cases, small populations of an invader can threaten native species that have much larger populations (Mooney and Cleland 2001).

Invasive Plants in Nonforest Vegetation

Many invasive plant species (both annual grasses and perennial forbs) have degraded the nonforest vegetation types of the IAP region by outcompeting native species and by directly affecting the frequency and intensity of wildfires (see following discussion). Although cheatgrass and medusahead are considered the most problematic of the invasive annual grasses, a number of deep-rooted, creeping invasive perennials, such as Russian knapweed (*Acroptilon repens*), squarrose knapweed (*Centaurea virgata*), Dalmatian toadflax (*Linaria dalmatica*), and Canada thistle (*Cirsium arvense*), are often some of the hardest invasive plants to manage (Ielmini et al. 2015).

Invasive Plants in Forest Vegetation

In general, invasive plants are unable to get the sunlight they require to survive in dense forests (Parendes and Jones 2000). To date, forests in western North America remain relatively unaffected by invasive plants (Oswalt et al. 2015).

However, forest ecosystems remain vulnerable (Dukes and Mooney 2004). Invasive plants are most often encountered in disturbed areas within forest vegetation types (e.g., along roads, streams, or trails, or in areas disturbed by harvesting, windthrow, or fire). The invasive plants encountered in forest vegetation types in the IAP region tend to be the same invasive plants encountered in nonforest vegetation types. When disturbance ceases in forests, however, populations of invasive species tend to decline as forest vegetation recovers.

Invasive Plants in Riparian Zones

Riparian zones in the Intermountain West may be invaded by either annual or perennial invasive plant species, but the most apparent are often perennials. Perennial invasive species with clonal or rhizomatous life forms, or that are capable of root sprouting, are ideally suited to survive in riparian habitats and compete with native vegetation. Perennial invasive species can attain large size, displace native vegetation, and significantly affect the structure of vegetation (Dudley 2009).

Invasive plants currently impacting riparian zones in the IAP region include the perennials saltcedar (*Tamarix* spp.), Russian olive (*Elaeagnus angustifolia*), camelthorn (*Alhagi pseudalhagi*), and perennial pepperweed (*Lepidium latifolium*), and the annual rabbitsfoot grass (*Polypogon monspeliensis*). Upland invasive plants that occur on the periphery of these ecosystems include Russian knapweed, ripgut brome (*Bromus diandrus*), red brome, cheatgrass, and invasive mustards (family Brassicaceae) (Chambers et al. 2013).

Climate Change and Invasive Plants

It is often assumed that climate change will favor nonnative invasive plants over native species (Dukes and Mooney 1999; Thuiller et al. 2008; Vilá et al. 2007; Walther et al. 2009). Although this may be an overgeneralization (Bradley et al. 2009; Ortega et al. 2012), numerous attributes of successful invaders suggest nonnative species could flourish with climatic changes, specifically increased atmospheric carbon dioxide levels, precipitation, and temperatures. For example, many invasive species are fast-growing early-seral species (ruderals) that tend to respond favorably to increased resource availability, including temperature, water, sunlight, and carbon dioxide (Milchunas and Lauenroth 1995; Smith et al. 2000; Walther et al. 2009). Many invasive species respond favorably to disturbance (Zouhar et al. 2008), which can increase resource availability (Davis et al. 2000). Invasive species may exploit postfire conditions better than many native species (Zouhar et al. 2008), despite native plant adaptations to fire. In bunchgrass communities, many invasive plants germinate and become established better than do native species when native vegetation is disturbed, even under equal propagule availability (Maron et al. 2012). Successful invaders also commonly have strong dispersal strategies and shorter generation times, which can

allow them to migrate quickly into freshly disturbed sites (Clements and Ditomaso 2011). Collectively, these attributes suggest that many invasive plants would benefit from increased disturbance under changing climate.

Invasive Plants and Climate Change Management Considerations

Climate change may both increase the intensity and duration of drought, and increase the intensity of precipitation events (Trenberth et al. 2003). Intense weather events associated with climate change can create disturbances in ecosystems that may make them more vulnerable to invasion. For example, mudslides, wind damage, and ice storms could damage forest ecosystems by uprooting trees and creating disturbed soil conditions ideal for invasion. Heavy rains, drought, wildfire, unusual movements of air masses, and other extreme climatic events can equally weaken the resilience of ecosystems and expose new areas to invasion (Bhattarai and Cronin 2014; Heller and Zavaleta 2009). Damage from these events, especially where invasive species are present or invade as a result, may affect the ability of these ecosystems to recover from the damage caused by such events. The affects of weather events can be exacerbated where invasive plants dominate the ground cover, yet fail to provide adequate levels of root structure to bind and hold soils. The failure to secure the soil can lead to increased erosion and consequent impacts on stream turbidity and water quality (WGISCC 2014).

Diez et al. (2012) provide examples of how extreme climatic events can affect each stage of the invasion process:

- Introduction/transport: Strong winds and storms can move seeds or propagules of invasive species into previously uninvaded locations;

- Establishment: Extreme climatic events such as drought or severe storms can weaken ecosystems or create significantly disturbed areas (e.g., mudslides, wildfire) that may facilitate successful invasive species establishment;

- Spread: The seeds or propagules of invasive species already within an area can be further spread by winds (e.g., associated with windstorms) and water (e.g., flooding); and

- Impact: Weather events may strengthen or compound the negative impacts of invasive species; for example, extended drought can increase the frequency or severity (amount of fire-caused mortality) of fire in areas invaded by invasive plants, thereby altering historical fire regimes.

Unless desirable plants are present to fill vacated niches, control of existing invasive plants may open niches only for the establishment of other undesirable plants.

The effectiveness of existing invasive species management measures will need to be reevaluated in light of climate change. Control activities may have to be modified in response to climate-induced changes in plant phenology

and distribution. Adjustments could include changes in the timing and level of herbicide applications and methods of mechanical control and management for invasive plants (WGISCC 2014). We also highlight the need to better understand how climate change will impact relationships between invasive plants and their biological control agents so managers can predict and advance biocontrol efficacy (Runyon et al. 2012). An integrated pest management strategy for invasive plants which considers all forms of pest control (cultural, mechanical, biological, and chemical) is

most likely to be successful through time (DiTomaso 2000; Masters and Sheley 2001). Current context and approach for invasive species management are described in box 8.1, and adaptation strategies for invasive species are described in Chapter 14.

Box 8.1—The Framework for Invasive Species Management

Policy-makers, resource managers, and researchers have generally accepted a hierarchy of actions associated with the management of invasive species: prevention, early detection with a rapid response to eradicate them, or if they gain a foothold and cannot be eradicated, then control and management (WGISCC 2014; Heller and Zavaleta 2009).

Prevention

Prevention is the most effective defense against biological invasions (NISC 2016). Prevention is the only tactic that ensures an invasive species does not become an additional stressor to a vulnerable ecosystem (WGISCC 2014). Unless measures are taken to prevent invasive plant propagules from hitching rides, the ongoing expansion of global commerce is likely to exacerbate the problem of biological invasions (Dukes and Mooney 2004).

Early Detection and Rapid Response

Where prevention fails to stop the arrival of an invasive species to an ecosystem, early detection and a rapid response to eradicate the invasive species can minimize harmful impacts to an ecosystem (Wittenberg and Cock 2001). Early detection of invasive plant populations, followed immediately by decisive management practices to eradicate an incipient population, is critical to preventing a species from becoming invasive. Rapid eradication depends on adequate preparedness, having the necessary methods, legal authorities, and resources to act on the detection before the invasion becomes entrenched. For this reason, eradication efforts should be considered within the broader, proactive conservation planning (WGISCC 2014).

Control and Management

Once an invasive plant has established and spread beyond a point where eradication is feasible, long-term control can still reduce that species' stress on an ecosystem. Reducing the extent or impact of an invasive plant infestation may directly enhance ecological resiliency of the affected resource. Long-term control should improve ecosystem functions of invaded areas while containing further spread of the invasive plant by protecting adjacent uninfested areas (WGISCC 2014).

Most often a single method is not effective to achieve sustainable control of invasive plants. A successful long-term management program should be designed to include combinations of mechanical, cultural, biological, and chemical control techniques as necessary. This is particularly true in revegetation programs in which seeding establishment is the most critical stage and is dependent upon the suppression of competitive species (DiTomaso 2000). The need to integrate control methods to get tolerable levels of invasive plant densities underscores the need for constant monitoring and evaluation of treatments. If a treatment does not result in desired or expected control, land managers need to be prepared to modify their treatments and resource expectations in the future, perhaps incorporating additional control methods or reducing potential resource benefits.

Forest Service Invasive Species Management Policy

The Forest Service Manual addresses invasive species management (FSM 2900) (Forest Service 2011) with five strategic objectives. The first three FSM 2900 strategic objectives mirror the framework outlined above (prevention, early detection and rapid response, control and management), but FSM 2900 adds two additional strategic objectives: restoration and organizational collaboration. The Forest Service seeks to proactively manage aquatic and terrestrial areas of the National Forest System to increase the ability of those areas to be self-sustaining and resistant to the establishment of invasive species. Where necessary, implementation of restoration, rehabilitation, and or revegetation activities following invasive species treatments is desirable to prevent or reduce the likelihood of the reoccurrence or spread of aquatic or terrestrial invasive species (U.S. Forest Service 2011). Cooperation with other Federal agencies, State agencies, local governments, tribes, academic institutions, and the private sector can help to: increase public awareness of the invasive species threat; coordinate invasive species management activities to reduce, minimize, or eliminate the potential for introduction, establishment, spread, and impact of aquatic and terrestrial invasive species; and coordinate and integrate invasive species research and technical assistance activities (U.S. Forest Service 2011).

Geologic Hazards

Background and Mechanistic Models for Hazard Assessment

Geologic hazards related to climate change primarily involve erosional geomorphic processes, such as flooding, mass wasting, periglacial activity, snow avalanches, and aeolian transport. Climate-driven changes in temperature, precipitation, and atmospheric circulation have direct impacts on the physical processes driving erosion (e.g., freeze-thaw, hydrological runoff, and windspeed). Over long periods of time, landscapes evolve to reflect the erosional regime to which they are exposed. Climate change can alter that regime by changing the timing, frequency, magnitude, and style of erosional events, thereby causing a transient geomorphic response that will persist until the system equilibrates with the change in physical regime. This period of transience and the new state toward which the system evolves can alter the potential for geologic hazards. However, climate change may play out differently within and between subregions; geologic hazards may increase in some cases, decrease in others, or show little to no change. Hence, site-specific assessments are frequently required.

The degree of geomorphic response to a given change in climate depends on the physical setting and the associated degrees of freedom for adjusting to the climate perturbation. For example, soil-mantled hillslopes or alluvial rivers will be more responsive to a change in precipitation and runoff because they are composed of loose, mobile material. In contrast, bedrock landscapes are likely to show much less response to the same climatic perturbation. Geomorphic responses and changes in the style and degree of erosion can be quantitatively predicted using regime diagrams (or state diagrams) which relate process and form to the driving physical variables. For example, figure 8.22 shows predicted domains for different types of erosional processes occurring on soil-mantled hillslopes as a function of topographic slope and drainage area (a surrogate for hydrological discharge). Each domain is based on mechanistic predictions for the style of erosion that will result for different combinations of area and slope (Montgomery and Dietrich 1994).

Using mechanistic frameworks, such as figure 8.22, one can map erosional process domains onto the landscape using geographic information systems and digital elevation models, allowing rapid prediction of how geomorphic processes (and hazards) may respond to climate change (in this case, climate-driven changes in precipitation and the runoff associated with a given drainage area). For example, figure 8.23 shows the predicted spatial distribution of shallow landslides in a mountain basin based on the above framework and given values of hydrology and soil characteristics; the results demonstrate that (all else equal) the risk of landsliding is expected to rise with climate-driven increases in rainfall (figs. 8.23a-d).

Similarly, figure 8.24 shows a state diagram for alluvial rivers, from which one can predict changes in channel
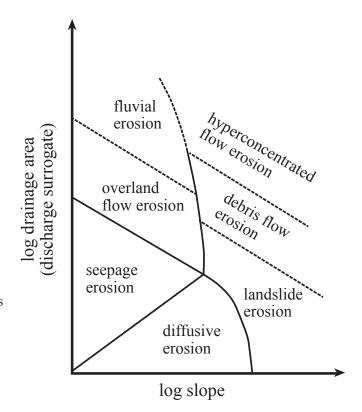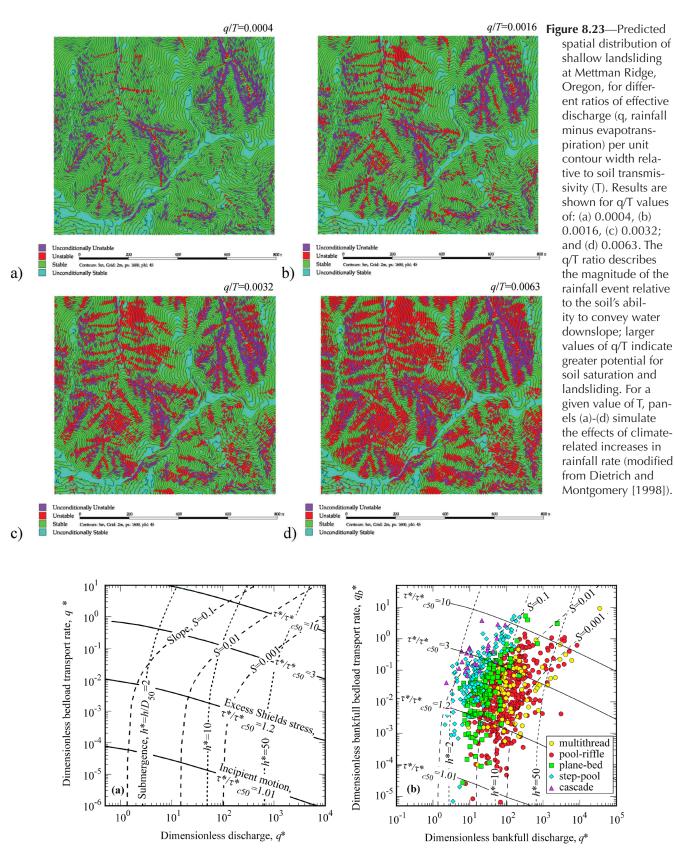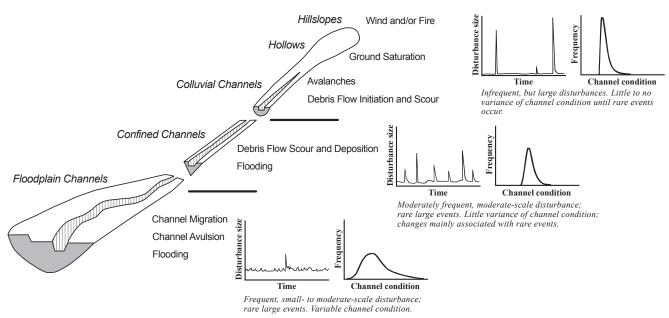

Figure 8.22—Domains for different types of erosional processes on soil-mantled landscapes (modified from Montgomery and Dietrich [1994]).

characteristics (depth, slope, grain size) or reach-scale channel morphology (pool-riffle, plane-bed, step-pool, cascade) as a function of climate-related changes in streamflow or sediment supply. Furthermore, by grouping channels into process domains (fig. 8.25), one can identify which portions of the river network (and associated ecosystems) may be susceptible to climate-related changes in a given type of disturbance.

An important factor not explicitly included in these state diagrams is vegetation. Grasses, shrubs, and trees alter geomorphic processes by (1) intercepting and shielding the ground from direct impact of precipitation, (2) creating surface roughness that slows erosion from wind and water, and (3) offering root strength that can dramatically increase erosional thresholds. For example, over the long term, vegetated hillslopes may become oversteepened (i.e., achieving steeper slopes than would be possible without the added effects of root strength and surface roughness). Climate-driven changes in forest health, vegetative cover, and species composition (and associated root strength and surface roughness) can cause hillslopes to rapidly unravel, exhibiting accelerated rates of surface erosion and mass wasting. For example, increased frequency and extent of landslides is commonly observed following forest clearing of steep terrain (e.g., Gray and Megahan 1981; Johnson et al. 2000; Montgomery et al.

Figure 8.23—Predicted spatial distribution of shallow landsliding at Mettman Ridge, Oregon, for different ratios of effective discharge (q, rainfall minus evapotranspiration) per unit contour width relative to soil transmissivity (T). Results are shown for q/T values of: (a) 0.0004, (b) 0.0016, (c) 0.0032; and (d) 0.0063. The q/T ratio describes the magnitude of the rainfall event relative to the soil's ability to convey water downslope; larger values of q/T indicate greater potential for soil saturation and landsliding. For a given value of T, panels (a)-(d) simulate the effects of climate-related increases in rainfall rate (modified from Dietrich and Montgomery [1998]).

Figure 8.24—State diagram for alluvial rivers showing: (a) contours of equilibrium channel slope (S), relative submergence ($h^* = h/D_{50}$, where h is flow depth and D_{50} is the median surface grain size), and excess Shields stress (τ^*/τ^*_{c50}, where τ^* is the dimensionless shear stress and τ^*_{c50} is the critical value for mobilization of D_{50}) as functions of dimensionless discharge (q^*) and dimensionless equilibrium bedload transport rate (q_b^*, transport rate = sediment supply); and (b) the same figure populated with field data for different reach-scale channel types evaluated at bankfull stage (from Buffington [2012], and after Parker [1990]).

Figure 8.25—Process domains in mountain rivers, showing headwater to lowland channel types and associated disturbance processes (schematic at left). Graphs show disturbance size relative to mean values (first right-hand graph) and variance of channel condition (second right-hand graph) as a function of these disturbances (floods, sediment inputs, changes in vegetation) and degrees of freedom associated with each process domain and channel type (from Buffington [2012]; modified from Montgomery [1999], and after Benda and Dunne [1997a, b], Church [2002], and Wohl [2008]).

2000; Swanston 1970) and may be a useful analog for potential effects of climate change in some settings. In terms of the figure 8.22 framework, climate-driven changes in vegetation alter the area-slope thresholds for different erosional processes, allowing one to mechanistically model the implications for geomorphic hazards. For example, spatially explicit predictions similar to figure 8.23 could be developed for different vegetation scenarios by altering the effective rainfall rate (rainfall minus interception), surface roughness, and root cohesion in standard erosion laws (Montgomery and Dietrich 1994) to simulate the effects of climate-driven changes in forest health, biomass density, or species composition on erosional processes and hazards.

A variety of other process-based models are also available for predicting hazard zones at landscape scales. Examples are the runout path of debris flows (Benda et al.

2007; NetMap 2017), the extent of floodplain inundation (Bates et al. 2010; LISFLOOD-FP 2017), the extent of critical streambed scour for salmonid embryos (Goode et al. 2012), and the extent of aeolian erosion as a function of vegetation type and density (Mayaud et al. 2017) for climate-related changes in physical and biological conditions.

Larger-scale geologic hazards, such as earthquakes and volcanic eruptions, are not directly influenced by climate change. However, the impacts of these events can be modulated by climate. For example, glaciers and ice patches present on Mount St. Helens during its 1980 eruption helped to generate lahars (muddy debris flows) that caused substantial erosion and sediment deposition during the event (Pierson 1985). Similarly, the densely forested landscape around the volcano produced massive loads of

Table 8.8—Relative size of floods in different hydroclimates.[a]

Discharge ratio	Snowmelt (Colorado Front Range)	Frontal rainfall (Klamath Mountains, California)[b]	Thunderstorm (Colorado Front Range)
Q_{ma}/Q_{ma} [c]	1.0	1.0	1.0
Q_5/Q_{ma}	1.3	1.3	1.1
Q_{10}/Q_{ma}	1.4	1.9	1.9
Q_{50}/Q_{ma}	1.8	3.5	4.5
Q_{100}/Q_{ma}	2.0	4.5	8.9

[a]Table from Buffington (2012). Data from Pitlick (1994), based on regional flood frequency curves for mountain basins with roughly comparable ranges of drainage area.
[b]Approximate average value for the three frontal rainfall systems examined by Pitlick (1994).
[c]Q_{ma} = mean annual flood.

wood that were delivered to lakes and rivers within the blast zone; in turn, complex geomorphic responses and shifting habitats ensued as that material was subsequently mobilized or sequestered during hydrological and atmospheric events in the decades after the eruption.

Potential Effects of Climate Change on Fluvial Erosion in the Intermountain Adaptation Partnership Region

In the IAP region, climate-related changes in hydroclimate are likely to be important drivers of increased erosional hazards. As used here, hydroclimate refers to the type of runoff regime (e.g., snowmelt, frontal rainfall, or thunderstorm/monsoonal), which has important implications for fluvial erosion and associated hazards. While rivers and their floodplains are adjusted to the local hydrological regime, each hydroclimate has substantially different physical characteristics. For example, the relative size of a given recurrence-interval flood systematically varies with hydroclimate (table 8.8). The 100-year flood (Q_{100}) is typically 9 times as large as the mean annual flood (Q_{ma}) in thunderstorm systems, 4.5 times as large in frontal rainfall systems, and only twice as large in snowmelt environments. This suggests very different potential for geomorphic work and erosion across hydroclimates. In most cases, global climate models predict subtle changes in the timing and magnitude of precipitation events (e.g., Goode et al. 2013), but where watersheds become transitional from one hydroclimate to another, substantial changes in state (and erosional hazard) may occur due to the flood statistics documented in table 8.8. These hazards may be compounded by concomitant changes in vegetation type and species composition (and thus changes in erosional thresholds as discussed earlier). Identifying regions or subbasins within watersheds where transitional hydroclimates are expected to emerge as a result of climate change may be critically important for planning.

Interactions

Large mortality events in forests are normally associated with the occurrence of several stressors (Allen et al. 2010; McDowell et al. 2016). The interactions among disturbances working over various spatial and temporal scales define the nature of forested landscapes (Jenkins et al. 2008). Changes in drought intensity and frequency, for example, have the potential to alter fire, and populations and impacts of tree-damaging forest insects and pathogens (Ayres and Lombardero 2000; Dale et al. 2001; Weed et al. 2013). In addition, bark beetle-caused tree mortality in conifer forests affects the quantity and quality of forest fuels (Jenkins et al. 2008). Complex interactions make it challenging to predict the effect of multiple stressors and whether threshold-type responses may occur (McDowell

et al. 2016). In this section, we explore some potential interactions between several ecological disturbances and discuss the likelihood of climate change effects.

Fire and Bark Beetle Interactions

Introduction

A large reduction in fire as a result of suppression efforts over the last century has substantially altered forest composition, structure, and ultimately vulnerability to insect pests (McCullough et al. 1998), particularly in low-elevation, dry forest types. Changes in stand structure, including increased homogeneity and density, and increased abundance of fire-intolerant, shade-tolerant conifers have increased susceptibility to several bark beetle species (Fettig et al. 2007). Reciprocally, mortality caused by bark beetles can change subsequent fire hazard (Hicke et al. 2012). For example, crown fire potential is increased in lodgepole pine stands immediately (1–4 years) after mountain pine beetle outbreak (red stage) as a result of rapidly desiccating needles still attached to the tree (Jolly et al. 2012). Disturbance interactions like these are a natural component of forests in the IAP region, and understanding their causes and consequences will help managers anticipate possible effects of climate change.

Effects of Bark Beetles on Fuels and Fire Behavior

Effects of bark beetle outbreaks on fire hazard (e.g., probability, severity, and intensity) are of considerable concern in many forest types in the IAP region. It has long been presumed that fire occurrence or intensity, or both, may increase following outbreaks of bark beetles (Hoffman et al. 2013), but studies demonstrating this interaction are few and have contradictory conclusions (Hicke et al. 2012; Parker et al. 2006). A growing body of literature utilizing physics-based models (e.g., Hoffman et al. 2012a, 2015; Linn et al. 2013), historical observations (e.g., Kulakowski and Jarvis 2011), and stand structure and fuels characterizations (e.g., Harvey et al. 2013) addresses the change in both fuels distribution and potential fire behavior after bark beetle outbreaks in many forest types. Outbreak severity, spatiotemporal heterogeneity in tree-level mortality, forest type differences associated with individual species traits, and species composition influence how we interpret the influence of bark beetle outbreaks on fire hazard.

A common approach to evaluate post-outbreak fire hazard is to group impacted stands into three phases that correspond to the bark beetle population stage (endemic, epidemic, and post-epidemic) (Jenkins et al. 2008). These phases can be similarly characterized based on canopy color associated with aerial fuel moisture conditions over time as trees die and deteriorate. Trees in the green phase are usually alive and undergoing a low-level endemic or initial epidemic attack. In this phase, photosynthesis is still occurring, water relations in the tree are close to normal,

and there are normal levels of fine canopy fuels. Red phase stands are related to an ending epidemic or to a recent post-epidemic beetle population stage. Here the needles are still on the tree, but in contrast to the previous phase, their moisture is reduced and the composition of the volatile compounds is different, making the canopy fine fuels more flammable (Gray et al. 2015; Jolly et al. 2012). Last, in gray-phase stands, the needles have fallen off the tree, drastically reducing aerial fine fuels, and making a short-term (1–3 years) contribution to the fine surface fuels. A fourth phase, not related to canopy color, is called an old phase. These stands comprise individuals remaining one decade or longer after the beetle epidemic; this is the phase when trees begin to fall and regeneration responds to created openings.

Hicke et al. (2012) conducted the most thorough review of the fire-bark beetle literature to date and noted that, despite varying approaches and research questions, much agreement exists on fire hazard after bark beetle outbreaks. Specifically, during the gray phase, there was strong agreement that surface fire hazard and torching potential increased, but crown fire potential was reduced. Similarly, agreement for reduced fire hazard in old-phase conditions was found. However, most disagreement occurred regarding fire hazard during the red phase, when trees retain their drying needles and changes in foliar chemistry can increase their flammability. Many studies have concluded that during this roughly 1- to 4-year period, fire hazard increases (Hoffman et al. 2012a; Jenkins et al. 2014; Jolly et al. 2012; Klutsch et al. 2011). Fire hazard also increases as the proportion of the stand killed by bark beetles increases, regardless of forest type (DeRose and Long 2009; Hoffman et al. 2012a; Jorgensen and Jenkins 2011; Page and Jenkins 2007). Many, though not all (see Linn et al. 2013), studies suggest as stands transition from red phase into gray phase, fire hazard decreases.

Characterization of bark beetle-caused mortality into phases simplifies the actual spatial and temporal variability associated with the developing insect population on a specific host, and the composition, condition, and arrangement of those hosts at tree, stand, and landscape levels. The rate at which erupting beetle populations build initially is influenced by the amount (proportion) of susceptible host; beetle population movement between stands and across the landscape is influenced by proportion of susceptible host and their arrangement (DeRose and Long 2012b; Hoffman et al. 2015). For example, mountain pine beetle populations can build quickly in homogeneous stands of drought-stressed, suitable lodgepole pines, resulting in relatively rapid mortality of the pine.

The interactions between fire and bark beetles in heterogeneous landscapes need to be discussed across a range of stand conditions and forest types. Forest types should be evaluated separately for fire hazard after bark beetle outbreaks because of varying intensities of bark beetle effects on its host, environmental conditions that characterize a particular forest type (e.g., elevation and aspect), and proclivity of a forest type to promote advance regeneration

(e.g., spruce-fir) or not (e.g., persistent lodgepole pine). The amount and arrangement of live fuel in post-outbreak stands are influenced by the presence or absence of advance regeneration, which varies by forest type.

The vast majority of research on beetle outbreak and fire hazard has been conducted in the lodgepole pine forest type (reviewed in Hicke et al. 2012), including study areas in the IAP region (Jenkins et al. 2014; Page and Jenkins 2007). Other forest types that have received notable attention in the IAP region include spruce-fir (DeRose and Long 2009; Jorgensen and Jenkins 2011), Douglas-fir (Guinta 2016; Harvey et al. 2013), and limber pine (Gray et al. 2015). These areas are impacted by the principal eruptive bark beetles in the region, the mountain pine beetle and spruce beetle. Much less research has been conducted in lower-elevation forest types such as ponderosa pine (Hoffman et al. 2012b; but see Hansen et al. 2015), pinyon-juniper types (Linn et al. 2013), and quaking aspen. Increased activity of pinyon ips beetles in some of these forest types merits research on their interactions with fire.

Effects of Fire on Bark Beetles

Fire can directly and indirectly influence bark beetle populations. Fire burning in stands of infested trees can directly kill bark beetles or their developing brood and therefore decrease populations (Martin and Mitchell 1980). However, indirect effects are more common, typically resulting from the effect of fire on host tree suitability and vigor. Trees scorched or wounded by fire are generally thought to be weakened, and as a result, are less resistant to bark beetle attack. But studies investigating the relationship between fire-caused damage to conifers and resin production or flow have reported variable results, ranging from temporary reductions in resin to elevated resin levels for up to 4 years (Davis et al. 2011; Davis et al. 2012; Perrakis and Agee 2006; Wallin et al. 2003). In addition, fire can indirectly increase bark beetle and other beetle attacks by eliciting host tree compounds that may attract bark beetles (Kelsey and Joseph 2003; Wallin et al. 2003).

Susceptibility of fire-damaged trees to bark beetle attacks generally increases with increasing damage level. However, trees must have enough live, suitable phloem for successful attack and brood production to occur (DeNitto et al. 2000; Parker et al. 2006). Populations of bark beetles are not expected to increase in areas of high burn severity where the majority of trees are killed and little to no viable phloem remains, whereas areas of intermediate fire severity are likely to provide the most suitable habitat for bark beetle brood production (Hood and Bentz 2007; Powell et al. 2012).

Besides suitable phloem availability, additional factors affecting fire-driven bark beetle population dynamics include prefire and postfire weather and climatic conditions, prefire bark beetle population levels (e.g., epidemic or incipient populations leading to greater potential for postfire bark beetle effects than endemic levels), and stand structure and composition where extensive tracts of susceptible host within and next to the fire perimeter will promote short-term

Table 8.9—Reciprocal interactions between fire and bark beetles.

Forest type or species	Bark beetle response to fire	Fire (fuels) response to bark beetles
Douglas-fir	Douglas-fir beetle response to fire damage depends on stand conditions: Presence of fire-damaged trees and fire severity Large trees High stand density index (Hood and Bentz 2007) and landscape conditions (Hood et al. 2007) Continuous tracts of susceptible stands, and favorable climate (e.g., drought)	Douglas-fir beetle outbreaks typically cause variable mortality Red-stage surface fuels are relatively unchanged (Harvey et al. 2013), but aerial fuels are more flammable Gray-stage potential fire behavior is likely reduced (Guinta 2016) Post-outbreak snag half-life is 10-20 years
Lodgepole pine	Mountain pine beetle contributes to tree mortality within fire boundary (Amman and Ryan 1991; Geiszler et al. 1984; Jenkins et al. 2014; Lerch 2013; Powell et al. 2012); response to fire depends on: Fire severity Populations prior to fire	Red-stage (1-4 years) potential fire behavior increases (Hicke et al. 2012; but see Simard et al. 2011). Severity of fire is related to severity of mortality (Hoffman et al. 2012a) Gray-stage potential fire behavior is likely reduced (Page and Jenkins 2007) Post-outbreak snag half-life is less than a decade
Ponderosa pine	Complex of bark beetles (western pine beetle, mountain pine beetle, roundheaded pine and pine engraver beetles) contribute to tree mortality within fire boundary and adjacent area following wildland and prescribed fires (Breece et al. 2008; Davis et al. 2012; Fettig et al. 2008, 2010; Fischer 1980; McHugh et al. 2003; Miller and Keen 1960; Miller and Patterson 1927); response to fire depends on: Presence of fire-damaged trees, severe fire effects Favorable climate (e.g., drought) Bark beetle populations prior to fire	Red stage potential fire behavior unknown Gray stage surface fuel increased and crown fuel decreased Post-outbreak snag half-life is less than a decade (Hoffman et al. 2012b)
Whitebark pine, limber pine	Little is known	Post snag half-life is several decades (Perkins and Swetnam 1996)
Jeffrey pine	Jeffrey pine beetle, red turpentine beetle and ips contribute to tree mortality within fire boundary (Bradley and Tueller 2001; Maloney et al. 2008)	Little is known
Pinyon-juniper	Little is known	Thought to increase potential fire behavior (Gaylord et al. 2013), and possibly fire spread in red and gray stage (Linn and others 2013)
Engelmann spruce	Spruce beetle populations may increase in fire-damaged, wind thrown trees (Gibson et al. 1999; Rasmussen et al. 1996)	Red-stage aerial fuels probably increase potential crown fire behavior (1-4 years) (Jorgensen and Jenkins 2011) Gray-stage potential fire behavior low (DeRose and Long 2009) Post-outbreak snag half-life >50 years (Mielke 1950).
Subalpine fir	Western balsam bark beetle response thought to be low, due to direct fire effects and competition with wood borers, but may increase in wind thrown trees (DeNitto et al. 2000)	Little is known
White fir-grand fir	Increased fir engraver activity observed on fire-damaged white fir (Fettig et al. 2008; Maloney et al. 2008; Schwilk et al. 2006)	Little is known
Quaking aspen	Little is known	Little is known

bark beetle outbreaks (Davis et al. 2012; Jenkins et al. 2008). Most bark beetle activity occurs within 1 to 3 years postfire when favorable conditions exist (Davis et al. 2012; Lerch et al. 2016; Tabacaru et al. 2016). One important exception is populations of Douglas-fir beetle, which may take longer to build when prefire populations are low, but populations can be sustained for several years (McMillin and Allen 2003; Rasmussen et al. 1996; Weatherby et al. 2001).

The use of both natural ignition fires and prescribed burns continues to increase in Western forest ecosystems where management goals include fuel reduction, restored functionality, and resilience. Therefore, information on the response of bark beetles to fire is needed to identify where burning can be used appropriately (Jenkins et al. 2014; McCullough et al. 1998; Tabacaru et al. 2016). Predicting tree death following fire is a necessary part of planning prescribed burns, managing stands, and developing salvage-marking guidelines after wildfire (Fowler and Sieg 2004; Hood and Bentz 2007; McCullough et al. 1998). Because bark beetles contribute to postfire tree mortality (reviewed in Jenkins et al. 2008, 2014), models that predict postfire survival are improved if they consider the effects of bark beetle attacks (Breece et al. 2008; Sieg et al. 2006). Conversely, not including bark beetles in predictive models may significantly underestimate delayed tree mortality caused by fire (Hood and Bentz 2007). Mortality levels (less than 10 percent) are typically acceptable in meeting fuels reduction objectives, but may conflict with restoration goals if large-diameter trees are preferentially killed (Perrakis et al. 2011). For example, Douglas-fir beetle shows preference for fire-damaged trees greater than 20 inches diameter (Hood and Bentz 2007).

Fire effects on specific bark beetles are described for host species that occur in the IAP region where there is information on interactions (table 8.9). Information is lacking on fire-bark beetle interactions for whitebark pine, limber pine, pinyon-juniper species, and quaking aspen. The recent ecological interest in whitebark pine and extent of pinyon-juniper forest types in the IAP region warrant further inspection for bark beetles impacting these trees. In addition, behavioral and population dynamics following fire have not been investigated for many bark beetle species, especially for thin-barked trees, where the phloem is easily degraded by direct fire effects.
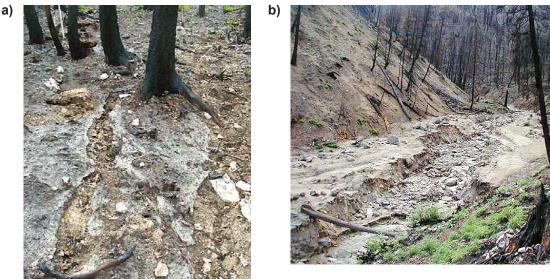
Climate Change Effects

Assuming there will be an increase in wildland fires and climate-driven host tree stress under a changing climate, there will be corresponding increases in likelihood of bark beetle outbreaks in general (Bentz et al. 2010; Hicke et al. 2012; Weed et al. 2013; Williams et al. 2013) and in the potential for intensified interactions between fire and bark beetles, hastening vegetation changes. Bark beetle population dynamics and wildfire behavior are at least partly driven by drought and warming temperatures (e.g., DeRose and Long 2012a,b; Kolb et al. 2016a; Raffa et al. 2008). Drought predisposes trees to bark beetle attacks (e.g.,

Gaylord et al. 2013), and dries fuels that contribute to fire initiation and increased fire spread and severity. Both the area burned and area affected by bark beetles has increased (Bentz et al. 2010; Littell et al. 2009). This trend is likely to continue.
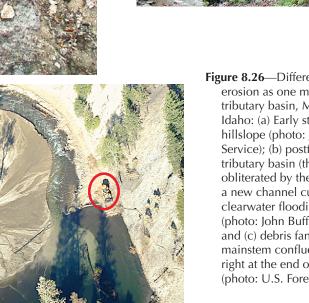
As temperatures increase, bark beetle population cycles may shift or intensify, creating an advantage over hosts. This advantage is not without constraints and may be limited by physiological control of beetle population cycles (Bentz and Powell 2014). With warming climate, increased population reproduction and longer growing seasons have the potential to reduce the time it takes to kill all or most suitable host trees in a stand or landscape. This is likely to result in significantly increased fire hazard during the 1 to 4 years of the red phase and possibly the gray phase. If such mortality occurred across the landscape, the potential for large, severe fires would be increased. However, recent work suggested otherwise in an area on the east side of the Cascade Mountains in the Pacific Northwest (Meigs et al. 2016).

Douglas-fir beetles, and to some extent bark beetles in ponderosa pine, have previously shown the strongest response to fire of all bark beetle species in the IAP region. The beetle attacks fire-damaged trees, leading to increased tree mortality both within and outside fire perimeters (Cunningham et al. 2005; Furniss 1965; Hood and Bentz 2007; McMillin and Allen 2003; Rasmussen et al. 1996) (table 8.9). Increased wildfire activity is likely to affect bark beetles most in forests dominated by Douglas-fir or ponderosa pine. There is little evidence that fire triggers sustained or widespread outbreaks of other bark beetle species outside of fire perimeters. Most bark beetle effects are expected to be relatively short-term pulses of increased mortality (1–2 years for pine bark beetles and 2–4 or more years for Douglas-fir beetle and spruce beetle). There may be increased bark beetle response to planned ignition fires (prescribed burns) under a warmer and drier climate, as more trees will be drought stressed, and postburn weather conditions may not be favorable for tree recovery. However, the potential increased beetle response to prescribed burns should be considered a word of caution and not a deterrent to the use of this practice (Fischer 1980; Tabacaru et al. 2016).

Insect Defoliation and Fire

Outbreaks of western spruce budworm are an important driver of forest dynamics in mixed conifer forest and may extend over tens to hundreds of miles and persist for more than a decade. In the last century, changes in land use and fire suppression have led to an increase in the amount and density of spruce budworm host tree species at the landscape level. This has altered the severity and frequency of both fire and western spruce budworm outbreaks. Despite the ecological and economic significance of these disturbances, the interactions among western spruce budworm, fire, and climate are not fully understood.

a)

b)

c)

Figure 8.26—Different scales and types of postfire erosion as one moves downstream in a steep tributary basin, Middle Fork of the Boise River, Idaho: (a) Early stages of post-fire rilling on a hillslope (photo: John Buffington, U.S. Forest Service); (b) postfire debris-flow passage in the tributary basin (the predisturbance channel is obliterated by the debris-flow deposit, with a new channel cut into the deposit during clearwater flooding at the end of the event) (photo: John Buffington, U.S. Forest Service); and (c) debris fan and backwater flooding at the mainstem confluence (note the bulldozer on the right at the end of the flooded road for scale) (photo: U.S. Forest Service).

Defoliating Lepidoptera and other groups can alter the accumulation and distribution of fuels and vegetation. With outbreaks, insolation at the soil surface may increase, affecting moisture levels of fuels such as dead wood, fallen needles or leaves, and other types of litter. Tree mortality or dead treetops resulting from insect attack influence the availability of fuels on the soil surface (e.g., dead wood and vegetation on the ground) and ladder fuels. These factors play a large role in determining the risk of fire ignition, and fire intensity and severity. Insect outbreaks, including those of western spruce budworm, can increase the probability of fire occurrence and forest fire severity because of increased dead fuel loads (Baskerville 1975; Graham 1923; Hummel and Agee 2003; McCullough et al. 1998; Parker et al. 2006; Pohl et al. 2006; Prebble 1950; Ryerson et al. 2003; Schowalter 1986; Stocks 1987; Swaine and Craighead 1924). Historically, many Douglas-fir forests were shaped by a combination of insect outbreaks and mixed-severity fires (Agee 1993; Hessburg et al. 1994, 2007), suggesting the potential for synergistic interactions.

The only studies to explicitly assess the statistical relationship between fire and western spruce budworm outbreak records reported a negative correlation between the disturbance types over a 3- to 6-year period (Lynch and Moorcroft 2008; Preisler et al. 2010). However, these studies examined outbreaks solely during the late 20th century, when fires were being actively suppressed (Lynch and Moorcroft 2008; Preisler et al. 2010). Flower et al. (2014b) found no evidence of a consistent relationship between the timing of fires and western spruce budworm outbreaks among 10 sites along a longitudinal transect running from central Oregon to western Montana. Before 1890, no consistent relationship was apparent in the timing of the two disturbance types. After ca. 1890, fires were largely absent and defoliator outbreaks became longer lasting, more frequent, and more synchronous (Flower et al. 2014a). Other research corroborates findings that the duration and intensity of western spruce budworm outbreaks have increased with the decrease in forest fire frequency in western Montana since 1910, although these authors note that the frequency of

budworm outbreaks was not affected (Anderson et al. 1987). Defoliation events thus appear to have no discernible impact on subsequent fire risk (Flower et al. 2014b). Recent studies examining other insect species have found that the observed effect of insect activity on subsequent fire behavior is highly dependent on time since outbreak and weather conditions (Hicke et al. 2012).
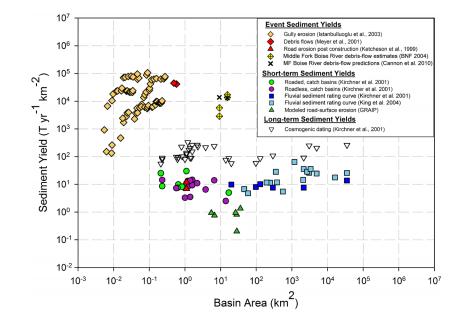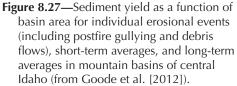
Wildland Fire and Erosion Interactions

As mentioned, recent climate warming has increased the frequency, extent, and severity of wildland fire in western North America (Westerling 2006). In terms of erosional processes, wildland fire removes vegetation (loss of interception, surface roughness, and root strength) and creates hydrophobic (water-repellent) soils, both of which increase the potential for surface erosion (fig. 8.26a) and generation of postfire debris flows in steep terrain during high-intensity rainfall or rain-on-snow events. Debris flows that are routed through tributary basins can dramatically alter channel and floodplain habitats through both scour and deposition (fig. 8.26b) and commonly deliver pulses of sediment and wood to mainstem rivers, which are deposited as debris fans at tributary junctions (fig. 8.26c). Fans can temporally dam mainstem rivers, inducing upstream flooding and sediment deposition (fig. 8.26c). Over time the fan erodes and the sediment pulse is routed through the downstream river, causing changes in channel morphology and aquatic habitat that can be either beneficial or detrimental depending on the size and volume of sediment (e.g., Lewicki et al. 2006). Moreover, elevated sediment loads can cause channel aggradation and subsequent flooding that put infrastructure (roads, bridges, campgrounds, dams) at risk.

The window for postfire erosion is typically several years to a decade, depending on the rates of postfire regrowth (Istanbulluoglu et al. 2004), during which time multiple, repeated erosional events may occur. Unlike landslide-related debris flows, which typically take thousands of years to collect enough colluvium to occur again (Dietrich et al. 1982), postfire debris flows in the IAP region are commonly produced by "bulking" events that can be generated each time severe runoff occurs during the window of vulnerability (Cannon et al. 2003, 2010). Bulking debris flows are caused by overland flow and gullying of exposed soil surfaces that contribute high sediment concentrations to the runoff event, causing a downstream change from clearwater flow, to hyperconcentrated flows, and finally to debris flows. The generation of such debris flows can be very rapid, occurring midway along the length of a hillslope or first-order channel. The rapidity of the events and the substantial window for repeated occurrence, makes postfire debris flows particularly hazardous.

Tools are available for predicting postfire erosion at both plot scales (e.g., Robichaud et al. 2007a, b) and basin scales (e.g., USGS 2017). Burned Area Emergency Response activities can reduce plot- and hillslope-scale erosion, but postfire debris flows occur on scales that are not feasibly mitigated.

Sediment yields from postfire debris flows in the IAP region are typically orders of magnitude larger than background sediment loads in rivers (fig. 8.27). Consequently, climate-driven increases in wildland fire are likely to elevate sediment loads above long-term averages, potentially putting downstream reservoirs at risk given that such facilities were designed under conditions of historically lower sediment yields. While massive postfire debris flows and their sediment loads are impractical to mitigate, low-gradient portions of river networks may be able to store substantial amounts of the load, acting as capacitors and thereby offering natural mitigation (Goode et al. 2012). Moreover, despite the dramatic effects and negative connotations of postfire debris flows, they can have important ecological benefits (e.g., providing supplies of wood that promote

Figure 8.27—Sediment yield as a function of basin area for individual erosional events (including postfire gullying and debris flows), short-term averages, and long-term averages in mountain basins of central Idaho (from Goode et al. [2012]).

channel complexity and supplies of gravel needed for salmonid spawning habitat). Many aquatic and terrestrial organisms in western basins have evolved with, and are adapted to, this type of disturbance, but climate-driven changes in fire regime (frequency, extent, severity) could create levels of disturbance that overwhelm species response and population resilience.

Defoliator and Bark Beetle Interactions

Physiological stress to trees caused by needle loss during defoliator outbreaks can predispose them to bark beetle attacks. However, bark beetle attacks do not make trees more susceptible to attack by defoliating insects, because unlike bark beetles, most insect defoliator outbreaks are not driven by host physiological stress (Mattson and Addy 1975; Redak and Cates 1984). The most common defoliator and bark beetle interactions in the IAP region are the western spruce budworm and Douglas-fir tussock moth defoliation events, with subsequent Douglas-fir beetle and fir engraver attacks. Interactions between Douglas-fir tussock moth and Douglas-fir beetle are more common than Douglas-fir tussock moth and fir engraver, because Douglas-fir is the preferred host for Douglas-fir tussock moth in the IAP region. Similarly, much of the mortality and top kill in larger trees during a western spruce budworm outbreak is caused by Douglas-fir beetle in Douglas-fir and fir engraver in true fir (Azuma and Overhulser 2008; Johnson and Denton 1975; Powell 1994). Growth loss, top kill and mortality following western spruce budworm outbreaks are related to the duration of the outbreak, stand conditions, and associated droughts (Alfaro et al. 1982; Ferrell and Scharpe 1982; Fredericks and Jenkins 1988). Mortality predictions for anticipated western spruce budworm outbreaks should include associated bark beetle mortality (Wickman 1978b).

Defoliation severity and duration influence host resistance and subsequent bark beetle attack. In the Douglas-fir tussock moth system, Douglas-fir tussock moth and fir engraver abundance associated with defoliation are regulated by host resistance, directly by resin, or indirectly by limiting the supply of susceptible hosts (Wright et al. 1979). Douglas-fir tussock moth acts as a stress factor to reduce host resistance, allowing Douglas-fir beetle and fir engraver to attack more trees successfully. Douglas-fir beetle and fir engraver activity generally increase after western spruce budworm and Douglas-fir tussock moth defoliation events, though this increase is variable. The increase is influenced by factors such as defoliation intensity, logging activity, drought, presence of root disease, tree-damaging storm events, host tree size and availability (percent of a stand), and stand conditions in the IAP region (Ferrell and Sharpe 1982; Fredericks and Jenkins 1988; Johnson and Denton 1975; Weatherby et al. 1992) and other areas of the West (Azuma and Overhulser 2008; Hadley and Veblen 1993; Klein and Bennett 1995; Lessard and Schmid 1990; Negrón et al. 2014; Wickman 1963, 1978b; Wright et al. 1984).

Bark beetle populations rise and continue killing trees for 2 to 3 years after the short-lived Douglas-fir tussock moth outbreak crashes. Generally, Douglas-fir beetle activity begins increasing during a Douglas-fir tussock moth outbreak when trees are over 80 percent defoliated, and peaks 1 to 2 years following the outbreak (Negrón et al. 2014; Weatherby et al. 1997). Some studies suggest that Douglas-fir trees completely defoliated (or nearly so) may not be the optimal host for beetle brood production because of loss of nutrients, with trees becoming a sink for beetles rather than a source (Fredericks and Jenkins 1988; Weatherby et al. 1997; Wright et al. 1979). Similarly, fir engraver populations increased in trees that were 80 percent defoliated; attacks by Douglas-fir tussock moth lasted 2 years, and 50 percent of attacks occurred on trees defoliated over 90 percent (Wright et al. 1984).

The attack pattern of Douglas-fir beetle and fir engraver following western spruce budworm outbreaks is less clear, perhaps because of the extensive duration and fluctuation of defoliation severity of western spruce budworm outbreaks. Douglas-fir beetle prefers to attack trees heavily defoliated by western spruce budworm (McGregor et al. 1983; Sturdevant et al. 2012). During both Douglas-fir tussock moth and western spruce budworm outbreaks, attacks occur at the tops of trees, making ground observations more difficult (Azuma and Overhulser 2008; Weatherby et al. 1997; Wright et al. 1984).

Site conditions, such as moisture, can influence bark beetle mortality associated with Douglas-fir tussock moth and western spruce budworm outbreak events. After a Douglas-fir tussock moth outbreak in British Columbia, Douglas-fir beetle played only a minor role as a mortality agent (Alfaro et al. 1987). However, a higher percentage of trees were killed by Douglas-fir beetle in eastern Oregon (Wickman 1978b) and central Idaho (Weatherby et al. 1992). Negrón et al. (2014) found no difference in Douglas-fir beetle attack level following light or heavy defoliation of Douglas-fir in Colorado; Douglas-fir beetle activity was attributed to dry site conditions. High host mortality during overlapping western spruce budworm and bark beetle outbreaks suggests that stand susceptibility to western spruce budworm epidemics may be an important precursor to Douglas-fir beetle outbreaks (Hadley and Veblen 1993). Overall, trees with over 90 percent defoliation appear to have a high probability of being killed by bark beetles, and dry sites, even with less defoliation, will be more attractive to bark beetles than wetter sites. In addition, Douglas-fir beetle populations can build in defoliated trees to infest other stressed trees (Wickman 1978b).

Changes in stand composition and structure can be influenced by defoliator events followed by bark beetle mortality. Stand trajectories are differently impacted by mortality caused by successive attacks of western spruce budworm and Douglas-fir beetle (Azuma and Overhulser 2008; Hadley and Veblen 1993). Hadley and Veblen (1993) suggested that stand structure altered by increasing mortality among the climax species would favor seral species such

as lodgepole pine in Colorado. However, another study spanning the large western spruce budworm outbreak and associated Douglas-fir beetle and fir engraver mortality of the 1980s found that western spruce budworm host species stocking did not change over a 20-year period in Oregon and Washington (Azuma and Overhulser 2008). Azuma and Overhulser (2008) found that the number of trees severely defoliated was not related to any factors, such as aspect, slope, elevation, or climax tree species, other than the number of host trees available. Negrón et al. (2014) reported that stand trajectories were set back to a seral stage favoring ponderosa pine after Douglas-fir tussock moth and Douglas-fir beetle activity in Douglas-fir of the Colorado Front Range.

Changes in the Defoliator-Bark Beetle Dynamic in Response to Climate Change

Warming temperatures and altered precipitation regimes in the future could affect the incidence and duration of bark beetle attacks on defoliated trees because bark beetles target stressed trees. Warm and dry conditions occurring during defoliator outbreaks are likely to accelerate the loss of trees from bark beetles. Drought-stressed trees are likely to lose needles, and defoliation levels over 90 percent could increase, thereby increasing the potential for bark beetle attack. More frequent and severe wildfires will influence bark beetle response to defoliation events, primarily because bark beetle populations increase after wildfires and could be available to utilize pulses of defoliated hosts.

Bark Beetle and Disease Interactions

Bark beetles have the potential to affect forest pathogens, and vice versa. These interactions may be either direct or indirect (Paine et al. 1997; Parker et al. 2006). Insect vectors, for example, directly aid in the dissemination and introduction of pathogens into new host trees (Cardoza et al. 2008; Klepzig and Six 2004). Feeding insects may benefit nutritionally with pathogen colonization (Bentz and Six 2006). Conversely, fungi and other micro-organisms present in diseased or decaying wood may have antagonistic effects on invading insects (Cardoza et al. 2006; Six and Bentz 2003). Indirect effects on bark beetle and pathogen interaction typically occur through alterations to host trees and habitat (Parker et al. 2006).

Bark Beetle and Dwarf Mistletoe Interactions

Bark beetle-dwarf mistletoe interactions are complex and not completely understood, but they appear to vary with the specific dwarf mistletoe, bark beetle, and host condition. Dwarf mistletoes can increase or decrease the susceptibility of host trees to bark beetles, or have no effect at all (Hawksworth and Wiens 1996). Dwarf mistletoe-caused reductions in tree growth and phloem thickness in the bole may decrease mountain pine beetle performance. However, evidence for dwarf mistletoe infestation decreasing phloem

thickness in lodgepole pine remains inconclusive (Agne et al. 2014). Shore et al. (1982) observed higher mountain pine beetle attack rates in lodgepole pines without dwarf mistletoe in British Columbia. In contrast, mountain pine beetle preferentially attacked ponderosa pine infected with dwarf mistletoe in Colorado (Frye and Landis 1975; Johnson et al. 1976; McCambridge et al. 1982). Although no relationships between mountain pine beetle and dwarf mistletoe were observed in areas where mistletoe infestation ratings were low, there was a significant positive trend in beetle attacks in stands with higher infestation ratings (Johnson et al. 1976).

Pine engraver beetles (*Ips* spp.) may preferentially attack ponderosa pine and pinyon pine heavily infested by dwarf mistletoe (Kenaley et al. 2006; Negrón and Wilson 2003). During periods of drought in the Southwest, *Ips* species primarily focused their attacks on suppressed and intermediate size classes of ponderosa pine heavily infected by dwarf mistletoe (Kenaley et al. 2008). Similarly, Douglas-fir beetles concentrated their attacks on heavily dwarf mistletoe-infested Douglas-fir during initial stages of a drought event in the Southwest (McMillin 2005); more than 60 percent of Douglas-fir trees having dwarf mistletoe ratings of 4 or greater (high infection) were killed by Douglas-fir beetles, whereas 30 percent of trees having a rating of 2 or less (low infection) were attacked. Most of the heavily infested trees were attacked just before or at the beginning of the drought, particularly the largest diameter trees; low to moderately infected trees were attacked later. These severely infected, large-diameter trees probably provided a reservoir of beetles during endemic population levels. However, trees of all infestation levels were attacked once populations increased to high levels.

Bark beetle outbreaks can also affect dwarf mistletoe dynamics, affecting tree growth within a stand. The net effect of bark beetle outbreaks on dwarf mistletoe is probably a moderate short-term reduction in stand-level dwarf mistletoe infestation, and a greater availability of resources for dominant and codominant trees, allowing them to release, and potentially become more tolerant of diseases or other stressors. In stands with heavy mistletoe infestation, changes in stand structure following bark beetle outbreaks can also facilitate dwarf mistletoe dissemination if surviving trees are infected by dwarf mistletoe. Increased incidence of dwarf mistletoe in post-outbreak stands can reduce growth and productivity and slow stand recovery over time (Agne et al. 2014; Shore et al. 1982). The magnitude of effects caused by the interactions between bark beetles and dwarf mistletoes is likely to intensify under both warmer/drier and warmer/wetter climates because of increased host tree stress, elevated tree mortality, and potential range expansion of dwarf mistletoes (Kliejunas 2011).

Bark Beetle and Root Disease Interactions

Root diseases have long been associated with endemic-level bark beetle populations and may serve as refugia for these populations (Tkacz and Schmitz 1986). Root disease-infected trees maintain endemic populations of mountain

pine beetle and may help to trigger populations during the incipient phase of an outbreak (Geiszler et al. 1980; Goheen and Hansen 1993; Hunt and Morrison 1986). Hinds et al. (1984) showed a significant association between the presence of Armillaria root disease, bark beetle infestation, and ponderosa pine mortality under endemic conditions in the Black Hills of South Dakota; they found 75 percent of mountain pine beetle-infested trees had Armillaria root disease. Endemic populations of fir engraver also regularly attack and accelerate the death of root disease-infected white fir and grand fir trees (Goheen and Hansen 1993). However, other stressors such as drought, high stand density, and severe defoliation, may override this pattern (Guyon 1992). Many bark beetle species, including Douglas-fir beetle and spruce beetle, prefer to infest fresh downed trees with impaired defenses (Franceschi et al. 2005). Significant wind events in and adjacent to root disease centers can consequently result in substantial amounts of suitable host material for bark beetle colonization and brood production (Hebertson and Jenkins 2008). These interactions may become more pronounced under warmer and drier climates, as forests affected by root disease become further stressed by drought, and become more susceptible to bark beetle attack (Allen et al. 2010).

Bark Beetle and White Pine Blister Rust Interactions

The combination of white pine blister rust and mountain pine beetle has already caused major population changes in white pines in the western United States (Keane and Arno 1993; Loehman et al. 2011a). Schwandt and Kegley (2004) found that mountain pine beetles were more likely to attack blister rust-infected whitebark pines when populations were at endemic levels, but this selection pattern was reversed when populations were at epidemic levels. Similarly, Dooley and Six (2015) suggest that preference of mountain pine beetle for blister rust-infected trees is likely to be curvilinear, with beetles initially responding positively to increasing infection severity, then showing a negative response when severity becomes high. However, others have found that mountain pine beetles preferred whitebark pines stressed by white pine blister rust and preference increased as infection increased (Bockino and Tinker 2012; Six and Adams 2007).

Climate change has resulted in an increase in areas thermally favorable to bark beetle reproductive success in whitebark pine ecosystems (Bentz et al. 2016; Bockino and Tinker 2012). Larson (2011) concluded that where blister rust infections were most severe prior to the recent mountain pine epidemic, the effects of both disturbances could be amplified and impacts on whitebark pine increased. During recent severe mortality of whitebark pine and limber pine caused by mountain pine beetle and secondary bark beetles, many potentially blister rust-resistant or -tolerant trees were killed. This could result in decreased whitebark pine regeneration and potentially the accelerated loss of the species.

However, in areas where moderate blister rust infections occurred before the mountain pine beetle epidemic, the combined effects of the disturbances may result in increased resistance to blister rust, because beetle attacks may be focused on rust-infected trees. In summary, climate-rust-beetle interactions now and in the future are complex and not uniform (Larson 2011).

Insects as Vectors of Pathogens

In the IAP region, black stain root disease is caused by *Leptographium wageneri* var. *wageneri* on pinyon pines, and *L. wageneri* var. *ponderosum* on Jeffrey and ponderosa pines. The fungus causing this root disease is vectored in part by root-feeding bark beetles and other insects (Bishop and Jacobi 2003; Goheen and Cobb 1980; Harrington et al. 1985). The biology of these beetles is not well known, but they have been shown to attack the roots of drought-weakened pines (Goheen and Hansen 1993). In turn, black stain root disease on ponderosa pine has been demonstrated to predispose trees to attack by other bark beetles (both *Dendroctonus* and *Ips* spp.), either through increased attraction or reduced resistance of weakened, infected trees (Goheen and Hansen 1993). Successful vectoring of the fungus by root-feeding bark beetles may be dependent on moisture conditions, with both beetles and fungi favoring high soil moisture.

Summary

The interactions between bark beetles and disease represent important and complex forest ecosystem dynamics that can have an array of impacts on the structure and function of our forests. Climate change will have demonstrable impacts on the frequency and intensity of bark beetle and disease outbreaks, particularly at the margins of host ranges and in interactions facilitated by stress on host ecosystems (Kliejunas 2011). Although episodic mortality has occurred historically, some ecosystems may already be responding to climate change. Forests may become increasingly vulnerable to higher tree mortality rates and die-off in response to future warming and drought in the presence of forest insects and diseases, even in environments that are not normally considered water limited. This greater vulnerability further suggests risks to ecosystem services, including the loss of sequestered forest carbon and associated atmospheric feedbacks (Allen et al. 2010).

Fire and Nonnative Pathogens

The most important nonnative tree disease in the IAP region is white pine blister rust (Smith and Hoffman 2000). Climate change could indirectly affect white pine blister rust by changing the geographic range of both the pines and the alternate (*Ribes*) host. Both hosts may become exposed to inoculum earlier or later in the year. The physiology of both hosts would be different at these different times of the year, possibly changing susceptibility. Resistance may change during different stages of a host's seasonal growth or under

changing temperature regimes (Sniezko et al. 2011) (see also the *White Pine Blister Rust* subsection above).

With warming, fires are currently projected to increase in size, frequency, and intensity (Flannigan et al. 2000; Westerling et al. 2011). These changes in fire may facilitate regeneration of white pines (Loehman et al. 2011a). Conversely, drought conditions may inhibit regeneration (McCaughey and Weaver 1990; Tomback et al. 1993). There is documentation of unsuccessful postfire regeneration in Colorado, even in stands previously dominated by limber pine with suitable conditions and a nearby seed source, and stand-replacing fires could cause extirpation of some limber pine populations (Huckaby 1991; Shankman and Daly 1988).

A study in Colorado illustrates the differences in patterns of reproduction in limber pine as compared to Great Basin bristlecone pine after fire-caused disturbance (Coop and Schoettle 2009). The study concludes that regeneration of bristlecone and limber pine may benefit from increases in natural disturbance, but that beneficial responses may require many decades. Regeneration can occur only if seed source and dispersal are present; survival will occur only if seedlings establish and can survive climatic stresses and the local frequency of fires. In addition, *Ribes* populations may increase after fire through regeneration by seed and sprouting from roots and rhizomes. However, re-burns soon after an initial fire can eliminate regenerating *Ribes* bushes before they can develop a seed bank for the next forest regeneration cycle (Zambino 2010).

White pines exist in multiple forest types and fire regimes, but most exist in infrequent, mixed- and high-severity fire regimes. The implications of changes in fire regimes in forests containing white pines threatened by white pine blister rust have been reviewed extensively for whitebark pine, the species that is currently at the highest risk (Keane and Arno 1993; Loehman et al. 2011b). In whitebark pine stands, fire can reduce shade-tolerant understory species such as fir, reduce rust- and beetle-infested older trees, promote stand conditions that favor whitebark pine seedlings, and provide openings for animals to plant seeds and facilitate plantings of rust-resistant seedlings (Keane and Parsons 2010; Trusty and Cripps 2011). In a modeling study based on Northern Rockies conditions, Loehman et al. (2011) predicted that the rate of canopy gap production could occur at a high enough rate to allow western white pine (*Pinus monticola*) regeneration to survive, despite pressure from white pine blister rust. The few stands of western white pine and sugar pine (*Pinus lambertiana*) in the IAP region may be sufficiently different that the model parameters used for predicting trends are not applicable. Severe fires may reduce mycorrhizal communities and populations to the point that establishing white pine regeneration, either planted or natural, becomes very difficult, but more frequent low-severity fires have not appeared to affect mycorrhizae (Trusty and Cripps 2011). Severe fire that kills rust-resistant pine trees may ensure

continued high rust-induced mortality in the future, because it dampens the rate of rust-resistant adaptations (Keane et al. 2012). Alternatively, where rust-resistant five-needle pines survive fire, they may provide the seeds for populating future landscapes that are resilient to both rust infection and fire mortality.

As white pine blister rust slowly kills pine trees, dead foliage and wood added to the fuel bed may increase fire intensity, which may then increase tree mortality (Loehman et al. 2011a). In stands dominated by five-needle pines, white pine blister rust infection often results in the slow, progressive thinning of the shade-intolerant pine overstory, allowing shade-tolerant competitors to occupy the openings. This creates substantially different canopy fuel conditions, such as lower canopy base heights, higher canopy bulk densities, and greater canopy cover, which facilitate more frequent and intense crown fires (Keane et al. 2002; Schwandt et al. 2010).

Conclusions

Ongoing and projected climate change for geographic areas encompassed by the IAP indicates a likelihood of varied shifts and changes to important disturbance regimes. Ecological disturbances are often specific to particular vegetation communities, elevations, and geographic areas. However, we acknowledge there is a lack of information for many of the multifaceted biological systems we have discussed in this chapter. The geographic and ecological diversity of the IAP region adds to the complexity of changes in the timing, magnitude, frequency, and duration of disturbance events, as well as the interactions of disturbances on a landscape. Climate-caused variations to ecological disturbances are difficult to describe without fully understanding how the changes will affect vegetation on our landscape (Chapters 6, 7). Although high levels of uncertainty exist, expected increases in disturbances, such as wildland fire, can and often do lead to specific changes in biodiversity and habitat heterogeneity (Grime 1973; McKinney 1998), affecting additional agents of change (i.e., invasive species, insects, and geologic hazards) and their respective interactions.

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