Chapter 8: Effects of Climate Change on Ecological Disturbance in the Northern Rockies Region

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Introduction

This chapter describes the ecology of important disturbance regimes in the Forest Service, U.S. Department of Agriculture (USFS) Northern Region and the Greater Yellowstone Area, hereafter called the Northern Rockies 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*—insect, disease, fire, weather, even human activity—and the effects of that agent on the landscape (table 8.1). More specifically, a disturbance regime is the cumulative effect of multiple disturbance events over space and time (Keane 2013). Disturbances disrupt an ecosystem, community, or population structure and change elements of the biological environment, physical environment, or both (White and Pickett 1985). The resulting 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 biological diversity in the form of shifting, heterogeneous mosaics of diverse communities and habitats across a landscape (McKinney and Drake 1998), and biodiversity is generally highest when disturbance is neither too rare nor too frequent on the landscape (Grime 1973).

A changing climate may already be altering characteristics of disturbance agents, events, and regimes, with additional effects expected in the future (Dale et al. 2001). Climate changes 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 (*Dendroctonus* spp.) outbreaks and wildfires, can result in highly visible, rapidly occurring, and persistent changes in landscape composition and structure. Understanding how altered disturbance patterns and multiple disturbance interactions might result in novel and emergent landscape behaviors is critical for addressing climate change impacts and for designing land management strategies that are appropriate for future climates (Keane et al. 2015).

We summarize five disturbance types present in the Northern Rockies region that are sensitive to a changing climate. Wildfires, bark beetles, white pine blister rust (*Cronartium ribicola*), other forest diseases, and nonnative plant invasions acting individually or synergistically can transform landscape patterns and ecological functions. This chapter provides background that can help managers understand the important role of disturbances on Northern Rockies landscapes, and anticipate how, when, where, and why climate changes may alter the characteristics of disturbance regimes.

Wildfire

Overview

Wildland fire is ubiquitous throughout forest ecosystems of the Northern Rockies and was historically the most important and extensive landscape disturbance in the region (Hejl et al. 1995). Wildfire emerged as a dominant process in North America after the end of the last glacial period, about 16,500 to 13,000 years B.P., commensurate with rapid climate changes and increased tree cover (Marlon et al. 2009). In the Northern Rockies region, many forest types are fire-prone and fire adapted, meaning that fire is an integral and predictable part of their maintenance and ecological functioning. Wildfire, as well as other disturbances such as insect outbreaks, disease, drought, invasive species, and storms, is part of the ecological history of most forest ecosystems, influencing vegetation age and structure, plant species composition, productivity, carbon (C) storage, water yield, nutrient retention, and wildlife habitat (Agee 1993).

Climate and fuels are the two most important factors controlling patterns of fire in forest ecosystems. Climate controls the frequency of weather conditions that promote fire, whereas the amount and arrangement of fuels influence fire intensity and spread. Climate influences fuels on

Table 8.1—Characteristics used to describe disturbance regimes.[a]

Disturbance characteristic	Description	Example
Agent	Factor causing the disturbance	Mountain pine beetle is the agent that kills trees
Source, cause	Origin of the agent	Lightning is a source for wildland fire
Frequency	How often the disturbance occurs or its return time	Years since last fire or beetle outbreak (scale dependent)
Intensity	A description of the magnitude of the disturbance agent	Mountain pine beetle population levels; wildland fire heat output
Severity	The level of impact of the disturbance on the environment	Percent mountain pine beetle tree mortality; fuel consumption in wildland fires
Size	Spatial extent of the disturbance	Mountain pine beetles can kill trees in small patches or across entire landscapes
Pattern	Patch size distribution of disturbance effects; spatial heterogeneity of disturbance effects	Fire can burn large regions but weather and fuels can influence fire intensity and therefore the patchwork of tree mortality
Seasonality	Time of year at which a disturbance occurs	Species phenology can influence wildland fire effects; spring burns can be more damaging to growing plants than fall burns on dormant plants
Duration	Length of time that disturbances occur	Mountain pine beetle outbreaks usually last for 3–8 years; fires can burn for a day or for an entire summer
Interactions	Disturbances interact with each other, climate, vegetation, and other landscape characteristics	Mountain pine beetles can create fuel complexes that facilitate or exclude wildland fire
Variability	Spatial and temporal variability of the above factors	Highly variable weather and mountain pine beetle mortality can cause highly variable burn conditions resulting in patchy burns of small to large sizes

[a] From Keane (2013).

longer time scales by shaping species composition and productivity (Dale et al. 2001; Marlon et al. 2008; Power et al. 2008), and large-scale climatic patterns such as the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) are important drivers of forest productivity and susceptibility to disturbance (Collins et al. 2006; Kitzberger et al. 2007). Current and past land use, including timber harvest, forest clearing, fire suppression, and fire exclusion through grazing have affected the amount and structure of fuels in the United States (Allen et al. 2002; Falk et al. 2011; Pausas and Keeley 2014).

Disturbance effects can overwhelm the direct effects of climate changes on ecosystems. As described in other chapters in this publication, climate changes influence forests directly; for example, it has been suggested that drought and heat stress 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 climate changes on forest ecosystems will be caused by altered disturbances, often occurring with increased frequency and severity. The warmer, drier conditions expected with climate change are likely to increase fire frequency, fire season length, and cumulative area burned in the coming decades in the western United States (Flannigan et al. 2006; McKenzie et al. 2004). Climate changes may also increase the frequency or magnitude of extreme weather events that affect fire behavior (Kurz et al. 2008b; Lubchenco and Karl 2012). Although shifts in vegetation composition and distribution caused by climate alone may occur over decades or centuries, wildfires can temporarily or persistently reorganize landscapes over a period of days (Overpeck et al. 1990; Seidl et al. 2011).

The role of fire in ecosystems and its interactions with dominant vegetation is termed a “fire regime” (Agee 1993). Fire regimes are 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 (table 8.2). These characteristics vary across vegetation types 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). Ecosystems in the Northern Rockies have been subject to a range of historical fire regimes, including (1) frequent (1–35 years), low- or mixed-severity fires that replaced less than 25 percent of the dominant overstory vegetation; (2) moderate-frequency (35–200 years), mixed-severity fires that replaced up to 75 percent of the overstory; and (3) infrequent (200+ years), high-severity fires that replaced greater than 75 percent of

Table 8.2— Risk assessment for fire regime changes.[a]

Fire regime component	Predicted direction of change	Main driver(s) of change	Projected duration of change	Likelihood of change
Ignitions	Unknown	Changes in lightning frequency and anthropogenic ignitions	Unknown	Unknown
Area burned	Increase	Increased fire season length, decreased fuel moistures, increased extreme fire conditions	Until a sufficient proportion of the landscape has been exposed to fire, thus decreasing fuel loads and increasing structural and species heterogeneity	High
Fire frequency	Increase	Increased ignitions, increased fuel loads, decreased fuel moistures, increased fire season length	In forested systems until a sufficient proportion of the landscape has been exposed to fire, reducing fuel loads and continuity; in grass- and shrubland systems, until global climate stabilizes	Moderate
Average fire size	Increase	Increased fire season length, decreased fuel moistures, increased extreme fire conditions	Until a sufficient proportion of the landscape has been exposed to fire, thus increasing the likelihood that previous fires will restrict growth of current year fires	High
Fire season length	Increase	Increased temperatures, decreased precipitation, decreased winter snowpack, decreased runoff	Until the global climate system stabilizes; predicted to increase as climate changes become more severe	High
Fire severity	Increase	Decreased fuel moistures, increased extreme fire conditions	In dry forest types, until fires decrease surface fuel loads; in mesic forests, if increased fire frequency decreases fuel loads	Moderate

[a] Developed using expert opinion and information from literature as summarized in this chapter.

the dominant overstory vegetation (fig. 8.1). More-detailed information on fire regimes specific to individual vegetation species and vegetation types can be found in Chapter 6 of this volume.

Wildland fire behavior is influenced by variability in environmental conditions including vegetation type and distribution, climate, weather, and topography. Despite major human influences on western U.S. wildfires since Euro-American settlement, climate is generally considered to be the primary control on fire regimes in the region, influencing vegetation production and condition as well as the physical environment (Marlon et al. 2012). Where rates of vegetation production outpace decomposition, sufficient biomass is available to support fires, although higher elevation regions with abundant fuels do not always have sufficiently dry conditions to sustain a fire. In these systems, short-duration drying episodes generally do not create dry enough conditions to sustain a fire, but 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 in the Northern Rockies region, during which time there are ample sources of ignition from lightning strikes and humans. Therefore, the active fire 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 (Littell et al. 2009).

At annual time scales, weather is the best predictor of fire characteristics such as area burned and fire size. Correlations between weather and annual area burned by fire or the number of large fires are similar for both pre-20th-century fires and fires that have occurred during the past few decades. Fire-weather relationships have been constructed for forested ecosystems of the Pacific Northwest (Hessl et al. 2004; Heyerdahl et al. 2002, 2008a) and Northern Rockies (Heyerdahl et al. 2008b; Littell et al. 2009; Westerling et al. 2003, 2006), based on tree-ring and fire-scar records and independently reconstructed climate, or observations of fire

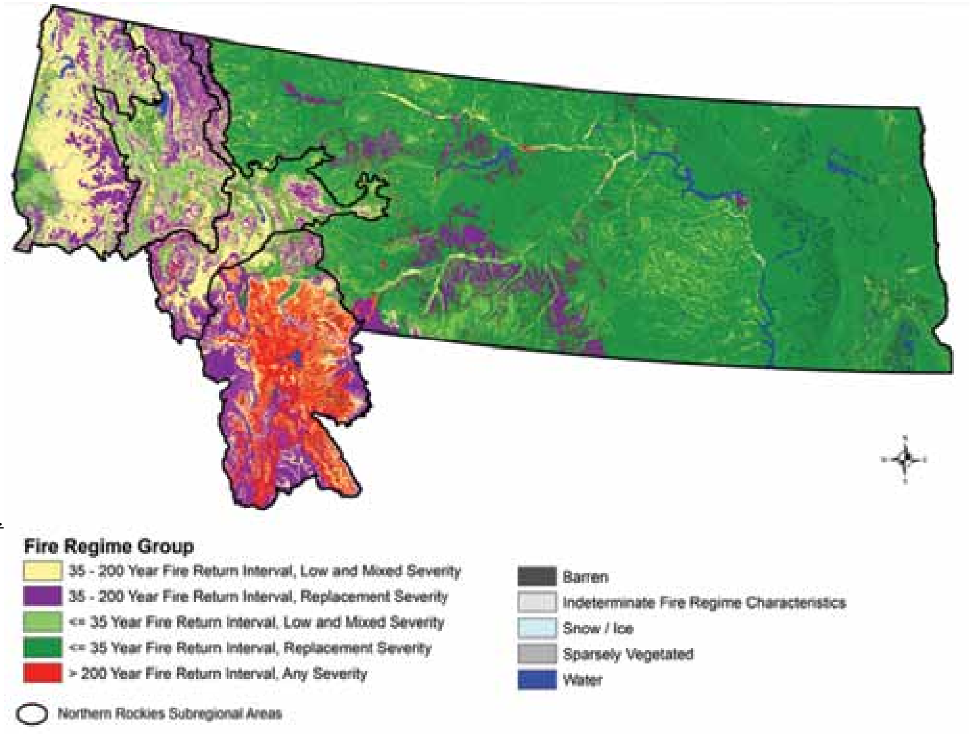

Figure 8.1—Fire regime groups for the Northern Rockies, LANDFIRE mapping program. The fire regime group layer characterizes the presumed historical fire regimes within landscapes based on interactions among vegetation dynamics, fire spread, fire effects, and spatial context (see http://www.landfire.gov/NationalProductDescriptions12.php).

events and weather in the seasons leading up to and during the fire where records are available. Regionally, widespread fire years are correlated with drought (Heyerdahl et al. 2008b; Morgan et al. 2008), and these regionally synchronous fires have generally occurred in the Northern Rockies (Idaho and western Montana) during years with relatively warm spring-summers and warm-dry summers (Heyerdahl et al. 2008a; Morgan et al. 2008).

In nonforested systems in the eastern Northern Rockies, precipitation amount, at both short (weeks to months) (Littell et al. 2009) and long (decades to centuries) (Brown et al. 2005) time scales is the dominant control on fire. During the fire season, the amount and timing of precipitation largely determine availability and combustibility 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). In contrast to the grasslands of the southwestern United States, antecedent precipitation has not been found to be a significant driver of large fires in the northern grasslands; rather, 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).

Humans are also important drivers of wildfire, via altered ignition patterns associated with land clearing and land cover change, agriculture, introduction of exotic species, and fire management (fuels treatments and fire suppression/exclusion). Grazing and the introduction of nonnative species have altered ecological processes that affect fire, including fuel loading and continuity, forest composition and structure, nutrient cycling, soils, and hydrology (Marlon et al. 2009; Swetnam et al. 1999). For many sagebrush ecosystems of low to moderate productivity, fire intervals are 10 to 20 times shorter today than what is estimated for pre-20th-century conditions (Peters and Bunting 1994; Whisenant 1990; see also Chapter 7), because of the spread and dominance of the nonnative annual cheatgrass (*Bromus tectorum*). Dry forests, shrublands, and grasslands in the region exist in a state of "fire deficit" as the result of fire exclusion, leading to less frequent wildfire, higher stand densities, higher fuel quantities, and higher fuel continuity. This has increased the potential for crown fires in forests with a history of low-severity fire regimes (Agee 1998; Peterson et al. 2005) and in some forests with mixed-severity regimes (Taylor and Skinner 2003).

Wildfire Shapes Landscape Patterns

The composition and structure of forests in the Northern Rockies is determined by climate, elevation, topographic position, and history of fire. In general, fire regimes vary along environmental gradients, with fire frequency decreasing and fire severity increasing with elevation (although aspect and slope position can influence fire patterns). For example, low-severity fires are typical in many ponderosa pine (*Pinus ponderosa*) forests at low elevations. Historically, fires here 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 rare (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. Conversely, high-severity fires occurring at intervals of more than 300 years are typical in subalpine forests and tend to result in high mortality of mature trees ("stand replacement") because

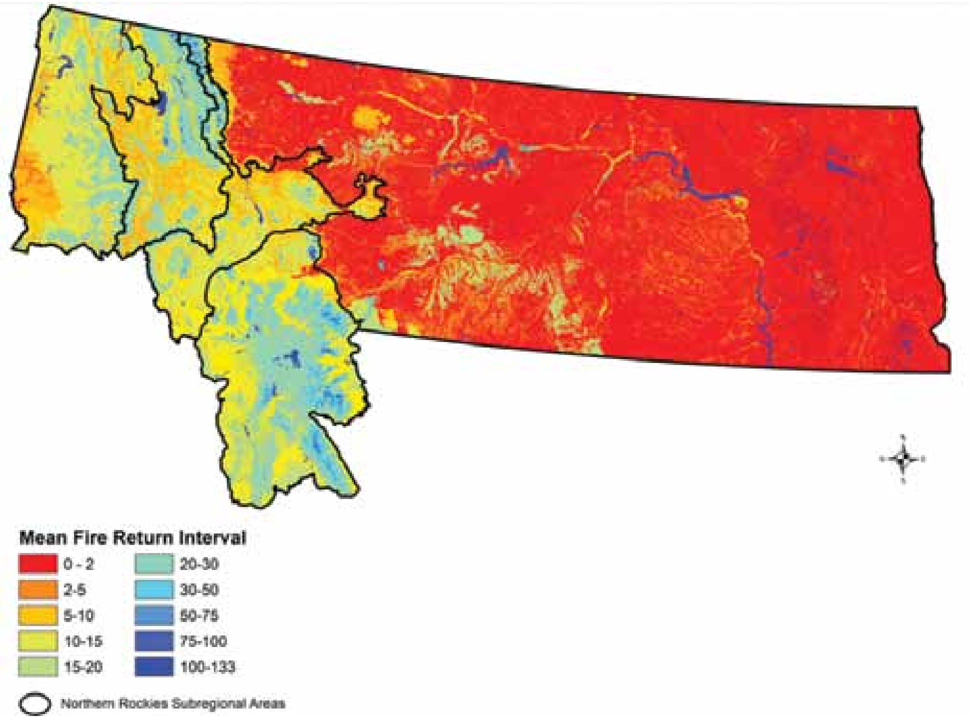

Figure 8.2—Mean fire return interval for the Northern Rockies, LANDFIRE mapping program. The mean fire return interval layer quantifies the average period between fires under the presumed historical fire regime (see http://www.landfire.gov/NationalProductDescriptions13.php for more information).

long intervals between fires result in dense, multi-storied forest structures that are susceptible to crown fires (Agee 1998) (fig. 8.2).

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. 8.3). 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 not altered fire regimes (Romme and Despain 1989; Schoennagel et al. 2004). For example, large, stand-replacing fires occasionally occurred in lodgepole pine (*Pinus contorta* var. *latifolia*) forests in Yellowstone National Park (Romme 1982), and many (but not all) lodgepole pine trees can regenerate prolifically when heating from fires releases seed from serotinous cones (Schoennagel et al. 2003).

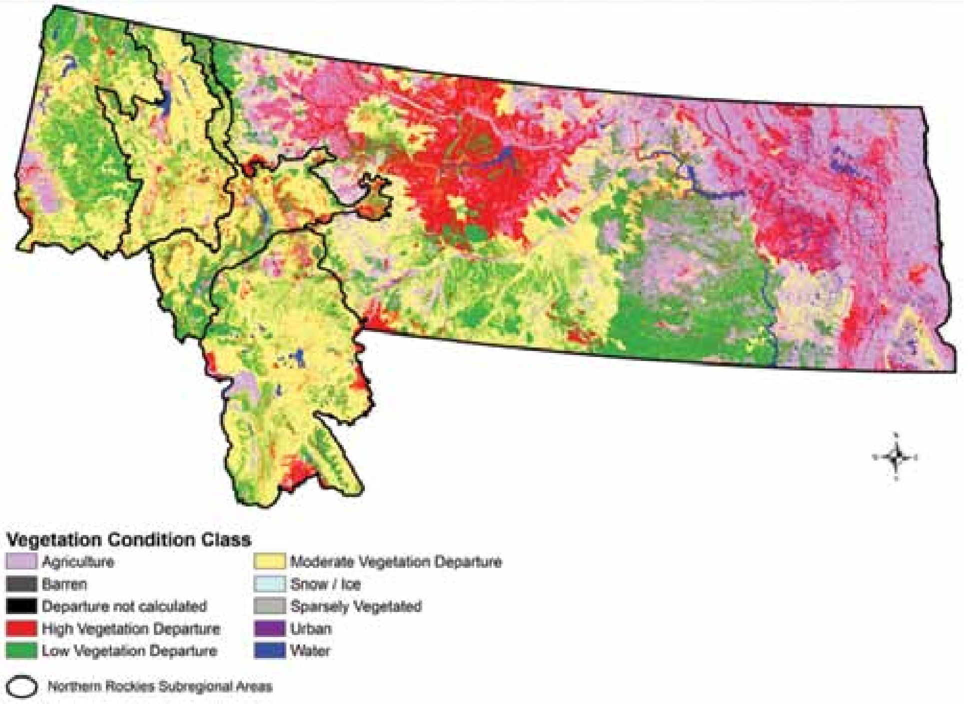

Figure 8.3—Vegetation condition class for the Northern Rockies, LANDFIRE mapping program. The vegetation condition class layer quantifies the amount that current vegetation has departed from the simulated historical vegetation reference conditions (see http://www.landfire.gov/NationalProductDescriptions10.php).

Wildfires and Forest Carbon Sequestration

Concerns about projected changes in global climate have raised an expectation that forests can help mitigate climate changes via management for increased carbon sequestration and storage (Sommers et al. 2014). Forests contain large reservoirs of carbon in soils (~45 percent of total storage), aboveground and belowground live biomass (~42 percent), dead wood (~8 percent), and litter (~5 percent) (Pan et al. 2011). The carbon sequestration potential of Earth's forests is about 33 percent of global emissions from fossil fuels and land use (Denman 2007), and North American forests currently offset about 13 percent of annual continental fossil fuel emissions (Pacala et al. 2007). The potential for forests 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 (Loehman et al. 2014).

Carbon typically accumulates in woody biomass and soils for decades to centuries until a disturbance event such as wildfire releases this stored carbon into the atmosphere (Goward et al. 2008). Wildfire in forested ecosystems is one of the primary disturbances that regulate patterns of carbon storage and release (Kasischke et al. 2000). The amount and rate of carbon release from a wildfire depend on the extent and severity of the fire, as well as pre-disturbance site conditions and productivity (Bigler et al. 2005; Dale et al. 2001; Falk et al. 2007). For example, high-severity fires typical of mid-to-upper elevation forests in the Northern Rockies 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 carbon is stored in woody biomass as forests regrow. Low-severity fires such as those that occur in low-elevation dry forest types typically release less carbon per fire event (although total emissions are dependent on area burned) at more frequent intervals than with stand-replacing regimes, and favor long-lived and fire-resistant (or tolerant) forest species that typically survive multiple fire events (Ritchie et al. 2007). Carbon losses from wildland fire are balanced by carbon capture from forest regrowth across unmanaged fire regimes and over multiple decades, unless a lasting shift in dominant plant lifeform occurs or fire return intervals change (Kashian et al. 2006; Wiedinmyer and Neff 2007).

There are several important ideas to consider when managing forests and fires for carbon resources. First, as stated above, unless structural or functional ecosystem shifts occur, net carbon balance in disturbance-adapted systems at steady state is zero when assessed over long time periods and at large spatial scales. Under these conditions, although a fire may result in a temporary loss of stored carbon from a forest to the atmosphere (i.e., the forest temporarily becomes a carbon source), this effect is transitory and balanced by carbon accumulation as the forest regrows. The time required for the postfire environment to shift from carbon source to sink varies among forest types and climates. For example, in simulations of effects of stand-scale fuels treatments on carbon-fire relationships in Northern Rockies forests, postfire carbon recovery occurred in 10 to 50 years, depending on vegetation type and whether stands were treated before fire to reduce woody fuels (Reinhardt and Holsinger 2010).

Second, quantifying or projecting wildland fire emissions is difficult because their amount and character vary greatly from fire to fire, depending on biomass carbon densities, quantity and condition of consumed fuels, combustion efficiency, and weather (Loehman et al. 2014). Emissions measured for an individual fire event may not be characteristic of large-scale emissions potential, because of complex ecological patterning and spatial heterogeneity of burn severity within fire perimeters. Although long intervals between wildfires can allow carbon to accumulate for years to centuries, disturbance-prone forests will eventually lose stored carbon to the atmosphere, regardless of management strategies designed to limit or prevent disturbance events.

Third, wildfire confers many important ecological benefits not measurable in carbon units (e.g., nutrient release and redistribution, stimulation of plant growth, increased productivity in soil systems from decomposition of burned material, initiation of vegetation succession and forest regeneration, increased availability of resources for surviving trees). Thus, it will be important to develop accounting methods that can assess ecological benefits in carbon-equivalent units so that they can be weighed against carbon losses from disturbance.

Finally, climate changes in combination with other ecosystem stressors may be sufficient to cause structural or functional changes in ecosystems and thus alter carbon dynamics of landscapes. For example, if climate changes increase wildfire frequency, extent, or severity in forested ecosystems, forests will likely lose carbon to the atmosphere that will not be rapidly replaced by new growth. This will cause forests to act as carbon sources for a period of time until disturbance regimes and biomass stabilize. Future landscapes could have the potential to store less, or more, carbon than under current climate and disturbance regimes.

Potential Future Wildfire Regimes and Wildfire Occurrence

Potential climate-driven changes to regional fire regimes in the mid-to-late 21st century include longer fire seasons and increases in fire frequency, annual area burned, number of high fire danger days, and fire severity as compared with modern fire patterns (Bachelet et al. 2003; Brown et al. 2004; Dillon et al. 2011; Krawchuk et al. 2009; Rocca et al. 2014; Westerling et al. 2006) (figs. 8.4, 8.5). In particular, lengthening of the fire season (the period of the year when fires can burn) will allow for more ignitions, greater likelihood of fire spread, and a longer burning duration. A longer burning window combined with regionally dry fuels will promote larger fires and increased annual area burned relative to modern recorded fire activity. Earlier onset of

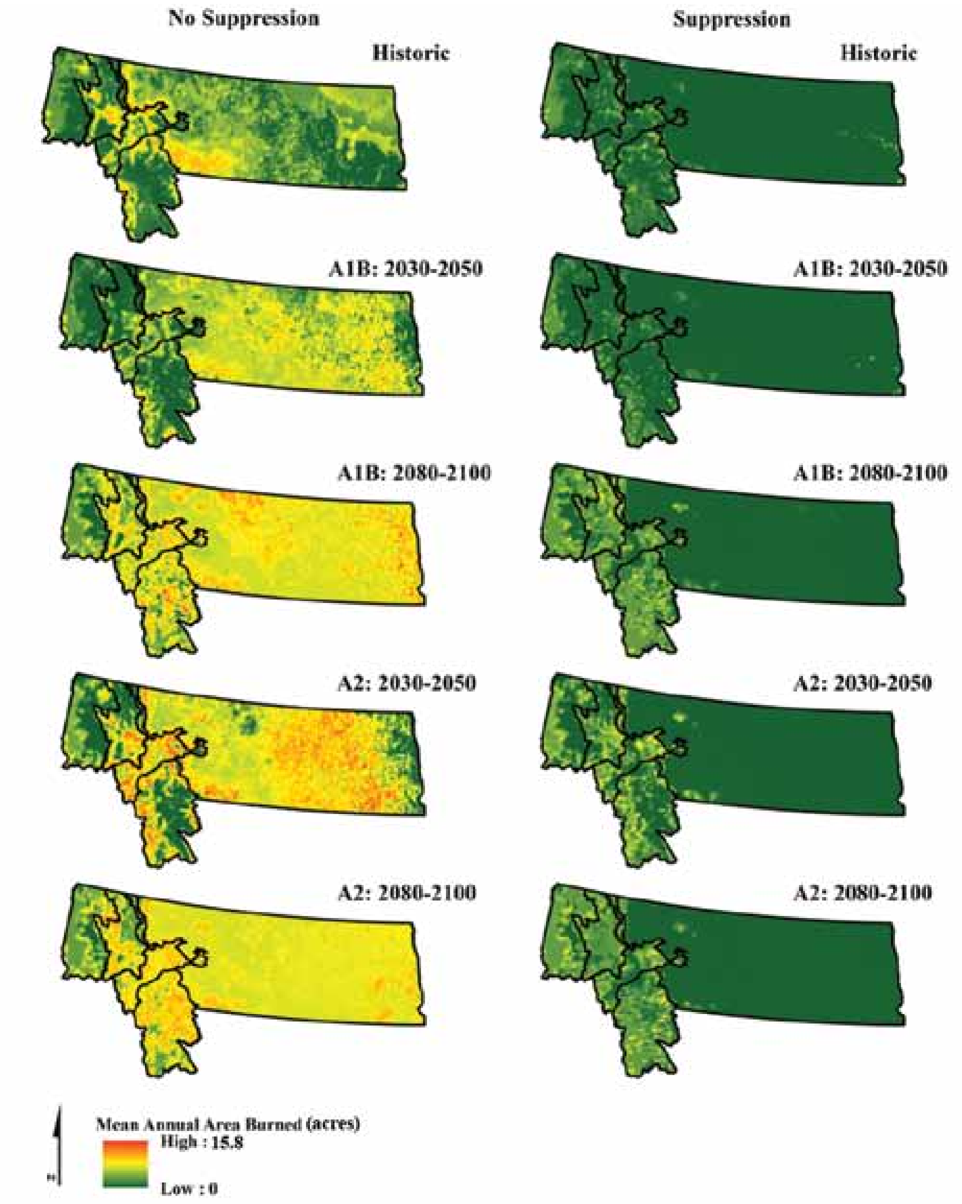

Figure 8.4—Changes in mean annual area burned (acres) for current levels of fire suppression and no fire suppression, A1B (moderate) and A2 (high) emission scenarios, and for the time periods 2030–2050 and 2080–2100, as projected by the MC2 dynamic global vegetation model.

snowmelt will reduce fuel moisture during fire season, making a larger portion of the landscape flammable for longer periods of time (McKenzie et al. 2004; Miller et al. 2011). This shift may be especially pronounced in mid- to high-elevation forested systems where fuels are abundant.

Earlier snowmelt, higher summer temperatures, longer fire season, and expanded vulnerable area of high elevation forests have produced observed increased wildfire activity compared to the mid-20th century, particularly in the Northern Rockies region (Westerling et al. 2006). Annual area burned by Western wildfires in the 20th century was greater in years with low precipitation, high drought severity, and high temperatures (Littell et al. 2009). Wildfire activity in the western United States is expected to increase if climates become warmer and drier in the future. Among western U.S. forests, mid-elevation forests of the Northern Rockies are projected to have a high risk of climate-induced increase in fire (Westerling et al. 2006), and increases in the area burned by fire are likely in lower and middle elevations of mountainous areas (Littell et al. 2009). However, in areas that are fuel limited, fires may become more infrequent where there is insufficient moisture for fine fuel accumulation (Littell et al. 2009).

The potential effects of climate change on wildfire area have been assessed by using statistical and ecological process models for the western United States (McKenzie et al. 2004; Spracklen et al. 2009), Pacific Northwest (Littell et al. 2010), Northern Rockies (Holsinger et al. 2014; Loehman et al. 2011a,b; Rocca et al. 2014), and the Greater Yellowstone Area (Westerling et al. 2011). For a mean temperature increase of 4 ºF, the annual area burned by wildfires is expected to increase by a factor of 1.4 to 5 for most western States (McKenzie et al. 2004), ultimately leading to greater damage, growth reductions, and mortality in forest ecosystems. The effects of future climate on fire severity (i.e., the proportion of overstory mortality) are less certain because

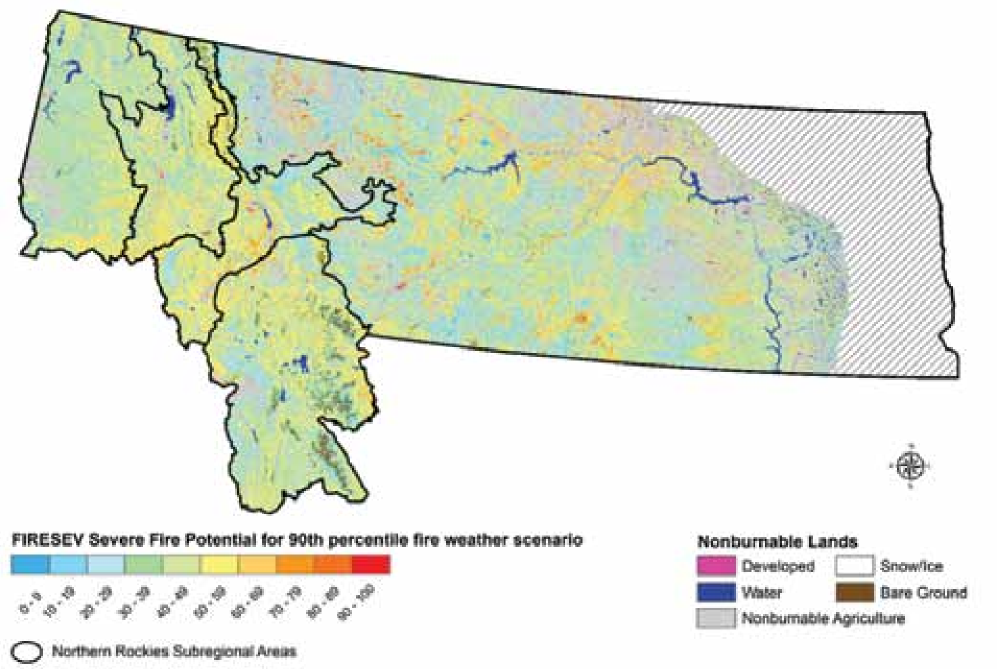

Figure 8.5—Severe fire potential (probability) for 90th percentile fire weather scenario, with non-burnable areas added in from the LANDFIRE 2008 Fire Behavior Fuel Model layer (data source: Dillon et al. 2011).

severity may be more sensitive than area burned to arrangement and availability of fuels. The risk posed by future fire activity in a changing climate can be assessed by its likely effects on human and ecological systems. At the wildland-urban interface, higher population and forest density have created forest conditions that are likely to experience more area burned and possibly higher fire severity than in the historical record (Dillon et al. 2011) (figs. 8.4, 8.5).

Although fire size in historical sagebrush landscapes is poorly understood, it is generally accepted that recent large fires have been fueled by woodland encroachment and higher fine fuel loads from weed invasions (e.g., cheatgrass). These changes in fire regime and vegetation-fuel structure affect large areas in the semiarid western United States and cascade through all trophic levels. Effects are particularly harmful on landscapes where postfire recovery is slow. The trend for larger, more damaging fires in sagebrush ecosystems is expected to continue until aberrations in fuel conditions that drive fire are corrected (Keane et al. 2008).

Interactions with Other Disturbance Processes

Wildland fires and insect outbreaks are the two primary natural disturbance processes in conifer forests of western North America (Hicke et al. 2012; Jenkins et al. 2012). The interaction of wildland fire and bark beetles has been studied since the early 20th century (Evenden and Gibson 1940; Miller and Patterson 1927; Weaver 1943), with research primarily focused on the potential for increased fire hazard following outbreaks. Multiple studies have cited changes in fire behavior, extent, and severity resulting from bark beetle-caused mortality in pine forests (see Hicke et al. 2012 for a summary). Drought and increased temperatures are key drivers of both wildland fires and bark beetle outbreaks. Climate change may be a causal factor in recent increases in annual area burned by wildfires (Littell et al. 2009) and area affected by bark beetle outbreaks (Bentz et al. 2010). Projections of warmer temperatures and increased drought stress suggest that the total area susceptible to or affected by beetle outbreaks and large or severe fires may increase in the coming decades (Williams et al. 2013). Acting independently or synchronously in space and time, wildland fires and bark beetle outbreaks can substantially influence forest structure, composition, and function; abruptly reorganize landscapes; and alter biogeochemical processes such as carbon cycling, water supply, and nutrient cycles (Edburg et al. 2012; Falk 2013; Fettig et al. 2013; Hansen 2014; Kurz et al. 2008a).

Unknowns and Uncertainties

Projections of future climate are somewhat uncertain because the ultimate magnitude of climate change and the severity of its impacts depend strongly on the actions that human societies take to respond to these risks (National Research Council 2010). Global climate models and their downscaled products may not accurately represent climate and weather at the regional and local scales that influence fire occurrence and behavior. For example, although associations between fire and quasi-periodic patterns such as ENSO and PDO have been identified, there is incomplete understanding of how these will respond to climate warming (McKenzie et al. 2004). In addition, precipitation trends are highly variable, and projections of future precipitation reflect both uncertainty and high variation (Intergovernmental Panel on Climate Change [IPCC] 2007, 2012; Littell et al. 2011). Lightning, an important ignition source for wildland fires, may increase in the future, thus increasing the potential for fire activity. For example, recent projections suggest that lightning strikes in the continental United States may increase by about 50 percent over the 20th century as the result of global warming-induced increase in updraft speeds and atmospheric water content (Romps et al. 2014). However, others have concluded that confidence in projections of increased thunderstorms and severe local weather events is low (Seneviratne et al. 2012).

Thus, the influence of climate changes on future fire patterns is not precisely known. Long-term changes in climate are unlikely to produce simple linear responses in global fire regimes (e.g., warmer temperatures do not always lead to increased fire frequency) because fire activity is influenced by precipitation, which is not projected accurately by climate models (Grissino-Mayer and Swetnam (2000). Other research suggests that increases in burned area can be expected in a warming climate, 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). In addition, climate drivers interact with legacies of human land use and local vegetation and fuel conditions at large spatial scales, making linear climate-fire predictions difficult. Specifically, decades-long fire exclusion and timber harvesting in some forests of the western United States have resulted in densely stocked stands and heavy down woody fuels accumulation that have probably contributed to the anomalous size and intensity of recent fires (Grissino-Mayer and Swetnam 2000; Naficy et al. 2010).

Bark Beetles

Overview

Bark beetles (Coleoptera: Curculionidae, Scolytinae) make up a large subfamily of insects, although less than 1 percent of the more than 6,000 species found worldwide cause significant economic impacts. In the Northern Rockies region, bark beetles of economic concern feed in the phloem of living conifers and can have extreme population amplifications over short time periods, the hallmark of outbreak species. Larval feeding, in addition to colonization by beetle-introduced fungi, typically results in death of the tree, and new host material is therefore required for each beetle generation. Historically, pulses of bark beetle-caused tree mortality have been extensive across the northern portion of the Rocky Mountain region. Between 1999 and 2013, bark beetle-caused tree mortality had substantial impacts in the Northern Rockies across an average of 1.4 million acres each year (fig. 8.6). Mountain pine beetle (*Dendroctonus ponderosae*, hereafter referred to as MPB) caused the majority of tree mortality (82 percent of acres with mortality detected) with a cumulative impact across 8.7 million acres during this time period (fig. 8.7). Across western North America between 1997 and 2010, bark beetle-caused tree mortality resulted in a transfer of carbon that exceeded that of fire-caused tree mortality (Hicke et al. 2013).

Both bark beetle populations and their host trees are being influenced by a warmer climate. Many bark beetle life history traits that affect population success are temperature-dependent (Bentz and Jönsson 2015), and warming temperatures associated with climate change have directly influenced bark beetle-caused tree mortality in some areas of western North America (Safranyik et al. 2010; Weed et al. 2015b). Warming climate will also influence host tree distribution across the Northern Rockies region, and tree vigor, which affects susceptibility to bark beetle attack (Chapman et al. 2012; Hart et al. 2013).

Bark Beetles in the Northern Rockies

Bark beetles are relative specialists, feeding on a single tree species or several species within a single genus. In the Northern Rockies region, multiple tree species are affected by different bark beetle species (table 8.3). Populations of several beetle species, and MPB in particular, began building in 1999, with high populations continuing in some areas through 2013 (USDA FS n.d.) (figs. 8.6, 8.7). Trend analysis indicates that most subwatersheds have declining populations, although some specific locations had increases in 2012 and 2013

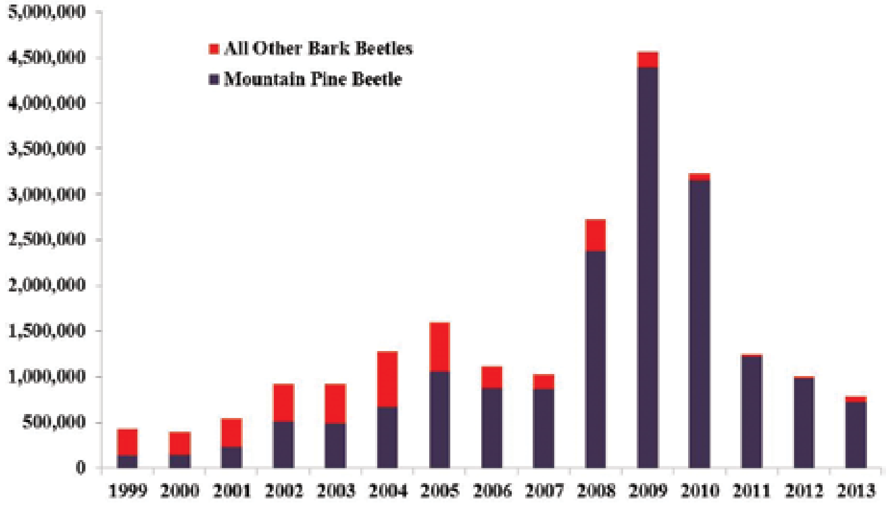

Figure 8.6—Area (acres) affected by bark beetles in the U.S. Forest Service Northern Region. Data based on Forest Health Protection aerial detections surveys.

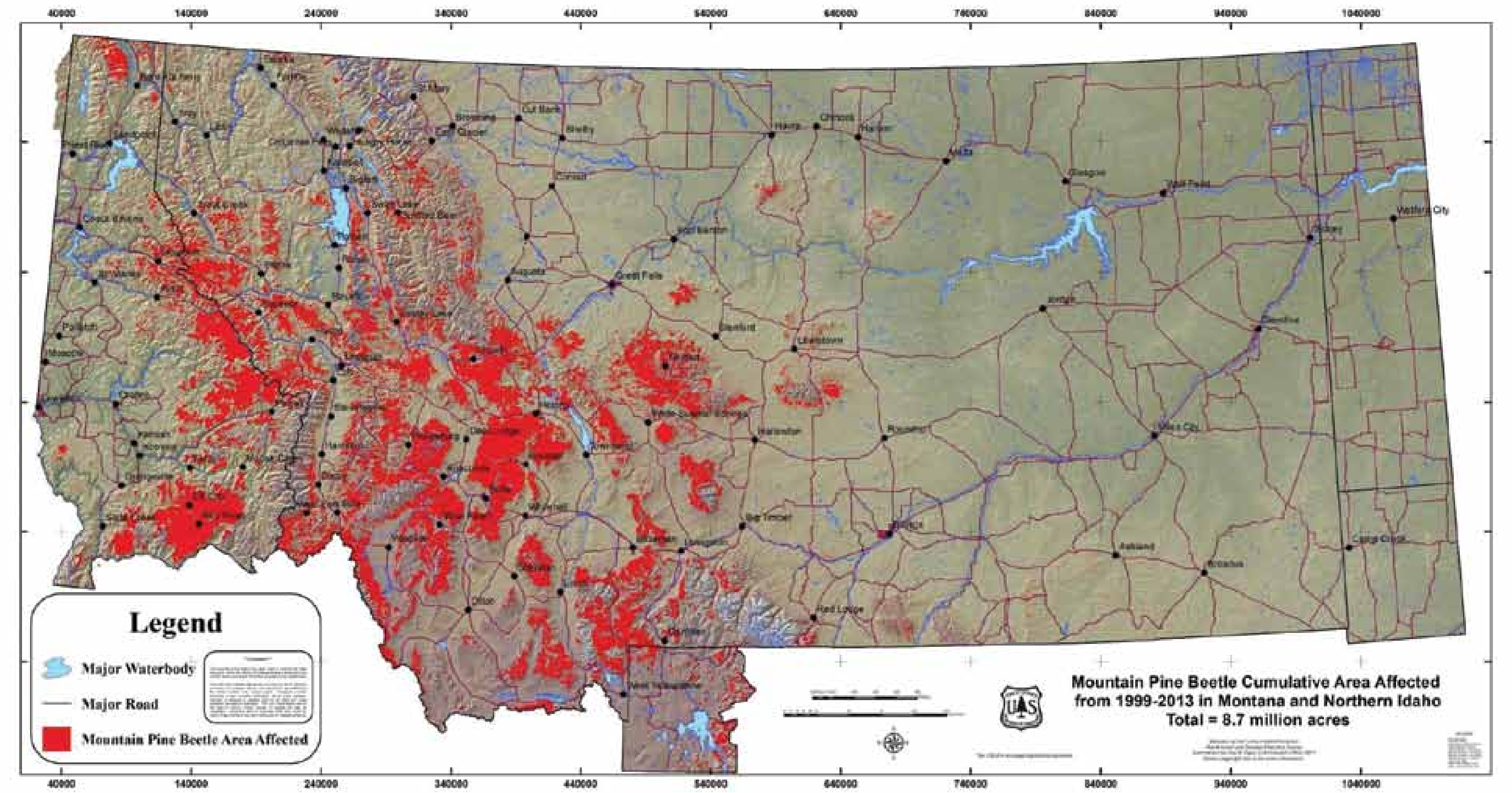

Figure 8.7—Cumulative area affected by mountain pine beetle between 1999 and 2013 in the Northern Rockies. Data based on Forest Health Protection aerial detection surveys.

Table 8.3—Bark beetle species that cause economic impacts in the Northern Rockies.

Bark beetle species		
Common name	**Scientific name**	**Host tree species**
Western pine beetle	*Dendroctonus brevicomis*	Ponderosa pine
Mountain pine beetle	*D. ponderosae*	Limber pine, lodgepole pine, ponderosa pine, western white pine, whitebark pine
Douglas-fir beetle	*D. pseudotsugae*	Douglas-fir
Spruce beetle	*D. rufipennis*	Engelmann spruce
Pine engraver beetle	*Ips* spp.	Lodgepole pine, ponderosa pine, western white pine
Fir engraver	*Scolytus ventralis*	Grand fir

(Egan 2014; Egan et al. 2013). Based on 2012 vegetation characteristics, susceptibility of Northern Rockies watersheds to future MPB outbreaks is spatially variable with many areas projected to lose more than 25 percent of total basal area (Krist et al. 2014).

Drivers of Bark Beetle Outbreaks

Bark beetle population outbreaks require forests with extensive host trees of suitable size and age (Fettig et al. 2013). For most irruptive species, preferred hosts are large, mature trees that provide a large amount of phloem resource for a developing brood. Large landscapes of these mature stands provide ideal conditions for years of bark beetle population growth.

Although suitable host trees are critical to outbreak development, beetle populations can exist for years at low levels until release is triggered by inciting factors. These triggers allow for rapid population growth that utilizes plentiful host trees. Triggers have been difficult to quantify but include factors that make food more readily available and that increase survival and reproduction of the beetles. Stand conditions (Fettig et al. 2013), drought (Chapman et al. 2012; Hart et al. 2013), and pathogens (Goheen and Hansen 1993) can make it easier for low levels of beetles to overwhelm and kill trees. Similarly, large areas of host trees recently killed by fire, wind, or avalanche provide pulses of accessible food, and have resulted in outbreaks of some species such as Douglas-fir beetle (*Dendroctonus pseudotsugae*) and spruce beetle (*D. rufipennis*) (Hebertson and Jenkins 2007; Shore et al. 1999), as well as secondary beetles including *Ips* species and fir engraver (*Scolytus ventralis*) (Livingston 1979). Weather favorable to beetle reproduction and survival also influences population fluctuations, and can both initiate and sustain outbreaks (Bentz et al. 2011; Powell and Bentz 2009; Régnière and Bentz 2007).

Given a susceptible forest, climate and weather directly drive bark beetle outbreaks by affecting beetle growth and survival through temperature-dependent life history traits. For example, the process of mass attack needed to successfully overcome tree defenses requires synchronous emergence of adults, a process mediated by temperature (Bentz et al. 1991). Diapause and development rate thresholds help in this synchrony (Bentz and Jönsson 2015; Hansen et al. 2001, 2011; Ryan 1959; Safranyik et al. 1990). These strategies also reduce the likelihood that life stages most sensitive to cold (eggs and pupae) are not present during winter. Development rates and thresholds also dictate life cycle timing, an important determinant of the number of generations per year.

The western pine beetle (*D. brevicomis*) and *Ips* species can be bivoltine (two generations in one year) in the Northern Rockies (Kegley et al. 1997; Livingston 1991), although multivoltine in more southern parts of their range. Other bark beetle species need at least 1 year to complete a generation (univoltine), and at higher elevations, where temperatures are cooler, 2 to 3 years may be required for a complete life cycle. Warm temperatures in the summer and spring extend the time that temperatures are above development thresholds, thereby allowing a reduction in generation time (Bentz et al. 2014; Hansen et al. 2001). Shorter generation times can lead to increased population growth, causing increased tree mortality. Winter temperature also influences bark beetle population success. Larvae cold-harden to survive subfreezing temperatures (Bentz and Mullins 1999; Miller and Werner 1987), although extreme fluctuations in temperature in spring and fall, in addition to long durations of temperatures below –31 °F, can cause extensive larval mortality (Evenden and Gibson 1940; Régnière and Bentz 2007; Safranyik and Linton 1991).

Bark Beetle Outbreaks Shape Landscape Patterns

Bark beetle disturbances play a significant role in successional pathways and biogeochemical cycles in Northern Rockies forests (DeRose and Long 2007; Edburg et al. 2012; Hansen 2014). At low population levels, bark beetles act locally as thinning agents, producing forest gaps that promote regeneration and the release and subsequent growth of neighboring host and nonhost trees, often producing uneven-aged stands (Mitchell and Preisler 1998). At outbreak population levels, tree mortality can approach 80 percent across landscapes of homogeneous host species and age, changing age-class distributions and overstory and understory species compositions. For example, in seral lodgepole pine forests, removal of the largest trees by MPB can hasten succession by climax species when fire is absent (Hagle et al. 2000; Roe and Amman 1970). Bark beetle disturbance can have long-term effects on forest structure and composition (Pelz and Smith 2012), and future landscape patterns in some forest types will be driven by tree mortality caused by large outbreaks of beetles.

Potential Future Bark Beetle Regimes and Occurrence

Climate change will have indirect and direct effects on bark beetle population outbreaks (table 8.4). Indirectly, changing temperature and precipitation regimes will influence the suitability and spatial distribution of host trees. Community associates important to bark beetle population success, including fungi, predators, and competitors, will also be affected by changing climate and thereby indirectly affect beetle population outbreaks. Direct effects will also occur as changing temperature regimes either promote or disrupt bark beetle temperature-dependent life history strategies that evolved through local adaptation for increased beetle population fitness and survival. Future bark beetle-caused tree mortality will therefore depend not only on the spatial distribution of live host trees and heterogeneity of future landscapes (see Chapter 6), but also on the ability of beetle populations and their associates to adapt to changing conditions when existing phenotypic plasticity is surpassed.

Projected changes in temperature and precipitation, in addition to a potential increase in extreme events such as windstorms, will significantly influence the spatial and temporal distribution of suitable host trees across future landscapes. For example, host tree defenses can be weakened by reduced water availability (Chapman et al. 2012; Gaylord et al. 2013; Hart et al. 2013). Increasing temperature is also associated with changing hydrologic regimes (see Chapter 4), including altered interseasonal timing of soil water availability facilitated by snowpacks that have progressively melted earlier in recent decades, and changes in the distribution of precipitation falling as rain versus snow (Regonda et al. 2005). These factors, along with other potential climate changes, may exacerbate physiological drought stress in host trees, which could indirectly benefit bark beetles that colonize stressed hosts in the late spring or summer (Raffa et al. 2008). Similarly, increased wind events could provide a reservoir of stressed trees used by some bark beetle species to surpass the endemic-epidemic threshold. Species currently considered secondary (i.e., those that infest stressed trees) could become primary tree killers as their favored habitat increases.

Warming temperatures will also directly influence bark beetle population success, although the effects will depend on the beetle species, as well as the seasonal timing, amount, and variability of thermal input. For example, across MPB habitats in the western United States from 1960 to 2011, minimum temperatures increased 6.5 °F. This increase in minimum temperature resulted in an increase in MPB survival and subsequent beetle-caused tree mortality in many areas of the Northern Rockies (Weed et al. 2015a). As climate continues to change, however, extreme within-year variability in winter warming could be detrimental to insect survival. Bark beetles produce supercooling compounds as temperatures decrease and catabolize compounds as temperatures warm. 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 species overwinter at the base of tree boles, gaining protection from predators and excessive cold temperatures when insulated beneath snow. Reduced snow levels in a warming climate could therefore add to increased overwinter mortality.

Warming at other times of the year could similarly have both positive and negative effects on bark beetle populations. Phenological flexibility allows some species to shift voltinism pathways, developing on a semivoltine (one generation every 2 years) life cycle in cool years, and a univoltine life cycle in warm years (Bentz et al. 2014; Hansen et al. 2001). Warming temperatures could also cause species that are

Table 8.4—Risk assessment for mountain pine beetle outbreaks.[a]

Elevation	Direction of change	Main driver(s) of change	Projected duration of change	Likelihood of change
<3,300 ft	Increase if host trees available	Temperature–caused shift to bivoltinism[b]	Increasing risk through 2100	High
3,300–6600 ft	Decrease	Temperature-caused disruption of seasonality	Decreasing risk through 2100	High
6,600–10,000 ft	Increase initially, then decrease	Initially temperature-caused shift from semivoltine[c] to unvioltine[d], then disruption of seasonality	Decreasing risk through 2100	High
>10,000 ft	Increase	Temperature-caused shift from semivoltine to univoltine	Increasing risk through 2100	High

[a] Developed using model simulations and expert opinion and information from literature as summarized in this chapter.
[b] Two generations in one year.
[c] One generation in two years.
[d] One generation in one year.

currently bivoltine (e.g., western pine beetle, *Ips* species) to become multivoltine. These types of voltinism shifts can lead to rapid increases in beetle populations and subsequent tree mortality. Some thermal regimes allow these life cycle shifts yet maintain seasonal flights. However, other thermal regimes that result in voltinism shifts could also disrupt seasonality. For example, warm summers could accelerate development, resulting in reduced generation time, but could also result in cold-sensitive life stages entering winter. Existing developmental thresholds and diapause strategies that serve synchrony currently reduce the likelihood of this happening. As existing phenotypic plasticity is surpassed, rapid warming without adaptation could lead to lower overall population fitness in some areas as a result of poor seasonal timing (Régnière et al. 2015).

Expected Effects of Climate Change

Although many bark beetle species in the Northern Rockies region can cause economic impact, the influence of climate change on population outbreaks has been most studied in MPB. It is clear that multiple aspects of climate change can positively influence MPB, including increasing winter temperature (Régnière and Bentz 2007; Weed et al. 2015b) and reduced precipitation (Chapman et al. 2012). But changing thermal regimes can have both positive and negative effects on MPB population growth through phenological synchrony and generation timing. Acknowledging potential other climate effects, here we describe expected direct effects of climate change using a temperature-dependent mechanistic demographic model of MPB population growth that is based on phenological synchrony (Powell and Bentz 2009). The effect of future temperatures on univoltine population growth rate relative to historical conditions is projected. Although current climates apparently prevent MPB from successfully completing two generations in a single year (Bentz and Powell 2015; Bentz et al. 2014), we also evaluated if future thermal regimes would promote bivoltinism. The model was driven with downscaled temperatures from two global climate models (GCMs: CanEMS2, CCSM4) and two emissions scenarios (Representative Concentration Pathways RCP 4.5 and RCP 8.5) based on the multivariate adaptive constructed analogs approach (University of Idaho n.d.). Although indirect effects of climate clearly affect host tree vigor, stand composition, and distribution across a landscape, these effects are currently not included in our demographic model. We report our model results, however, in conjunction with hazard categories developed by Krist et al. (2014) based on stand conditions conducive to MPB population growth (table 8.5). Model output was considered only for locations where pines currently grow. Model projections are presented in figures 8.8 and 8.9, and tables 8.4 and 8.5, and are summarized next. See Bentz et al. (2016) for spatial displays (for the CanEMS2 GCM).

Table 8.5—Pine and mountain pine beetle (MPB) metrics by elevation category. Pine forests <6,600 ft have relatively low current hazard for MPB and low univoltine growth potential, although bivoltine potential is moderate. Pine forests >6,600 ft have relatively high current stand hazard conditions for MPB and relatively high univoltine growth potential, although bivoltine potential is zero.

	<3,300 ft	3,300–6,600 ft	6,600–10,000 ft	>10,000 ft
Current stand density pine (trees per acre [standard deviation])[a]	46.4 (58.7)	142 (206)	471 (434)	223 (223)
Proportion of area (percent) [b] rated as:				
Low hazard	97	69	30	18
Moderate hazard	2	13	14	13
High hazard	1	18	56	68
MPB potential for population success (2015–2025), based on simulation with CanEMS2 GCM, emission scenario RCP-45				
Univoltine population growth rate (R)	0.00	0.44	1.62	0.65
Bivoltine (percent of points within elevation category projected to have a thermal regime supporting bivoltinism for >50 percent of years between 2015 and 2025)	24	5	0	0
MPB potential for population success (2015–2025), based on simulation with CanEMS2 GCM, emission scenario RCP-85				
Univoltine population growth rate (R)	0.04	0.86	2.0	1.05
Bivoltine (as above)	35	7	0	0

[a] From Blackard et al. (2009).

[b] Current MPB hazard based on host stand conditions (from Krist et al. 2014).

The proportion of areas with thermal requirements for MPB bivoltinism has historically been low in the Northern Rockies region (figs. 8.8, 8.9). Stands at elevations less than 3,300 feet currently have relatively few pines and low hazard to MPB, and population growth of univoltine populations was historically very low. This is most likely because it was too warm, and adult emergence synchrony was disrupted. Growth rate is projected to decrease further in current (2000–2009) and future climates relative to historical periods (fig. 8.8). However, the proportion of simulation points at less than 3,300 feet with thermal regimes that allow for bivoltinism is projected to increase through 2100, particularly when the RCP 8.5 scenario temperature projections are used (fig. 8.8). The availability of pines at less than 3,300 feet in future climates may be restricted.

- Pine stands at 3,300 to 6,600 feet were also projected to have lower univoltine population growth rates in current and future climates than historically, and some small proportion of stands will have increasing probability of bivoltinism (fig. 8.8).
- The highest density of pine currently occurs at 6,600 to 10,000 feet, the elevation range also associated with most (56 percent) of the high-hazard stands (table 8.5). These stands are predicted to have higher univoltine population growth rates than historically, through 2030–2050. Thermal regimes for bivoltinism are unlikely at this elevation (fig. 8.8).
- Population growth rates were historically very low in stands above 10,000 feet until 2000–2009; rates are projected to increase through 2100 (fig. 8.8). These stands historically were too cool for bivoltinism and are projected to remain too cool in future climates.
- Pine forests below 6,600 feet currently have low stand hazard for MPB and low univoltine growth potential in the near future (2015–2025), although bivoltine potential is moderate. Pine forests above 6,600 feet have high current stand hazard for MPB and high univoltine growth potential between 2015 and 2025, although bivoltine potential is zero. Pine stands above 6,600 feet, particularly between 6,600 and 10,000 feet, have the highest risk of MPB-caused tree mortality in the near future.
- The Grassland subregion contains a small amount of "Great Plains ponderosa pine," and historically temperatures were too warm for univoltine MPB population success (fig. 8.9). A high proportion of locations in these areas is projected to become thermally suitable for bivoltinism (fig. 8.9), although pine occurrence in future climates may be limited.
- In the Western Rockies, Central Rockies, and Eastern Rockies subregions, univoltine population growth is projected to decrease beginning in the 2000–2009 period, although a small proportion of locations at the lowest elevations will become thermally suitable for bivoltinism by 2080–2100.
- In the Greater Yellowstone Area subregion, univoltine population growth remains relatively high until the 2080–2100 time period (fig. 8.9) with a small proportion of locations at the lowest elevations with the potential to become bivoltine at that time (fig. 8.9).

Interactions with Other Disturbance Processes

Bark beetle-caused tree mortality is influenced by and can influence fire, although the relationships are complex and dynamic (Hicke et al. 2012; Jenkins et al. 2014). In fact, any disturbance that influences the distribution and vigor of host trees will influence bark beetle outbreaks. Moreover, the pattern of bark beetle-killed trees across a landscape will have cascading effects on a myriad of abiotic and biotic processes such as fire, wildlife habitat, and vegetation succession and dynamics (Saab et al. 2014). During non-outbreak years, many bark beetle species survive in trees infected with root diseases. The amount of root disease in trees stressed by climate change may increase, which in turn can result in higher populations of bark beetles causing increased tree mortality (see *Root Disease* section).

Unknowns and Uncertainties

It is important to acknowledge sources of uncertainty in models that describe relationships among climate, bark beetle populations, and their host trees, in addition to uncertainties with projections of future climate. Mechanistic-based phenology models are good tools for projecting beetle population response in a changing climate (Bentz and Jönsson 2015). This type of model incorporates the important role of seasonality and allows for emergent population processes when driven by climate change projections. However, data are lacking on temperature-dependent relationships of most bark beetle species in the Northern Rockies, hindering development of conceptual and empirical models. Moreover, one of the greatest sources of uncertainty is the lack of understanding of potential adaptations in bark beetle developmental traits to a rapidly changing climate. With few exceptions (Addison et al. 2013, 2014), little is also known about climatic effects on the wide array of bark beetle community associates including fungi, bacteria, parasites, and predators.

Host trees will also respond to climate change, and responses will have cascading effects on bark beetle populations. Further investigation, especially in water-limited systems, is needed to increase quantitative understanding of how climate-induced changes in trees influence bark beetle population success at different spatial scales. Due to this limited understanding, predictive models that incorporate the integrated effects of climate and bark beetle disturbances on vegetation pathways are lacking, constraining our ability to make projections for future forests (Anderegg et al. 2015).

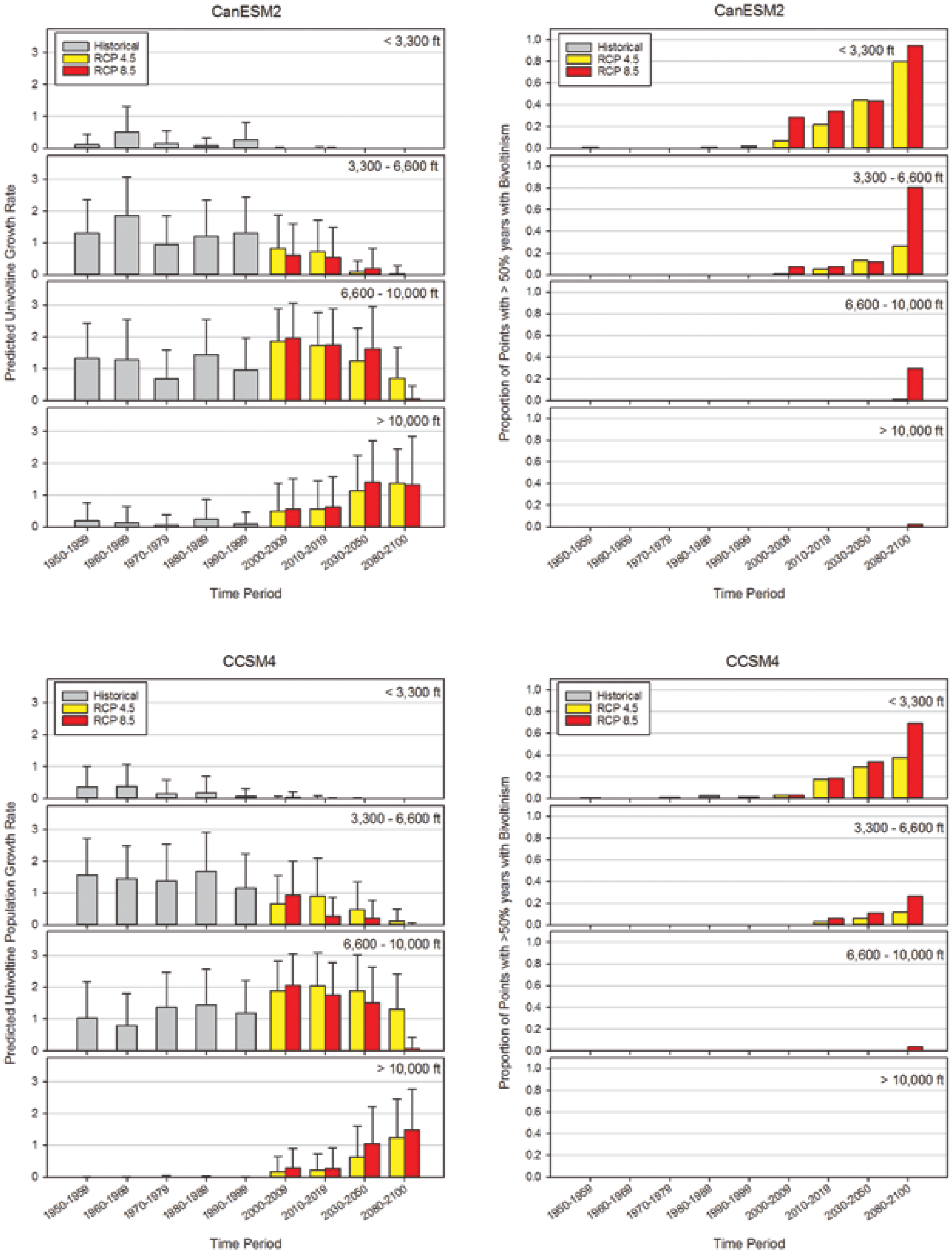

Figure 8.8—Left panel: projected mountain pine beetle (MPB) population growth rate (mean, standard deviation) of univoltine populations (one generation per year) over decades (historical) and 20-year periods (projected) from 1950 to 2100. Shown are the mean and standard deviation among locations of decadal (historic) and 2-decadal (projected) growth rates. Right panel: proportion of simulation points in which bivoltinism (two generations in one year) is projected for more than 50 percent of years in each time period. Projections are based on a temperature-dependent model of MPB development and population growth (Powell and Bentz 2009) using temperatures from the CanESM2 and CCSM4 GCMs and two emission scenarios (Representative Concentration Pathways [RCP] 4.5 and 8.5). Model output is shown by elevation category (in feet). Simulation points are geographic locations of downscaled temperatures where pines occur (sample size = 17,616).

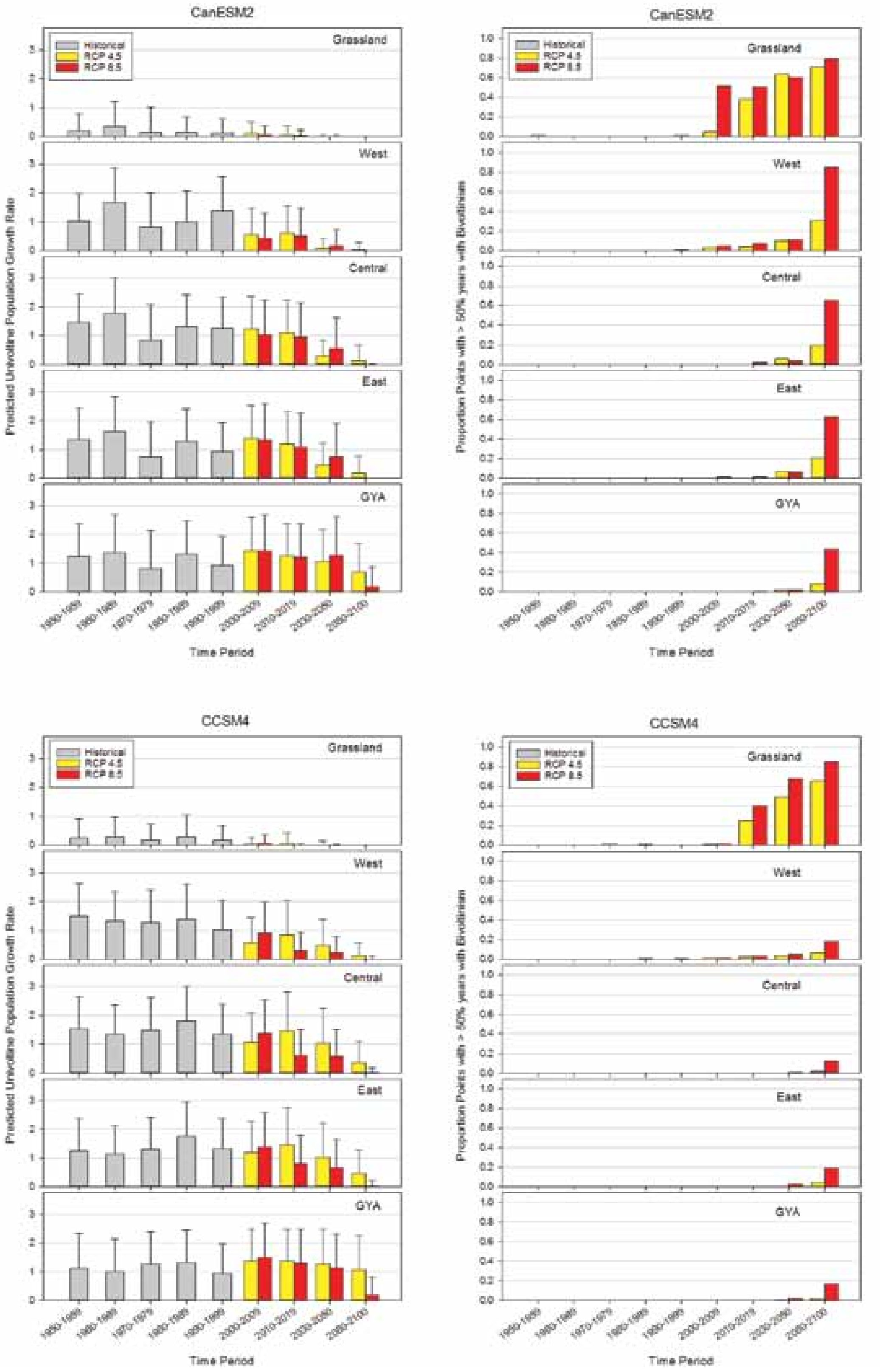

Figure 8.9—Left panel: Projected mountain pine beetle (MPB) population growth rate (mean, standard deviation) of univoltine populations (one generation per year) over decades (historical) and 20 year periods (projected) from 1950 to 2100. Shown are the mean and standard deviation among locations of decadal (historic) and 2-decadal (projected) growth rates. Right panel: proportion of simulation points where bivoltinism (i.e., two generations in one year) is projected for more than 50 percent of years in each time period. Predictions are based on a temperature-dependent model of MPB development and population growth (Powell and Bentz 2009) using temperatures from the CanESM2 and CCSM4 GCMs and two emission scenarios (RCP 4.5, RCP 8.5). Model output is shown by Northern Rockies Adaptation Partners (NRAP) subregion. Simulation points are geographic locations of downscaled temperatures where pines occur (sample size = 17,616).

White Pine Blister Rust

Overview

White pine blister rust (*Cronartium ribicola,* hereafter referred to as WPBR) is a nonnative fungus that was inadvertently introduced to western North America from Europe around 1910 (Bingham 1983; Tomback and Achuff 2011). The WPBR fungus infects only five-needle pine species, and all nine North American white pine species are susceptible. Three white pines occur in the Northern Region: western white pine (*Pinus monticola*), whitebark pine (*Pinus albicaulis*), and limber pine (*Pinus flexilis*). WPBR has been found across most of the ranges of these three pines in the Northern Region, and it has caused greater than 90-percent mortality in western white pine. WPBR presence in whitebark and limber pine is variable, but highest in the warmer, moister parts of their ranges (Tomback and Achuff 2010).

The life cycle of WPBR requires two hosts, with two spore-producing stages on white pine and three separate spore-producing stages on three potential alternate hosts: *Ribes*, *Pedicularis,* and *Castilleja* species. Pine infection begins when basidiospores produced on *Ribes* leaves in late summer are wind dispersed to nearby pines. The basidiospores germinate on pine needles and fungal hyphae grow through the stomata into the cell tissues, needles, and stem (Patton and Johnson 1970).

Cankers form on white pine branches and main stems as the phloem is first invaded by hyphae and then becomes disrupted by blister-like structures that are filled with powdery yellow aeciospores (Hudgins et al. 2005). As tree branches and stems are girdled, branches and tops die back to the canker. Continued downward growth of the persistent cankers and poor competitive ability then kill infected trees. Depending on where the canker occurs, cone production often decreases or is prevented well before tree death.

The released aeciospores infect *Ribes* and the other alternate host species (Schwandt et al. 2013). This can occur at long distances from infected pines, as aeciospores are hardy and can disperse as much as 60 miles (Frank et al. 2008). At most locations and for most alternate hosts, infected leaves produce urediniospores that spread only short distances from leaf to leaf or plant to plant (Newcomb 2003). These recurrent infections keep rust alive through the growing season until conditions are suitable for pine infection. For most alternate hosts, leaf infections produce hair-like structures (teliospores) that produce basidiospores in fall or when night temperatures are cool; other hosts with less vigorous leaf infections may produce teliospores directly. Locations where synergistic pairs of alternate hosts occur—one that readily spreads urediniospores, and one that produces pine-infecting basidiospores—are especially favorable for pine infection (Zambino 2010).

Basidiospores have a narrow weather window for production, dispersal, and successful infection of pine needles: they infect best in periods of high humidity (>98 percent) with moderate temperatures (between 60 and 68 ^{o}F) (Bega 1960). Conditions for infection are determined by temperature, with a 48-hour optimum for infection at 64 ^{o}F, though up to 5 days may be required at 39 ^{o}F (McDonald et al. 1981). Temperatures exceeding 77 ^{o}F are lethal for teliospores. Basidiospores are short-lived and most often cause infections within a few feet of *Ribes* plants, but they can be carried long distances or upslope on moist air masses, lofted in thermals over bodies of water, or carried downslope on cold air currents to infect trees at the interfaces with temperature inversions (Van Arsdel et al. 2005; Zambino 2010).

The time required for WPBR to kill its host varies by species, distance of infection from bole (Schwandt et al. 2013), and bole circumference. Typically WPBR kills western white pine in 5 to 10 years, and whitebark pines (*P. albicaulis*) after 20 years (Hoff and Hagle 1990). WPBR-caused tree mortality greatly affects stand structure and species composition, but the most serious impact of WPBR is the long-term impact on white pine regeneration capacity, with direct mortality of rust-susceptible seedlings and saplings and the loss of cone and seed production following branch dieback and top kill. Native pine populations show some heritable resistance to WPBR, but the frequency of resistance is low and variable (Zambino and McDonald 2004). Studies in the 1970s of natural stands that originated in the late 1920s estimated that fewer than 1 in 10,000 trees lacked cankers (were rust-resistant) (Hoff et al. 1980). But resistance may have increased in the 35 years since this

Table 8.6—Risk assessment for white pine blister rust.[a]

	Direction of change	Main driver(s) of change	Predicted duration of change	Likelihood of change
Infection frequency and severity	Little to moderate Increase	Possibility of increased wave years in high elevation ecosystems	Until a sufficient proportion of the landscape has populations of rust-resistant pine trees, there will always be high infections regardless of climate	Low

[a] Developed using expert opinion and information from literature as summarized in this chapter.

report, as a result of additional rounds of regeneration under natural selection (Klopfenstein et al. 2009; McDonald et al. 2004, 2005; Zambino and McDonald 2005).

Effects of Climate Change on White Pine Blister Rust

Climate changes may cause WPBR infections to occur earlier and with greater incidence in pine stands (table 8.6). Specific weather conditions required for basidiospore germination and infection of pine needles may occur more frequently and for longer periods in the future (Koteen 1999). “Wave” years are projected to increase in the future for whitebark pine (Keane et al. in press); these years have hot and humid weather conditions throughout most of the growing season that facilitate infections on pine and alternate hosts, followed by moist but cooler weather events for teliospore and basidiospore production and pine infection. For most temperate pine forests (western white and limber pine), however, Sturrock et al. (2011) speculate that wave years will actually decrease because of hotter, drier projected climates. Further, Helfer (2014) suggests that warmer temperatures could negatively affect rusts and that higher concentrations of atmospheric carbon dioxide (CO_2) could cause declines in rust populations. He also states that the highly variable and extreme weather projected in the future will aid in WPBR spore dispersal, resulting in expansion of its range and higher spore loads on existing pines.

The highly variable and novel climatic conditions projected in the future may serve to accelerate mutations of WPBR to create populations that may overcome the native rust resistance in five-needle pines (Simberloff 2000). Alternatively, changing climates may lead to suitable climates for WPBR variants that are in locations other than North America. Most rust infection and mortality occur regardless of tree condition and vigor, so it is doubtful that any direct responses of the tree or the *Ribes* hosts to future climates, such as increased growth, will enhance or degrade the ability of the host to ward off infections. However, climate-mediated changes in host regeneration dynamics could restrict or expand host ranges (Helfer 2014). As a result, this could alter WPBR range. Some predict higher leaf biomass for the two host species with warmer, enriched CO_2 environments, and more leaves could provide additional germination surfaces and a higher chance for rust infection on both hosts.

Distribution and frequency of synergistic alternate host species combinations (Zambino 2010) could also change. In higher elevation areas, new climates (i.e., warming temperatures along with high precipitation) may facilitate the expansion of *Ribes* into areas that were historically too cold and snowy to support certain hosts. On the other hand, in low-elevation upland areas where *Ribes* is currently abundant, drought may cause decline of the host. Moreover, drought may cause extended and extensive stomatal closure in the pines, thus preventing hyphae entry. The shifting of mosaics of the *Ribes* host populations into new higher elevation areas, driven by drought in lower elevations, may spread WPBR into areas where it has not yet occurred.

Interactions with Other Disturbance Processes

The interaction of fungal pathogens and their hosts with other disturbances may be a key factor in future WPBR infections (Ayres and Lombardero 2000). The interactive effects of wildland fire on WPBR are probably most important, but they are mostly minor and primarily indirect under future climates. The exception is the possibility that smoke may kill rust spores produced at the time of the fire (Hoffman et al. 2013).

White Pine Blister Rust and Wildland Fire

Fire indirectly affects WPBR by changing the size, distribution, and abundance of its hosts. Most five-needle pines of the western United States are somewhat fire-adapted with thick bark, high canopies, and deep roots (Ryan and Reinhardt 1988). Mixed- and high-severity fires are currently common in most forests where WPBR is present (Arno et al. 2000; Murray 2007) and are projected to increase in size, frequency, and intensity (Westerling et al. 2011). Increases in fires and burned areas can create favorable conditions for pine regeneration because most five-needle pine seeds are dispersed by rodents and birds and are thus better adapted to spread into postfire landscapes than seeds of their tree competitors (Lanner 1989; Morgan et al. 1994). *Ribes* populations may increase after fire through regeneration by seed and sprouting from roots and rhizomes. Therefore, fire will often favor *Ribes* regeneration over other species not adapted to fire. However, re-burns soon after an initial fire can eliminate regenerating *Ribes* individuals before they can develop a seedbank for the next forest regeneration cycle (Zambino 2010).

Severe fires that kill rust-resistant pine trees may ensure continued high rust mortality in the future because it dampens the rate of rust-resistant adaptations (Keane et al. 2012). However, where rust-resistant five-needle pines survive fire they can provide the seeds for populating future landscapes that are resilient to both rust infection and fire mortality. Fire exclusion generally increases competition stress (Heward et al. 2013), weakening pine trees. Stress from competition does not increase rust infection (Parker et al. 2006), but may facilitate mortality in pines trees under stress after being girdled by blister rust.

Trees infected with WPBR are weakened, and may be more susceptible to fire-caused damage and mortality (Stephens and Finney 2002). Ladder fuels of trees attacked or killed by WPBR may increase crowning owing to abundant pitch, which can extend from base to rust bole cankers, and from dead red crowns of girdled trees. As branches and tops of white pines die back, they add dead foliage and wood to the fuelbed, which may increase fire intensity and fire-caused tree mortality. In contrast, western white pine needles gradually added to the fuel bed are more similar to normal needle shed, and are quickly degraded in moist, productive environments. Mortality from WPBR often results in the elimination or 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; Reinhardt et al. 2010). Many shade-tolerant competitors are also more susceptible to fire damage, resulting in higher postfire tree mortality in rust-infected landscapes.

White Pine Blister Rust and Mountain Pine Beetle

Interactions between native MPB populations and WPBR are rarely studied because they are difficult to quantify over time. In their endemic phase, MPB populations may weaken pines and facilitate infection by WPBR, but these interactions are strongly governed by climate and biophysical environment (Tomback and Achuff 2011). However, the ubiquitous presence of WPBR spores and the resistance to the disease in pine species ensure that most five-needle pines at many sites will eventually become infected and die from WPBR, regardless of MPB endemic levels (Hoff et al. 2001). More importantly, MPB influences WPBR through regulation of the tree species that are host to both disturbance agents and killing of host trees that are resistant to the rust (Campbell and Antos 2000). For example, although whitebark pine stands in the Greater Yellowstone Area show little WPBR-related mortality, levels of MPB-related mortality are high (Kendall and Keane 2001; Macfarlane et al. 2013). Many stands of healthy five-needle pines in Yellowstone have been subjected to a major MPB outbreak over the last decade as a result of high densities of large diameter trees coupled with prolonged warm, dry conditions. These outbreaks resulted in substantial mortality of rust-resistant whitebark pine trees (Logan et al. 2008).

Effects of WPBR on MPB infestations are also highly variable and subtle. Archibald et al. (2013) found less MPB activity in trees that had high WPBR damage, whereas Bockino and Tinker (2012) found that whitebark pine selected as hosts for MPB had significantly higher WPBR infection, but this varied by tree size (diameter), stand type, and disturbance pattern (Larson 2011). Kulhavy et al. (1984) found that more than 90 percent of western white pine trees infected by bark beetles had either WPBR or some type of root disease, whereas Six and Adams (2007) found little evidence of interaction effects between MPB and WPBR. Simulations of MPB disturbance under current climate result in a decline in both lodgepole pine and whitebark pine, and a corresponding increase in subalpine fir (*Abies lasiocarpa*) and Douglas-fir (*Pseudotsuga menziesii*), with little change from the addition of WPBR (fig. 8.10). These trends are enhanced under a warmer climate, in which lodgepole pine declines are greater and stands are replaced primarily by Douglas-fir, but WPBR interaction has only minor effects on species composition (Keane et al. 2015).

White Pine Blister Rust, Fire, and Mountain Pine Beetle

Studies of interactions among fire, beetles, and rust are rare, but we posit that MPB and WPBR serve to reduce five-needle pine populations and create fuelbeds that may support wildfires that are more intense than historical counterparts, potentially resulting in high mortality of the dominant vegetation. Although fire reduces pine abundance in the short term, it apparently ensures the long-term persistence of pine by eliminating competitors (Keane and Morgan 1994). Modeling studies have shown that decades to centuries are required to reestablish populations of rust-resistant white pines after die-off (such as would occur with MPB), and increased frequency and extent of wildfire under climate change favored white pine regeneration and persistence over shade-tolerant species in some regions, even with WPBR infection and losses of some white pine to fire (Loehman et al. 2011a,b). The largest decline in whitebark pine has been found in those areas affected by both WPBR and MPB, but not fire (Campbell and Antos 2000).

Interactions among fire, MPB, and WPBR can occur only in areas that have the potential to support five-needle pines, which are rare in many landscapes. However, recent simulation efforts have found that fire frequency under current climate is 10 percent lower when all three disturbances are allowed to interact, and average tree mortality is also lower (fig. 8.10). In a warmer climate, fire frequency decreases, high-severity fires increase, and interactions among disturbances create different landscapes than when each disturbance acts separately (or in the absence of disturbance) (Keane et al. 2015) (fig. 8.11).

Unknowns and Uncertainties

It is difficult to mechanistically simulate WPBR population dynamics because the disease is governed by processes from fine-scale (e.g., microclimate, spore production and germination, tree size and health) to coarse-scale (e.g., spore dispersal, wind, alternate host distributions, topographic controls) processes. Therefore, the representation of WPBR in most models will tend to be both stochastic and empirical, and this will tend to reduce the robustness of model predictions and add to the uncertainty of future WPBR predictions.

White pine trees will also directly respond to climate change, and responses will have interacting effects on WPBR infection potential. The key to the future abundance of white pines on the Northern Rocky Mountain landscapes will hinge on the ability of the three pine species to develop rust-resistant populations that are resilient to climate change. This probably will not happen without human intervention. The rapid pace of predicted climate change coupled with the

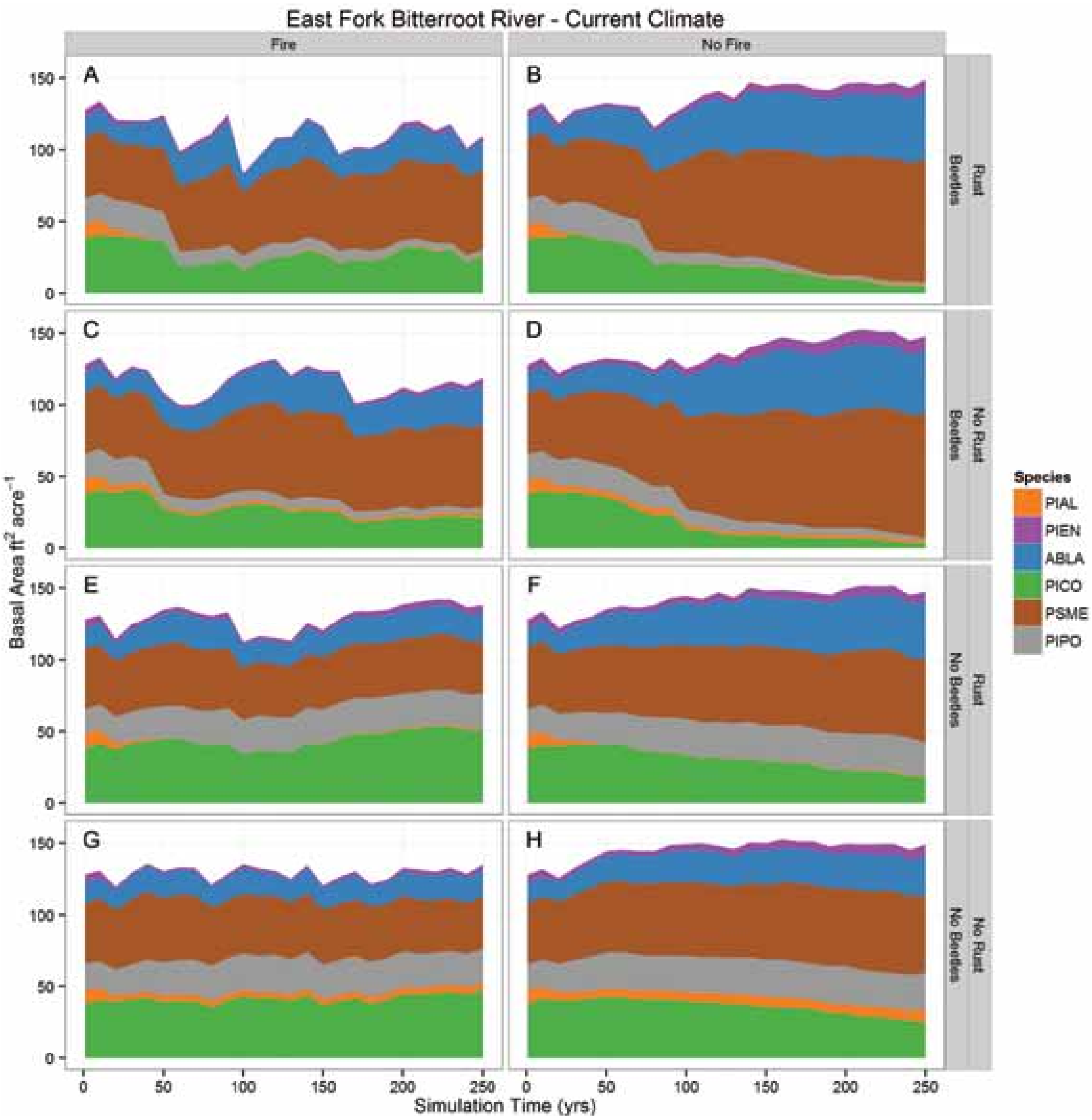

Figure 8.10—Landscape composition of species cover types using the plurality of basal area for current climate for the East Fork of the Bitterroot River landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): (a) fire, WPBR, and MPB; (b) no fire, WPBR, MPB; (c) fire and MPB; (d) MPB only; (e) fire and WPBR; (f) WPBR only; (g) fire only; and (h) no disturbances. Species: PIAL-whitebark pine, PIEN-Engelmann spruce, ABLA = subalpine fir, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine. Produced using the FireBGCv2 mechanistic ecosystem-fire process model (Keane et al. 2015).

long maturation times of the three pine species may exacerbate the species decline. It is essential that natural resistance is fostered by land management agencies to ensure that these valuable species and the forests that they create are not lost forever.

Forest Diseases

Overview

Forest diseases are found in all forest ecosystems of the Northern Rockies region. They are one of three major disturbance groups that affect ecosystem development and change, but the overall impacts of forest diseases on various resources are difficult to quantify. This is partly due to our inability to separate predisposing effects of some of the most important diseases, which act over a long term, from mortality caused by short-term factors such as insect outbreaks and drought. Forest diseases tend to be more cryptic and chronic in their effects, so estimating their occurrence and abundance is difficult. Here we rely mostly on older studies and observations to quantify disease effects in what were formerly called commercial timberlands. Spatial distributions of most forest diseases have not changed much, although the effects of individual diseases may change due

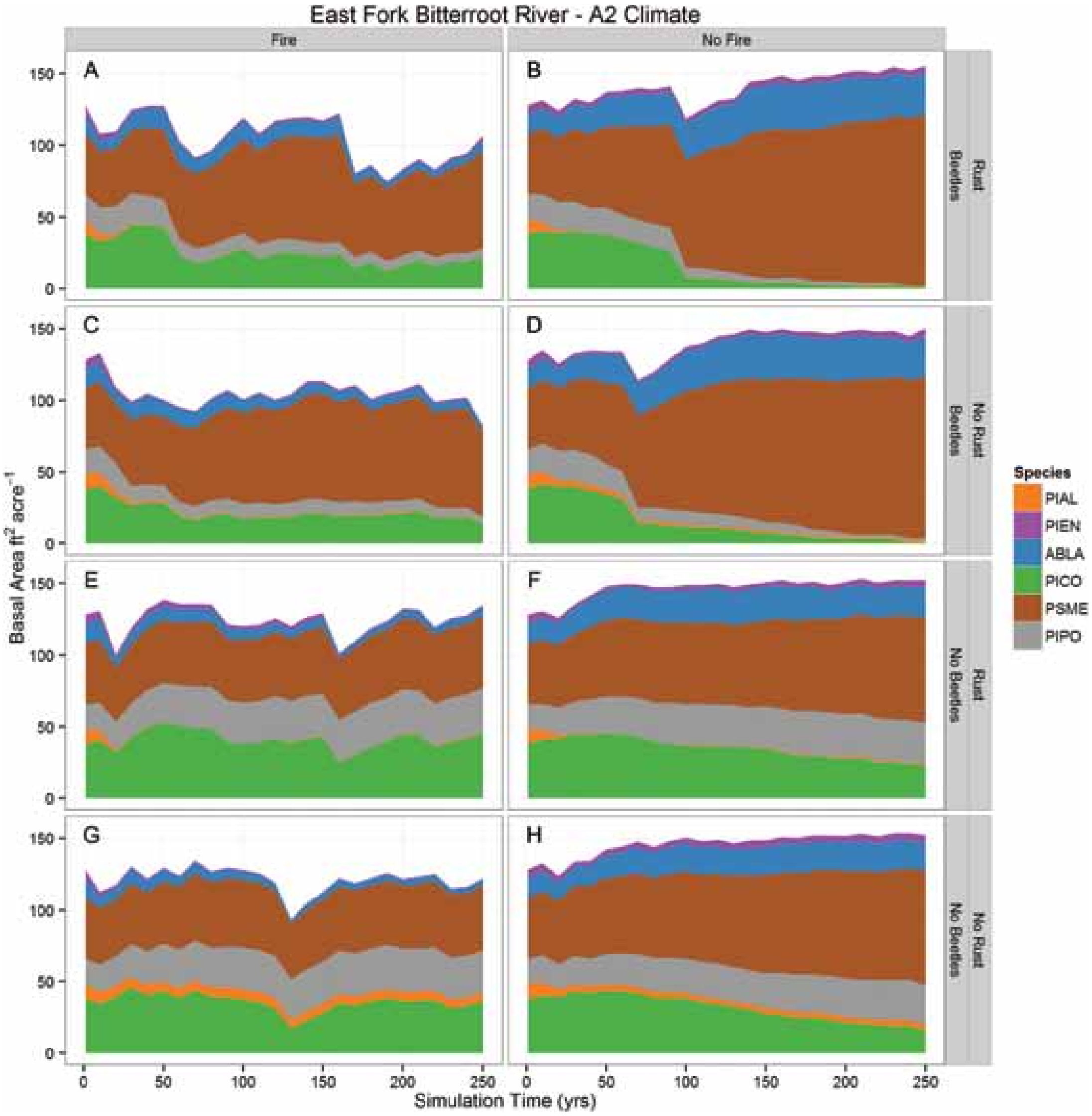

Figure 8.11—Landscape composition of species cover types using the plurality of basal area for a warmer climate (A2 emission scenario) for the East Fork of the Bitterroot River landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): (a) fire, WPBR, and MPB; (b) no fire, WPBR, MPB; (c) fire and MPB; (d) MPB only; (e) fire and WPBR; (f) WPBR only; (g) fire only; and (h) no disturbances. Species: PIAL = whitebark pine, PIEN = Engelmann spruce, ABLA = subalpine fir, PICO = lodgepole pine, PSME = Douglas-fir, and PIPO = ponderosa pine. Produced using the FireBGCv2 mechanistic ecosystem-fire process model (Keane et al. 2015).

to effects of climate on disease organisms, hosts, and environmental predisposition.

We focus on the major groups of forest diseases in the Northern Rockies known to have significant effects on ecosystems and ecosystem services, and for which at least some information is available on effects of climate.

Dwarf Mistletoe

Dwarf mistletoes (*Arceuthobium* spp.) are a group of parasitic seed plants that are widespread across the Northern Rockies region and primarily cause reduced tree growth and productivity, but in some cases also cause tree mortality. Five species of dwarf mistletoe are found in the region, mostly on these primary hosts: *A. americanum* on lodgepole pine, *A. campylopodum* on ponderosa pine, *A. cyanocarpum* on limber pine, *A. douglasii* on Douglas-fir, and *A. laricis* on western larch (*Larix occidentalis*). Mistletoes may occasionally infect trees of other species when they are growing interspersed with infected primary hosts.

Approximately 28 percent of lodgepole pine forest is infested by *A. americanum*. *Arceuthobium cyanocarpum* occurs primarily east of the Continental Divide, although the area affected has not been estimated. Douglas-fir is infested in more than 13 percent of its range by *A. douglasii*. About 38 percent of the western larch type is infested by *A. laricis*. The distribution of *A. campylopodum* in the region is limited to a portion of Idaho, where it occurs on ponderosa pine. Drummond (1982) estimated that 2.1 million acres of national forest lands were infested by the three most important species of dwarf mistletoe in the Northern Rockies. An estimated 31 million cubic feet of wood are destroyed by these pathogens each year.

Root Disease

Root disease is a major cause of tree growth loss and mortality in the Northern Rockies region. These diseases are primarily a problem west of the Continental Divide, but also affect local areas east of the divide. Various species of fungi cause root disease; the two most important native pathogens in the Northern Rockies region are *Armillaria* species and *Heterobasidion irregulare,* which causes annosus root diseases. These and other root diseases co-occur in many mesic to moist forests west of the divide. Armillaria root disease kills conifers of all species when they are young, but is especially damaging to Douglas-fir, subalpine fir, and grand fir (*Abies grandis*) because these species remain susceptible throughout their lives (Kile et al. 1991). In addition, root diseases often affect canopy closure and create small gaps. The effects of these root pathogens are persistent on a site and have impacts on multiple generations of trees. Armillaria and other root diseases influence forest species composition, structure, and successional trajectories by accelerating a transition to species that are more tolerant of root disease or by maintaining stands of more susceptible species in early-seral stages (Byler and Hagle 2000). They can also affect ecosystem services by affecting visual and recreational resources.

At least 3.3 million acres in the Northern Rockies have moderate to severe root disease, with up to 60 percent caused by *Armillaria ostoyae* (Smith 1984; USDA FS 2007). A recent evaluation of USFS Forest Inventory and Analysis data in the Northern Region identified 2.3 million acres of national forest lands with moderate to severe root disease (Lockman et al., in preparation). Shrub fields have replaced forest cover on 3 percent of forest lands in Idaho and Montana as a result of severe root disease. A study of Ecosection M333d (Bailey 1983), which includes the southern Idaho Panhandle National Forest and southern Kootenai National Forest, found evidence of root disease on 94 percent of the area (Byler and Hagle 2000). Root disease has reduced forest canopy cover in affected stands in northern Idaho and western Montana by an average of 20 to 30 percent.

The National Insect and Disease Forest Risk Assessment (Krist et al. 2014) identified locations where significant tree mortality and basal area losses from insects and diseases could occur between 2013 and 2027, modeling the potential for damage in standing live basal area across all ownerships from a variety of insects and pathogens. Root disease had the highest basal area loss as a percentage of total basal area; projected losses ranging from 0 to 20 percent in most national forests.

Needle Disease

Needle diseases have historically been of limited significance in the Northern Rockies region; 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 casts usually cause loss of needles in the year following a season that has been favorable for infection. In western larch, needle cast and needle blight are observed in the year of infection.

Needle casts and needle blights in lodgepole pine, ponderosa pine, western white pine, Douglas-fir, grand fir, and western larch generally cause little damage in the Northern Rockies region, although periodic outbreaks can cause severe damage in local areas (Lockman and Hartless 2008). These diseases are favored by long, mild, damp springs. Their occurrence at epidemic levels depends on favorable weather conditions and presence of an adequate host population.

Abiotic Disease

Most abiotic diseases result from the effects of adverse environmental factors on tree physiology or structure. This group of diseases can affect trees directly or interact with biotic agents, including pathogens and insects. A number of abiotic and environmental factors can affect foliage or individual branches, or entire trees, tree physiology, and overall tree vigor. The most significant abiotic damage is tree mortality.

Forests in the Northern Rockies region are periodically damaged by weather extremes, such as temperature and drought. Factors such as air pollutants and nutrient extremes occur infrequently or locally. An injury known as “red belt,” caused by strong, dry, warm Chinook winds in winter that induce twig and needle necrosis and desiccation, often afflicts conifers on the east side of the Continental Divide, primarily Douglas-fir and lodgepole pine (Bella and Navratil 1987). 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. A well-studied decline of western white pine called pole blight occurred in the Northern Rockies in the 1930s and 1940s (Leaphart and Stage 1971). This disease occurred on pole-size trees, often in plantations that were growing on shallow soils with low moisture storage capacity that were exposed to extended drought.

Canker Disease

Canker diseases affect tree branches and boles, typically in trees that are poorly adapted to the sites in which they are growing. Damage is caused by breakage at the site of the cankers, or by mortality of branches and boles beyond girdling cankers. Although canker fungi are most active on trees under stress, lack of specific data on climate effects makes it difficult to infer the effects of climate change.

Broad-Scale Climate Drivers of Forest Diseases

Climatic variability and change can alter patterns of pathogen distribution and abundance through (1) direct effects on development and survival of a pathogen, (2) physiological changes in tree defenses, and (3) indirect effects on abundance of natural enemies, mutualists, and competitors (Ayres and Lombardero 2000). Sturrock et al. (2011) suggest that climate change will affect pathogens, hosts, and their interaction; changes in these interactions may become the most substantial drivers of future disease outbreaks.

Fungi cause most forest diseases in the Northern Rockies region. Fungus life cycles are significantly influenced by climate-related factors such as timing and duration of precipitation, humidity, and temperature for spore germination, fungus growth, and inactivation. Fungus life cycles are short compared to their hosts, so fungi can respond more rapidly to a changing climate than their hosts, with potentially serious consequences (Boland et al. 2004). Dwarf mistletoe reproduction and infection are also affected by temperature and moisture (Hawksworth and Wiens 1996), and dwarf mistletoes are generally most prevalent in sites that have undergone past disturbances.

Overall health of host trees has a major role in determining if a pathogen successfully infects a tree or kills it. Many forest diseases, such as canker diseases, are caused by "facultative pathogens" that attack weakened hosts under specific environmental conditions. Impacts of climate change on host physiology may modify host resistance and alter stages and rates of development of pathogens (Coakley et al. 1999). Drought, or limited soil moisture availability, is a major driver that affects the incidence and severity of facultative pathogens. Soil moisture deficit, flooding, and water table fluctuation can all predispose trees to pathogens. Even if there are areas that may have a net gain in precipitation, projected longer growing seasons could cause recurring water deficit stress. Some diseases may be considered threshold diseases; that is, they are damaging but only under certain climatic conditions (Hepting 1963). These diseases may become more damaging if thresholds that trigger infections are reached more frequently, such as in recurring drought.

Effects of Climate Change on Forest Diseases

One of the difficulties of predicting sensitivity to a changing climate is that the scales available for GCMs, pathogen/disease models, and microsite environments do not always match (Seem 2004). For example, some GCM projections provide only mean monthly and annual estimates, rather than daily data useful for modeling forest diseases. In addition, pathogen ecology and effects are sensitive to local site and environmental conditions that may not be well represented by GCMs. There is also considerable uncertainty and lack of knowledge of impacts of a changing climate on future forest conditions and interactions with pathogens (Woods et al. 2005, 2010). Compared to trees, for which available soil moisture is critical, pathogens are affected more by precipitation events, especially timing, duration, and pattern, all of which are poorly projected by climate models. Facultative pathogens respond to weakened or less vigorous hosts, and their importance could increase if climatic conditions less favorable to tree growth become more frequent.

A changing climate will affect forest disease occurrence and severity, through effects on the pathogen, the host, or their interaction (Sturrock et al. 2011) (table 8.7). Interactions between pathogens and abiotic stressors (e.g., temperature and moisture) may represent the most substantial drivers of increased disease outbreaks (Sturrock 2012). Epidemics also depend on relatively constrained conditions for spread and infection to occur. For example, increased drought could affect host susceptibility to pathogens and predispose hosts to disease outbreaks (Coakley et al. 1999). Although models usually generate mean climatic conditions, it is often the extremes that have the greatest influence on pest conditions (Hepting 1963). Increased host stress

Table 8.7—Risk assessment for forest diseases.[a]

Pathogen component	Direction of change	Main driver(s) of change	Projected duration of change	Likelihood of change
Needle disease	Significant increase if appropriate precipitation timing occurs	Increased precipitation in spring and early summer	May occur sporadically in association with weather events	High
Root disease	Little change	Host stress	While hosts are maladapted	Moderate
Dwarf mistletoe	Could decrease mistletoe populations	Temperature could influence flowering and seed production/dispersal	Unknown	Low
Abiotic disease	Significant increase	Temperature and decreased precipitation	Unknown	High

[a] Developed using expert opinion and information from literature as summarized in this chapter.

could result in increased disease occurrence and interactions among multiple agents (Coakley et al. 1999). There is likely to be an increase in declines and dieback syndromes (Manion 1991) caused by changes in disease patterns involving a variety of diseases.

A changing climate may indirectly affect competitors, antagonists, and mutualists that interact with plant pathogens (Kliejunas et al. 2009). Some of the most profound effects of temperature and moisture changes could be on soil microflora, and on and in roots and shoots, where a complex of organisms live in relationships at the transition between pathogenesis, symbiosis, and saprogenesis. The balance among organisms could be upset, for example, turning a normal mycorrhizal association to pathogenesis, shifting pathogens from saprogenic to pathogenic phases, or shifting the order of ascendency of competing organisms due to their different temperature or moisture optima; consequently a pathogen might even take dominance from a saprophyte (Hepting 1963). Given that root pathogens of trees can often exploit a large food reserve in a tree once a defense is breached and then use those reserves to bolster attacks on nearby trees, even small changes in the frequency of shifts in relationships among fungal communities could have large effects.

Despite considerable knowledge about climatic conditions required by specific forest pathogens, little has been done to determine how changing climates may affect these pathogens (Kliejunas et al. 2009). Recent modeling work by Klopfenstein et al. (2009) used a subset of GCMs to project how the geographic distribution of the climate envelope for *Armillaria solidipes* and Douglas-fir could change in the interior northwestern United States. Their analysis suggests that Douglas-fir will have a considerably smaller geographic space that matches its current climate envelope and that this space will shift, whereas only minor changes are projected for *A. solidipes*. They suggest that areas where Douglas-fir is maladapted could increase, which could increase its susceptibility to Armillaria root disease.

Klopfenstein et al. (2009) used information for climatic variables based on the current distribution of *A. solidipes* on its Douglas-fir host in a network of plots. Climate space for *A. solidipes* modeled for current and 2060 climate are shown in figure 8.12. These preliminary projections are not necessarily the current or future distribution of *A. solidipes*, but identify only the modeled climate space matching where the pathogen currently occurs. It is unknown how the climate envelope could change because the distribution of competitor fungi and hosts will change as well.

Spring precipitation is projected to increase in most of the mountainous area of the Northern Rockies (see Chapter 3). This may increase frequency and severity of years when needle diseases cause significant needle loss in conifer species. This could affect the energy balance of susceptible trees, with potential effects on yield and vigor, particularly for species that normally carry multiple years of needles and cannot re-flush later in the season in response to defoliation.

There may be elevation and location maladaptation in resistance to the increased needle disease pressure resulting from climate change, as areas of tree host ranges and disease occurrences shift in location. Lophodermella needle cast in lodgepole pine (caused by *Lophodermella concolor*) occurred in northern Idaho in the early 1980s (Hoff 1985), and has also had outbreaks at high elevation in some Idaho locations in recent years. Lodgepole pine at high elevation normally has only infrequent outbreaks because bud break occurs near or after the time when spring rains that favor infection have ended, whereas needles in lower elevation trees expand when spores are present and able to infect. A provenance study under natural conditions during the outbreak in the 1980s showed that low elevation populations were generally more resistant and had heritable resistance, but high elevation populations were susceptible. About 6

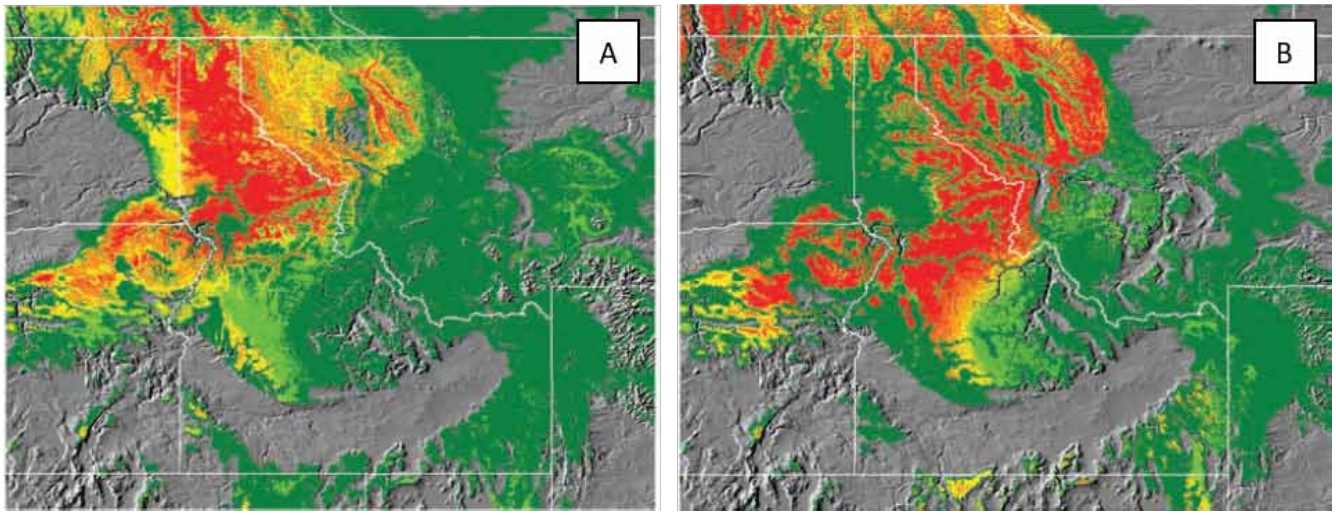

Figure 8.12—Modeled (a) current and (b) future (year 2060) climate space for *Armillaria solidipes* (Klopfenstein et al. 2009). Colors represent the probability of occurrence. Yellow = moderate, red = high.

percent of trees in this mixed provenance planting showed no infection, but 5 percent had almost complete defoliation. If moist conditions following bud break continue to occur at high elevation where natural selection for resistance has not occurred, recurrent needle disease outbreaks could stress trees and make lodgepole pine more susceptible to other factors (Hoff 1985).

Another example of a needle disease that may increase in the Northern Rockies region under climate change is Swiss needle cast (caused by *Phaeocryptopus gaeumannii*). This disease severely limits productivity of Douglas-fir west of the Cascade divide in Oregon and Washington, causing growth losses of up to 50 percent (Manter et al. 2005). Needle loss is very highly correlated with increasing winter temperatures and spring needle wetness. The disease, which is expected to become more severe in forests west of the Cascade crest in a warmer climate (Stone et al. 2008), has periods of local occurrence in northern Idaho (Navratil and Bella 1988) and Montana (Weir 1917). Milder winters and wetter springs that could increase the future distributions and severity of the disease might occur, but as yet, investigations and modeling have not been conducted to map and quantify potential effects.

Kliejunas (2011) performed a qualitative risk assessment of the effect of projected climate change on a number of forest diseases, several of which occur in the Northern Rockies. Dothistroma needle blight (caused by *Dothistroma septosporum*) provides a good example of potential effects of climate change. Kliejunas (2011) estimates that the risk potential is low if a warmer and drier climate occurs. A warmer and wetter climate could increase the risk potential to moderate. His assessment of the effect of climate change on dwarf mistletoes indicated a high risk potential regardless of precipitation levels because dwarf mistletoe survival and infection increases with temperature. His assessment of Armillaria root disease indicated a high to very high risk potential depending on moisture availability, with drier conditions increasing the potential.

Forest Pathogen Interactions

Direct effects of fire on pathogens are generally minimal. Fire directly and indirectly influences distribution, severity, and persistence of forest diseases; similarly, forest diseases influence fire behavior and severity. Diseases are generally host-specific, so removal of susceptible tree species by fire will usually reduce disease, whereas improving habitat for susceptible tree species will usually increase disease over time.

Forest pathogens are directly damaged by smoke and heat of fires. Smoke can inhibit dwarf mistletoe seed germination (Zimmerman and Laven 1987), and heat from fire can kill pathogens that cause root disease in the top 3 inches of soil (Filip and Yang-Erve 1997). Forest diseases are affected more by tree mortality from fire. Frequency and intensity of fire can affect persistence, as well as distribution and severity of certain diseases. High-intensity fires can completely remove a pathogen with its host, as with lodgepole pine-dwarf mistletoe (Kipfmueller and Baker 1998; Zimmerman et al. 1990), or remove species susceptible to root disease and prepare the site for regeneration of less susceptible seral species, such as pines and western larch (Hagle et al. 2000). Low-intensity fires often leave mosaics of pathogens along with their susceptible hosts, which can cause substantial increases of diseases such as dwarf mistletoe (Kipfmueller and Baker 1998). However, low-intensity fires in some habitats maintain species tolerant of root disease such as western larch (Hagle et al. 2000).

Human-caused fire exclusion has led to an increase in root disease and dwarf mistletoe (Hagle et al. 2000; Rippy et al. 2005), which can influence fire behavior and severity. Root disease creates pockets of mortality and scattered mortality; the resulting standing and down woody debris increases fuel loading, especially large fuels (Fields 2003). Increased litter accumulation and resinous witches' brooms from dwarf mistletoe infections can provide ladder fuels that may cause a ground fire to move into the canopy (Geils et al. 2002).

Climate effects that increase frequency or intensity of fires may affect incidence and severity of dwarf mistletoes (Zimmerman and Laven 1985). Fire affects dwarf mistletoes by changing canopy structure and stand density (Alexander and Hawksworth 1975; Dowding 1929); eliminating lower branches, which may have the heaviest infections and mistletoe seed production; thinning stem density, which may reduce lateral spread; and causing mistletoe shoots to abscise. Loss of shoots eliminates some infections directly, but even if infections remain within the bark, loss of shoots prevents seed production for several years, slowing mistletoe intensification within stands. Trees heavily infested with mistletoe often retain low infected branches and are prone to torching in fire, which could increase the risk of crown fire (Conklin and Geils 2008). Alternatively, torching in individual trees could eliminate the most heavily infected sources of mistletoe seed that infect understory regeneration.

An increase in severe weather events or fires could increase occurrence of other diseases. For example, root and bole wounds could be used as "infection courts" for root disease, and such wounds from management, windfalls, and fire are major avenues of infection for true firs and western hemlock (Smith 1989) and lodgepole pine (Littke and Gara 1986). Fire damage and other stresses can release root disease infections that have been walled off by host resistance responses (Hagle and Filip 2010). Relative importance of different root diseases could be altered under some climate change scenarios. Except as a sapling, western larch is considered resistant to Armillaria root disease due to its ability to generate multiple corky barriers at infection sites (Robinson and Morrison 2001). The response of this species to wounds and the thick bark that it generates also make it among the most resistant to fire damage, and a species more likely to persist and regenerate under increased fire frequency.

Illustrating interactions between bark beetles and disease, a study in lodgepole pine forests of central Oregon showed that altered stand structure following an MPB epidemic increases dwarf mistletoe in lodgepole pine stands, thereby reducing stand growth and productivity and slowing stand recovery (Agne et al. 2014). The influence of dwarf mistletoe on stand structure heterogeneity could increase landscape resistance and resilience to disturbances. Another example of complex interrelationships is the interaction between stem decay, bark beetles, and fire frequency in central Oregon lodgepole pine. After fire damaged the roots of lodgepole pines, stem decay fungi infected these damaged roots and over time caused extensive heartwood decay in the boles of these trees. Data show these decay-infected trees grew at a slower rate than uninfected trees and trees with stem decay were preferentially attacked by MPB years later (Littke and Gara 1986).

Nonnative Plants

Overview

Projecting how nonnative plants and climate change may interact to alter native plant communities, ecosystems, and the services they provide is challenging because of our limited ability to project how climate change will alter specific local abiotic conditions that define the fundamental niches of plants (Gurevitch et al. 2011; Thuiller et al. 2008). We start with knowledge of structure and function of current ecosystems, and then apply first principles of ecology to explore how climate change might alter these systems, their susceptibility to invasion, and invasiveness of introduced plants from a general perspective. We do not project changes in individual plant species, but define the parameters that bound potential community change based on climate projections and discuss how community invasibility might be affected across that range of potential conditions.

Effects of Climate Change on Nonnative Species

Hundreds of nonnative species have been introduced into the Northern Rockies region (Rice n.d.). Not all of these species are abundant, but recent surveys showed that nonnative plants account for an average of 40 percent of species present (richness), and 25 percent of those nonnatives have significant effects on native grassland flora (Ortega and Pearson 2005; Pearson et al. in review). Invasive plant species represent a threat to ecosystem integrity because they compete with native species in many plant communities and can alter ecological processes. These negative impacts can reduce biological diversity, forage for wildlife, and recreation opportunities. Most nonnative invasive species are herbaceous species (graminoids and forbs), but some are shrub and tree species that commonly occur in riparian areas (e.g., Russian olive [*Elaeagnus angustifolia*], tamarisk [*Tamarix ramosissima*]).

Although extensive work has been done to understand the biology of some of the most common nonnatives, such information is far from complete. Few studies have explored how changes in temperature and moisture related to climate change may affect nonnative plant populations in the Northern Rockies region.

It has historically been assumed that climate change will favor nonnative plants over native species (Dukes and Mooney 1999; Thuiller et al. 2008; Vila et al. 2007; Walther et al. 2009), but this may be an overgeneralization (Bradley et al. 2009, 2010; Ortega et al. 2012). Numerous attributes associated with successful invaders suggest nonnative species could flourish under certain climate change scenarios. For example, many nonnative plants are fast-growing early-seral species (ruderals) that tend to respond favorably to increased availability of resources, including temperature, water, sunlight, and CO_2 (Milchunas and Lauenroth 1995; Smith et al. 2000; Walther et al. 2009). Extensive work shows that nonnative species respond favorably to disturbance (Zouhar et al. 2008), which can increase resource availability (Davis et al. 2000). Nonnative species may also exploit the disturbances associated with postfire conditions better than many native species (Zouhar et al. 2008), despite the adaptations of native plants to fire. In bunchgrass communities, many nonnative plants recruit more strongly 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, both of which can allow them to migrate more quickly than slow-growing and slowly dispersed species (Clements and Ditommaso 2011). Greater plasticity of successful invaders could also favor their survival in place and ability to expand their populations (Clements and Ditommaso 2011). Collectively, these attributes suggest that many nonnative species would benefit if climate change results in increased disturbance.

Few studies have manipulated CO_2, moisture, or temperature to quantify the effects of climate change on nonnative versus native plants in the Northern Rockies region. Of the work that does exist, most has targeted grassland and sagebrush communities, presumably because these are among the most susceptible to invasion (Forcella 1992; see also Chapter 7). Experimentally increasing temperatures in a Colorado meadow system resulted in increases in native upland shrubs, with big sagebrush (*Artemisia tridentata*) increasing in drier conditions and shrubby cinquefoil (*Dasiphora fruticosa*) in wetter conditions (Harte and Shaw 1995). These different responses indicate the importance of background moisture in driving species-specific responses to elevated temperatures.

Recent experimental work in western Montana showed that reduced precipitation can significantly impact spotted knapweed (*Centaurea melitensis*), whereas native bluebunch wheatgrass (*Pseudoroegneria spicata*) populations were unaffected by the same drought stress (Ortega et al. 2012; Pearson et al., unpublished data). This result is consistent with historical observations of spotted knapweed declines following drought conditions (Pearson and Fletcher 2008). In Wyoming sagebrush-steppe systems,

Table 8.8—Prominent nonnative species in the Northern Rockies and their primary habitats.

Species	Habitat
Cheatgrass (*Bromus tectorum*)	Xeric shrublands and grasslands
Spotted knapweed (*Centaurea maculosa*)	Xeric shrublands and grasslands, dry forest openings
Rush skeletonweed (*Chondrilla juncea*)	Xeric shrublands and grasslands
Canada thistle (*Cirsium arvense*)	Wetland/riparian areas, disturbed sites in moist grasslands
Houndstongue (*Cynoglossum officinale*)	Highly disturbed mesic and xeric grasslands, roadsides
Leafy spurge (*Euphorbia esula*)	Riparian areas, mesic and xeric grasslands
Orange hawkweed (*Hieracium aurantiacum*)	Forest openings, moist meadows, roadsides
Yellow hawkweed complex (*Hieracium* spp.)	Forest openings, roadsides
St. Johnswort (*Hypericum perforatum*)	Xeric grasslands and shrublands
Dalmatian toadflax (*Linaria dalmatica*)	Xeric grasslands and shrublands
Yellow toadflax (*Linaria vulgaris*)	Mesic to xeric grasslands and shrublands, burned areas
Sulfur cinquefoil (*Potentilla recta*)	Xeric grasslands and shrublands
Common tansy (*Tanacetum vulgare*)	Riparian areas

bluebunch wheatgrass outperformed both cheatgrass and medusahead (*Taeniatherum caput-medusae*) in dry years, but the opposite was true in wet years (Mangla et al. 2011). Community-level studies in other grasslands have shown that drought periods can shift vegetation away from annual grasses and forbs and toward drought-tolerant native perennial grasses (Tilman and El Haddi 1992). Hence, heating and drying could favor drought-tolerant native species in dry grassland and sagebrush systems and reduce their susceptibility to invasion by nonnative species (see Chapter 7). However, these conditions might increase susceptibility of native vegetation to invasive species in wetter locations.

Xeric Grasslands and Shrublands

Of the many dominant cover types that occur in the Northern Rockies region, the most vulnerable to weed invasion are typically those on warm, dry (xeric) sites, although riparian and wetland sites can be invaded by several invasive plant species. The most susceptible plant communities tend to have low vegetation cover, high bare ground, and unproductive soils; various nonnative plant species exploit these more open sites. However, disturbances resulting from fire or vegetation management can provide opportunities for invasion in most kinds of dominant vegetation. Hundreds of nonnative plant species occur in the Northern Rockies, the most serious of which are described in table 8.8.

Xeric grasslands and shrublands are highly vulnerable to establishment of nonnative species (see Chapter 7). Many of the native plants in Northern Rockies grasslands are perennials that tolerate environmental variability over long time scales in contrast with the life history strategies of weedy invasive species (Grime 1977; MacArthur and Wilson 1967). Whether native or nonnative species benefit, or more specifically, which native or nonnative species benefit, will probably depend on the specific ways in which climate change plays out.

If temperature increases but precipitation does not, this will likely reduce resource availability and increase stress, potentially favoring nonnative species. Projections of the effects of climate change need to consider how nonnative plants respond, as well as how recipient communities and their invasibility may change. Many successful nonnative species flower later and have different phenologies from native species, allowing nonnative species to potentially exploit an empty niche (Pearson et al. 2012). Therefore, nonnative species may increase if this niche expands with climate change, or decline if the niche is disrupted.

Invasive species primarily spread into disturbed areas with sufficient bare ground and sunlight for germination and establishment, although some species such as spotted knapweed, houndstongue (*Cynoglossum officinale*), yellow sweet clover (*Melilotus officinalis*), and yellow toadflax (*Linaria vulgaris*) can readily establish in undisturbed plant communities. Nonforested landscapes (e.g., shrublands, grasslands) have been invaded in many areas of the Northern Rockies region (see Chapter 7). As fires and other disturbances increase in intensity and frequency, invasive species can occupy and potentially dominate native plant communities that were previously resistant to invasion, although numerous factors such as fire resistance of native species, propagule availability, and variation in burn severity can affect establishment (Zouhar et al. 2008). Native and domestic livestock grazing and browsing of native species can reduce plant vigor and open up sites for establishment of invasive species. Silvicultural prescriptions that decrease canopy cover also increase the likelihood that invasive species may establish and increase in both cover and density,

Table 8.9—Risk assessment for nonnative plant species.[a]

Invasive species component	Direction of change	Main driver(s) of change	Likelihood of change
Area infested	Variable by species, from low to high	Altered temperature and precipitation patterns; increased atmospheric CO_2; altered fire regimes	High
Species response to habitat disturbance	High	Increased fire frequency and severity, which can increase the amount of habitat vulnerable to nonnative invasion	High
Altered fire regimes	High	Increased fire frequency in areas with fire-tolerant and flammable invasive species (e.g., cheatgrass-fire cycle)	High

[a] Developed using expert opinion and information from literature as summarized in this chapter.

although subsequent succession may suppress those species as canopy closure returns.

Climate change is likely to result in a range of responses among invasive species, due to differences in their ecological amplitude and life history strategies (table 8.9). Bioclimatic envelope modeling indicates that climate change could result in both range expansion and contraction for five widespread and dominant invasive plants in the western United States. Yellow starthistle (*Centaurea solstitialis*) and tamarisk are likely to expand, whereas leafy spurge (*Euphorbia esula*) is likely to contract; cheatgrass and spotted knapweed are likely to shift in range, leading to both expansion and contraction (Bradley 2009; Bradley et al. 2009). Invasive species are generally inherently adaptable and capable of relatively rapid genetic change, which can enhance their ability to invade new areas in response to ecosystem modifications (Clements and Ditomaso 2011), including short-term disturbance (fire) or long-term stressors (e.g., prolonged drought, increased temperatures, chronic improper grazing). Increased concentrations of CO_2 in the atmosphere have been shown to increase the growth of weed species, which could have an influence on their invasiveness (Ziska 2003).

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