Chapter 7
Effects of Climate Change on Ecological Disturbance in the Northern Rockies

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Abstract Disturbances alter ecosystem, community, or population structures and change elements of the biological and/or physical environment. Climate changes can alter the timing, magnitude, frequency, and duration of disturbance events, as well as the interactions of disturbances on a landscape, and climate change may already be affecting disturbance events and regimes. Interactions among disturbance regimes, such as the co-occurrence in space and time of bark beetle outbreaks and wildfires, can result in highly visible, rapidly occurring, and persistent changes in landscape composition and structure. Understanding how 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

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land management strategies that are appropriate for future climates. This chapter describes the ecology of important disturbance regimes in the Northern Rockies region, and potential shifts in these regimes as a consequence of observed and projected climate change. We summarize five disturbance types present in the Northern Rockies that are sensitive to a changing climate—wildfires, bark beetles, white pine blister rust (*Cronartium ribicola*), other forest diseases, and nonnative plant invasions—and provide information that can help managers anticipate how, when, where, and why climate changes may alter the characteristics of disturbance regimes.

Keywords Disturbance • Wildfire • Beetles • Pathogens • Climate change • Resilience • Rocky Mountains

7.1 Introduction

The term *disturbance regime* describes the general temporal and spatial characteristics of a *disturbance agent*, such as insects, disease, fire, and human activity, and the effects of that agent on the landscape (Table 7.1). More specifically, a disturbance regime is the cumulative effect of multiple disturbance events over space and time (Keane 2013). Disturbances alter ecosystem, community, or population structures and change elements of the biological and/or physical environment (White and Pickett 1985). The resulting shifting mosaic of diverse ecological patterns and structures affects future patterns of disturbance, in a reciprocal, linked relationship that shapes the fundamental character of landscapes and ecosystems.

Climate changes can alter the timing, magnitude, frequency, and duration of disturbance events, as well as the interactions of disturbances on a landscape, and climate change may already be affecting disturbance events and regimes (Dale et al. 2001). Interactions among disturbance regimes, such as the co-occurrence in space and time of bark beetle outbreaks and wildfires, can result in highly visible, rapidly occurring, and persistent changes in landscape composition and structure. Understanding how 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. 2015a).

This chapter describes the ecology of important disturbance regimes in the Northern Rockies region, and potential shifts in these regimes as a consequence of observed and projected climate change. We summarize five disturbance types in the Northern Rockies that are sensitive to a changing climate—wildfires, bark beetles, white pine blister rust (*Cronartium ribicola*), other forest diseases, and nonnative plant invasions—and provide information that can help managers anticipate how, when, where, and why climate change may alter the characteristics of disturbance regimes.

Table 7.1 Characteristics used to describe disturbance regimes

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 fires effects; spring burns can be more damaging to growing plants than autumn burns on dormant plants
Duration	Length of time of 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	The spatial and temporal variability of the above factors	Highly variable weather and mountain pine beetle mortality can cause variable burn conditions resulting in patchy burns of small to large sizes

From Keane (2013)

7.2 Wildfire

7.2.1 Overview

Wildland fire was historically the most important and extensive landscape disturbance in the Northern Rockies region (Hejl et al. 1995). Wildfire emerged as a dominant process in North America after the end of the last glacial period, about 16,500–13,000 years before present, with rapid climate changes and increased tree cover (Marlon et al. 2009). In the Northern Rockies, many forest types are fire prone and fire adapted, meaning that fire is an integral and predictable part of their maintenance and ecological functioning.

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 7.2).

Table 7.2 Risk assessment for fire regime changes, based on expert opinion and information from literature summarized in this chapter

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 human-caused 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 forests, until fires decrease surface fuel loads; in mesic forests, if increased fire frequency decreases fuel loads	Moderate

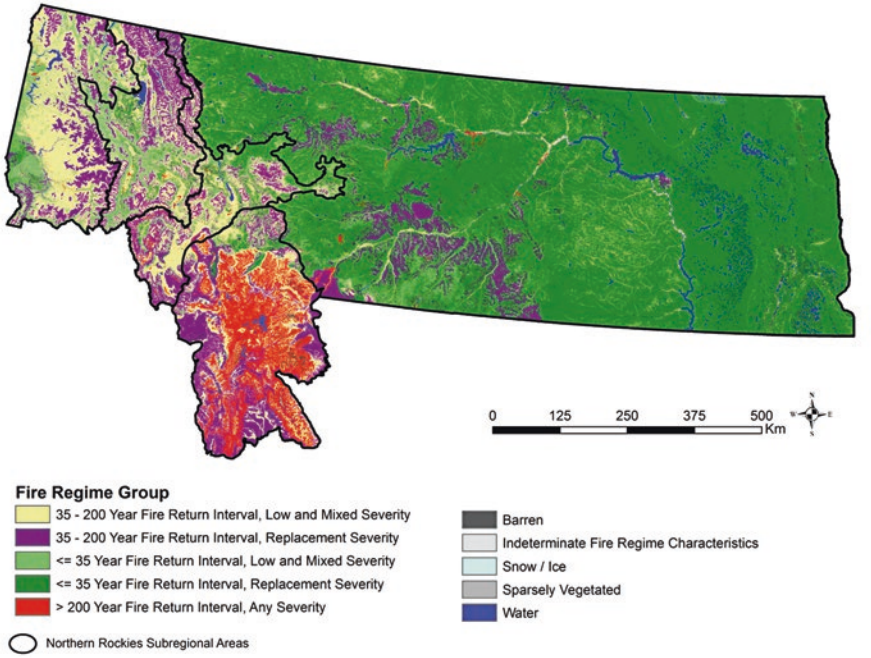

Fig. 7.1 Fire regime groups for the Northern Rockies, LANDFIRE mapping program. The fire regime group layer characterizes the presumed historical fire regimes within landscapes based on interactions among vegetation dynamics, fire spread, fire effects, and spatial context

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% of the dominant overstory vegetation; (2) moderate-frequency (35–200 years), mixed-severity fires that replaced up to 75% of the overstory; and (3) infrequent (200+ years), high-severity fires that replaced greater than 75% of the dominant overstory vegetation (Fig. 7.1).

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 in ponderosa pine forests burned frequently enough to maintain low fuel loads and open stand structure, resulting in a landscape in which fire-caused mortality of mature trees was rare (Agee 1998; Jenkins et al. 2011). Conversely, high-severity fires occurring at intervals of more than 300 years are typical in subalpine forests. These fires cause extensive mortality of mature trees because long intervals between fires result in dense, multi-layer forest structures that are susceptible to crown fires (Agee 1998).

Climate and fuels are the two most important factors controlling fire regimes 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 longer time scales by shaping species composition and productivity (Dale et al. 2001; Marlon et al. 2008) and large-scale climatic patterns such as the El Niño Southern Oscillation and Pacific Decadal Oscillation are important drivers of forest productivity and susceptibility to disturbance in the Northern Rockies (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, also affect the amount and structure of fuels (Falk et al. 2011).

At annual time scales, weather is the best predictor of fire characteristics such as area burned and fire size. In forest ecosystems, fuels lose moisture and become flammable in warm and dry summers typical in the Northern Rockies, 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). In these high-elevation systems short-duration drying episodes generally do not create sufficiently dry conditions to sustain a fire, but prolonged dry weather conditions (about 40 days without precipitation) can sufficiently dry fuels to carry large, intense fires once they are ignited (Schoennagel et al. 2004). 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 non-forested 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 (Westerling and Swetnam 2003; Gedalof et al. 2005). 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 nonnative species, and fire management (fuel 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 (Swetnam et al. 1999; Marlon et al. 2009). For many sagebrush ecosystems of low to moderate productivity, fire intervals are 10–20 times shorter today than what is estimated for pre-twentieth century conditions (Chap. 6), because of the spread and dominance of the nonnative annual cheatgrass (*Bromus tectorum*). In contrast, many 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 that historically experienced low-severity fire regimes (Peterson et al. 2005) and in some forests that experienced mixed-severity regimes (Taylor and Skinner 2003).

7.2.2 Potential Future Wildfire Regimes and Wildfire Occurrence

The most visible and significant short-term effects of climate changes on forest ecosystems are likely to be caused by altered disturbances, often occurring with increased frequency and severity. Climate changes are likely to increase fire frequency, fire season length, and cumulative area burned in the coming decades in the western United States, in response to warmer, drier conditions (McKenzie et al. 2004; Flannigan et al. 2006). Climate changes may also increase the frequency or magnitude of extreme weather events that affect fire behavior (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).

Earlier snowmelt, higher summer temperatures, and longer fire seasons have resulted in increased wildfire activity compared to the mid-twentieth century, particularly in the Northern Rockies (Westerling et al. 2006). Potential mid to late twenty-first century climate-driven changes to regional fire regimes 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 (Brown et al. 2004; Westerling et al. 2006; Rocca et al. 2014). In particular, lengthening of the fire season will allow for more ignitions, greater likelihood of fire spread, and a longer burning duration (Riley and Loehman 2016). 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 snowmelt will reduce fuel moistures during the fire season, making a larger portion of the landscape flammable for longer periods of time (McKenzie et al. 2004). This shift may be especially pronounced in middle to high elevation forested systems where fuels are abundant. 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 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 (Loehman et al. 2011; Holsinger et al. 2014; Rocca et al. 2014), and the Greater Yellowstone Area (Westerling et al. 2011). For a mean temperature increase of 2 °C, the annual area burned by wildfires is expected to increase by a factor of 1.4–5 for most western states (McKenzie et al. 2004). The effects of future climate on fire severity (i.e., the proportion of overstory mortality) are less certain because severity is more sensitive than area burned to arrangement and availability of fuels. The trend for larger, more damaging fires in sagebrush ecosystems is expected to continue until aberrations in fuel conditions that drive fire are altered (Keane et al. 2008).

7.2.3 Potential Interactions Between Wildfire and Other Disturbances

Interactions between fire and other disturbance agents will likely be a driver of ecosystem change under changing climate. Drought and increased temperatures are key drivers of both wildland fires and bark beetle outbreaks. Multiple studies have cited changes in fire behavior resulting from bark beetle-caused mortality in pine forests (reviewed in Hicke et al. 2012), with increased fire intensity persisting for approximately 5 years after fire, depending on local conditions.

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; Hansen 2014).

7.3 Bark Beetles

7.3.1 Overview

Bark beetles are an important forest disturbance agent in the Northern Rockies region. Bark beetles in the region feed in the phloem of living conifers and can have extreme population amplifications over short time periods. Larval feeding, in addition to colonization by beetle-introduced fungi, typically results in death of the tree. Bark beetles are relative specialists, feeding on a single tree species or several species within a single genus, and in the Northern Rockies, multiple tree species are affected by different bark beetle species.

Historically, pulses of bark beetle-caused tree mortality were extensive across the northern Rocky Mountain region. Recently, between 1999 and 2013, bark beetle-caused tree mortality in the Northern Rockies affected nearly 570,000 hectares each year. Mountain pine beetle (*Dendroctonus ponderosae*, hereafter referred to as MPB) caused the majority of tree mortality, cumulatively affecting about 3.5 million hectares over the 1999–2013 time period. 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).

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 non-host trees, often producing uneven-aged stands (Mitchell and Preisler 1998). At outbreak population levels, tree mortality can approach 80% 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). 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.

7.3.2 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 the perfect scenario 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 that allow for rapid population growth. Triggers include factors 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*) (Shore et al. 1999; Hebertson and Jenkins 2007), 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 (Régnière and Bentz 2007; Powell and Bentz 2009).

Climate and weather directly drive bark beetle outbreaks by affecting beetle growth and survival. 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 (Hansen et al. 2001, 2011; Bentz and Jönsson 2015).

Temperature is also an important determinant of the number of bark beetle 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), although multivoltine in more southern parts of their range. Other bark beetle species require at least one year to complete a generation (univoltine), and at higher elevations where temperatures are cooler, two to three 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 (Hansen et al. 2001; Bentz et al. 2014). 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). However, extreme fluctuations in temperature in spring and autumn, in addition to long durations of temperatures below −35 °C, can cause extensive larval mortality (Safranyik and Linton 1991; Régnière and Bentz 2007).

7.3.3 Potential Effects of Climate Change on Bark Beetles

Climate change will likely have direct and indirect effects on bark beetle population outbreaks (Table 7.3). Indirectly, changing temperature and precipitation regimes influence the suitability and spatial distribution of host trees. Fungi, predators, and competitors associated with beetles can also be affected by changing climate and thereby indirectly affect beetle population outbreaks. Direct effects may also occur as changing temperature regimes either promote or disrupt bark beetle temperature-dependent life history strategies. Future bark beetle-caused tree mortality will therefore depend not only on the spatial distribution of live host trees and heterogeneity

Table 7.3 Risk assessment for mountain pine beetle outbreaks, developed using model simulations and expert opinion and information from literature summarized in this chapter

Elevation	Direction of change	Main driver(s) of change	Projected duration of change	Likelihood of change
<1000 m	Increase if host trees available	Temperature–caused shift to bivoltinism[a]	Increasing risk through 2100	High
1000–2000 m	Decrease	Temperature-caused disruption of seasonality	Decreasing risk through 2100	High
2000–3000 m	Increase initially, then decrease	Initially temperature-caused shift from semivoltine[b] to unvioltine[c], then disruption of seasonality	Decreasing risk through 2100	High
>3000 m	Increase	Temperature-caused shift from semivoltine to univoltine	Increasing risk through 2100	High

[a] Two generations in 1 year
[b] One generation in 2 years
[c] One generation in 1 year

of future landscapes, but also on the ability of beetle populations and their associates to adapt to changing conditions (Bentz et al. 2016).

Projected changes in temperature and precipitation may cause significant stress to bark beetle host trees in the future. 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 temperatures are expected to alter the seasonal timing of soil water availability because of reduced snowpack and more precipitation falling as rain rather than snow (Regonda et al. 2005). Reduced soil water availability during the late spring and summer will lead to increased physiological drought stress in host trees that could indirectly benefit bark beetles that colonize stressed hosts in the late spring or summer (Raffa et al. 2008). Similarly, increased disturbance events could provide a reservoir of stressed trees used by some bark beetle species, leading to epidemic population levels.

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, an increase in minimum temperature between 1960 and 2011 was associated with an increase in MPB survival and subsequent beetle-caused tree mortality in the Northern Rockies (Weed et al. 2015). As climate continues to change, extreme within-year variability in winter warming could be detrimental to insect survival, so reduced snow levels could therefore contribute to increased 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 lifecycle in warm years (Hansen et al. 2001; Bentz et al. 2014). Warming temperatures could also cause species that are 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 disrupt seasonality (Régnière et al. 2015).

7.3.4 Projected Effects of Climate Change on Bark Beetle Populations

Mechanistic models can be used to explore the potential effects of changing climate on bark beetle populations. Here we describe results from a temperature-dependent mechanistic demographic model of MPB population growth that is based on phenological synchrony (Powell and Bentz 2009). The model was driven with downscaled temperatures from two GCMs (CanEMS2, CCSM4) and two greenhouse gas emissions scenarios (RCP 4.5 and 8.5). Climate data were downscaled using the multivariate adaptive constructed analogs approach (Abatzoglou and Brown 2012). Although indirect effects of climate clearly affect host tree vigor, stand composition, and distribution across a landscape, these effects were not included in the

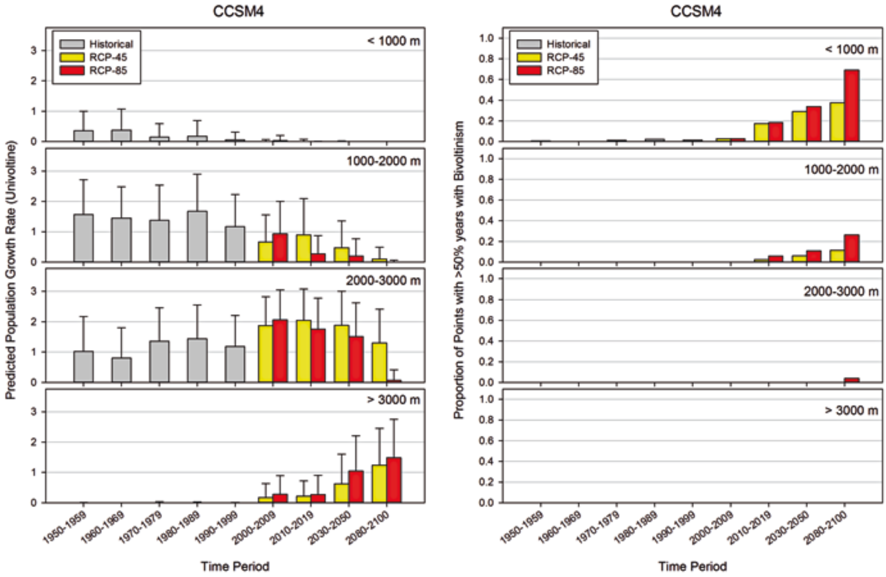

Fig. 7.2 Left panel: projected mountain pine beetle population growth rate (mean, standard deviation) of univoltine populations (one generation per year) over decades (historical) and 20-year periods (projected) from 1950 to 2100, for the RCP 4.5 and 8.5 emission scenarios (see section 7.3.4). Shown are the mean and standard deviation among locations of decadal (historical) and 2-decadal (projected) growth rates. Right panel: proportion of simulation points in which bivoltinism (two generations in 1 year) is projected for more than 50% of years in each time period

demographic model. Model output was considered only for locations where pines currently grow.

The proportion of areas with thermal requirements for MPB bivoltinism has historically been low in the Northern Rockies (Fig. 7.2). Stands at elevations <1000 meters currently have relatively few pines and low hazard for 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 and future climates relative to historical periods. However, the proportion of simulation points at <1000 meters with thermal regimes that allow for bivoltinism is projected to increase through 2100, particularly with greater temperature increases (under RCP 8.5) (Fig. 7.2). The availability of pines at <1000 meters in future climates may be restricted.

Overall, model results suggest that pine stands above 2000 meters, particularly between 2000 and 3000 meters, have the highest risk to MPB-caused tree mortality in the near future. The highest density of pine occurs at 2000–3000 meters, the elevation range also associated with a majority of stands with high hazard (56%). These stands are projected to have higher univoltine population growth rates than in the historical period. Thermal regimes for bivoltinism are unlikely at these elevations (Fig. 7.2). In stands above 3000 meters, population growth rates were historically very low until 2000–2009. However, rates are projected to increase through 2100 (Fig. 7.2). These stands have historically been, and will remain, too cool for bivoltinism.

7.4 White Pine Blister Rust

7.4.1 Overview

White pine blister rust (*Cronartium ribicola,* hereafter referred to as WPBR) is a nonnative fungus introduced to western North America from Europe around 1910 (Tomback and Achuff 2011). The life cycle of WBPR requires two hosts, with two spore-producing stages on white pine and three separate spore producing stages on alternate hosts: *Ribes*, *Pedicularis,* and *Castilleja*. The WPBR fungus infects three white pines found in the Northern Region: western white pine (*Pinus monticola*), whitebark pine (*P. albicaulis*), and limber pine (*P. flexilis*). WPBR has been found across most of the ranges of these three pines, causing over 90% mortality in western white pine. WPBR infections rates are highest in the warmer, moister parts of the ranges of whitebark and limber pine (Tomback and Achuff 2011).

The time required for WPBR to kill its host varies by species, distance of infection from bole, and bole circumference. WPBR kills western white pine in 5–10 years, and whitebark pine in 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. Native pine populations show some heritable resistance to WPBR, but the frequency of resistance is low and variable (Hoff et al. 1980), although resistance may have increased since this early report through additional natural selection (Klopfenstein et al. 2009).

7.4.2 Effects of Climate Change on WPBR

Climate change may cause WPBR infections to occur earlier and with greater frequency and intensity in pine stands. 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—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—may increase in the future for whitebark pine, although wave years may actually decrease for most temperate pine forests because of hotter, drier conditions in a changing climate (Sturrock et al. 2011). Warmer temperatures could negatively impact rusts, although extreme weather could facilitate WPBR spore dispersal, resulting higher spore loads and expansion of its range (Helfer 2014).

Climate-mediated changes in host regeneration dynamics could restrict or expand host ranges (Helfer 2014), thus altering WPBR range. The distribution and occurrence of synergistic combinations of alternate host species (Zambino 2010) could also change. Higher elevation areas may experience new climates that facilitate the expansion of *Ribes* into areas that were historically too cold and snowy. On the other hand, low-elevation upland areas where *Ribes* are currently abundant might experience drought that causes decline of the host. Moreover, drought may cause extended and extensive stomatal closure in pines, thus preventing hyphae entry.

7.4.3 Interactions with Other Disturbance Processes

Interactions 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).

Fire indirectly affects WPBR by changing the size, distribution, and abundance of its hosts. Mixed- and high-severity fires are currently common in most forests where WPBR is present (Arno et al. 2000), and these fires are projected to increase in size, frequency, and intensity (Westerling et al. 2011). Increased fire frequency and area burned can create favorable conditions for pine regeneration, because most five-needle pine seeds are dispersed by rodents and birds and are thus well adapted to spread into postfire landscapes. *Ribes* populations may increase after fire through regeneration by seed and sprouting from roots and rhizomes. However, re-burns soon after an initial fire can eliminate regenerating *Ribes* before they can develop a seed bank 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 they dampen the rate of rust-resistant adaptations (Keane et al. 2012). However, where rust-resistant pines survive fire, they can provide seeds for populating future landscapes that are resilient to rust infection and fire mortality.

Trees infected with WPBR are weakened, and may be more susceptible to fire-caused damage and mortality (Stephens and Finney 2002), and canopies of trees attacked or killed by WPBR may increase crown fire because of excessive pitch. Mortality from WPBR often results in elimination or thinning of the shade-intolerant pine overstory, allowing shade-tolerant competitors to occupy the openings and creating different canopy fuel conditions (Reinhardt et al. 2010). Many shade-tolerant competitors are more susceptible to fire damage, resulting in higher postfire tree mortality in rust-infected landscapes.

Mountain pine beetle also influences WPBR through regulation of the tree species that host 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 pines in Yellowstone have been subjected to a major MPB outbreak over the last decade, resulting in substantial mortality of rust-resistant whitebark pine trees (Logan et al. 2008).

Model simulations of MPB disturbance under current climate suggest a decline in both lodgepole pine (especially without fire) and whitebark pine, with a corresponding increase in subalpine fir (*Abies lasiocarpa*) and Douglas-fir (*Pseudotsuga menziesii*), and little change with the addition of WPBR (Fig. 7.3). These trends are enhanced under a warmer climate, in which lodgepole pine declines are greater and stands are mainly replaced by Douglas-fir, but WPBR interaction has minor effects on species composition (Keane et al. 2015a). Fire frequency under current climate is 10% lower when fire, MPB, and WPBR are allowed to interact, and average tree mortality is also lower (Fig. 7.3). 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. 2015a) (Fig. 7.4).

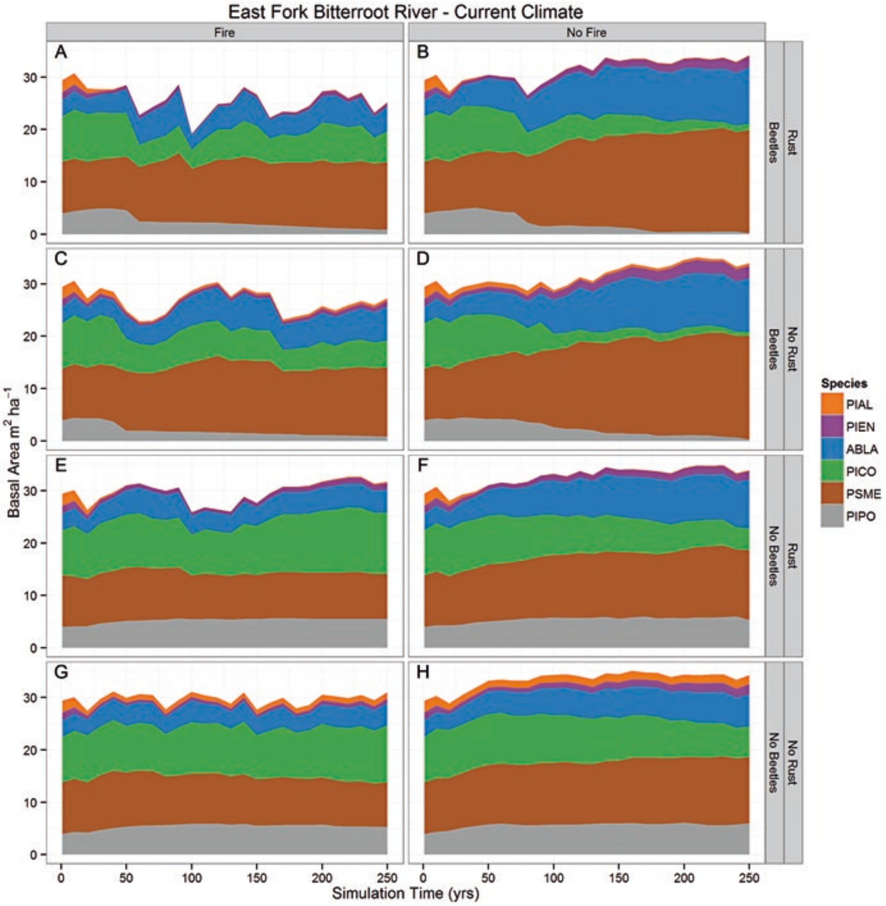

Fig. 7.3 Landscape composition of species cover types using the plurality of basal area for current climate for the East Fork of the Bitterroot River landscape with all combinations of fire, white pine blister rust, and mountain pine beetle. Species: PIAL = whitebark pine, PIEN = Engelmann spruce, ABLA = subalpine fir, PICO = lodgepole pine, PSME = Douglas-fir, and PIPO = ponderosa pine. Produced using the FireBGCv2 mechanistic ecosystem-fire process model (Keane et al. 2015a)

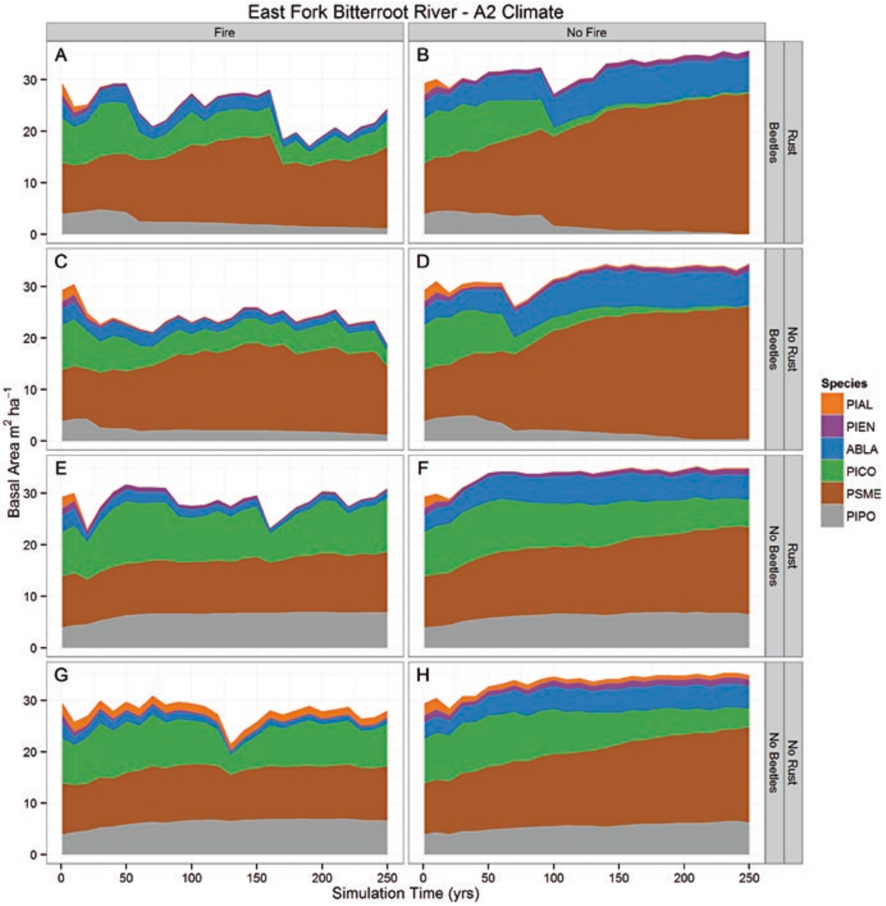

Fig. 7.4 Landscape composition of species cover types using the plurality of basal area for a warmer climate (A2 emission scenario) for the East Fork of the Bitterroot River landscape with all combinations of fire, white pine blister rust, and mountain pine beetle. Species: PIAL = whitebark pine, PIEN = 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. 2015a)

7.5 Forest Diseases

7.5.1 Overview

We focus on forest diseases in the Northern Rockies known to have significant effects on ecosystems and ecosystem services, and for which at least some information on climate effects is available. These include dwarf mistletoes, root disease, needle disease, abiotic disease, and canker disease. Climate drivers and potential effects of climate change on these diseases are discussed in the following sections.

Dwarf mistletoes (*Arceuthobium* spp.) comprise five species of parasitic seed plants found in the Northern Rockies. They mainly cause reduced tree growth and productivity, but in some cases, they also cause tree mortality. Drummond (1982) estimated that 850,000 hectares of national forest lands were infested by the three most important species of dwarf mistletoe in the Northern Rockies.

Caused by various species of fungi, root disease is a major cause of tree growth loss and mortality in the Northern Rockies. The two most significant native pathogens in the Northern Rockies region are Armillaria (*Armillaria* spp.) and annosus (*Heterobasidion annosum*) root diseases, which occur in many mesic to moist forests west of the Continental Divide. At least 1.3 million hectares in the Northern Rockies have moderate to severe root disease, with up to 60% caused by *Armillaria ostoyae* (USFS 2007). Armillaria kills conifers of all species when they are young, but it 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). 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).

Needle diseases have historically been of limited significance in the Northern Rockies; 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. However, periodic outbreaks can cause severe damage locally (Lockman and Hartless 2008). Needle diseases are favored by long, mild, damp springs, their occurrence at epidemic levels depending on favorable weather conditions and presence of an adequate host population.

Canker diseases, which affect tree branches and boles, typically occur in stressed 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.

Forests in the Northern Rockies periodically experience damage from weather extremes, such as high temperatures and drought. Conifers on the east side of the Continental Divide, primarily Douglas-fir and lodgepole pine, often experience twig and needle necrosis and desiccation caused by strong, dry, warm Chinook winds in winter (Bella and Navratil 1987). Drought injury can initiate a decline syndrome by predisposing trees to infection by less aggressive biotic agents, such as canker fungi and secondary beetles.

7.5.2 Effects of Climatic Variability and Change on 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

Table 7.4 Risk assessment for forest diseases, developed using expert opinion and information from literature summarized in this chapter

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

natural enemies, mutualists and competitors (Ayres and Lombardero 2000). Changing interactions between pathogens and their hosts may become a substantial driver of future disease outbreaks (Sturrock et al. 2011) (Table 7.4).

Fungi cause most forest diseases in the Northern Rockies, and fungus life cycles are directly influenced by climate-related factors such as timing and duration of precipitation, humidity, and temperature for spore germination, fungus growth, and inactivation. Dwarf mistletoe reproduction and infection are also affected by temperature and moisture (Hawksworth and Wiens 1996). Spring precipitation is projected to increase in most of the mountainous area of the Northern Rockies (Chap. 2). This may affect pathogens, specifically increasing the frequency of years when needle diseases cause significant needle loss in conifer species. For example, needle loss from Swiss needle cast (caused by *Phaeocryptopus gaeumannii*) is highly correlated with increasing winter temperatures and spring needle wetness (Stone et al. 2008).

Increased host stress in a changing climate could result in increased disease occurrence (Coakley et al. 1999). For example, low soil moisture (drought) affects the incidence and severity of pathogens. Flooding and water table fluctuation can also predispose trees to pathogens. Some diseases may become more damaging if thresholds that trigger infections, such as recurring drought, are reached more frequently.

Indirect effects of climate change on competitors, antagonists, and mutualists may also affect 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 lives. Given that root pathogens of trees can often exploit a large food reserve in a tree once a defense is breached and use those reserves to bolster attacks on nearby trees, even small changes in relationships among fungal communities could have large effects.

Kliejunas (2011) conducted a qualitative risk assessment of the potential effects of climate change on forest diseases, several of which occur in the Northern Rockies. Risk potential for Dothistroma needle blight, (caused by *Dothistroma septosporum*) was estimated to be low in a warmer and drier climate, but moderate in a warmer and wetter climate. Risk potential for dwarf mistletoes was rated as high regardless of precipitation levels because dwarf mistletoe survival and infection increases with temperature. Armillaria root disease risk potential was rated as high to very high depending on moisture availability, with drier conditions increasing risk.

7.5.3 Forest Pathogen Interactions

Fire directly and indirectly influences distribution, severity, and persistence of forest diseases, and forest diseases can influence fire behavior and severity. 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 upper soil profile (Filip and Yang-Erve 1997). High-intensity fires can completely remove a pathogen with its host (Kipfmueller and Baker 1998) or remove species susceptible to root disease (Hagle et al. 2000). In contrast, low-intensity fires can leave mosaics of pathogens along with their susceptible hosts, which can increase diseases such as dwarf mistletoe (Kipfmueller and Baker 1998). However, low-intensity fires in some habitats maintain species tolerant of root disease (e.g., western larch) (Hagle et al. 2000).

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

An increase in severe weather events and/or fires could increase occurrence of other diseases in a changing climate. For example, root and bole wounds could be used as "infection courts" for root disease, and such wounds from windfalls and fire are major avenues of infection for true fir 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).

Pathogens, insects, and fire can also interact. For example, root damage from fire in lodgepole pine can lead to stem decay fungi, which over time can cause extensive heartwood decay in the boles of trees (Littke and Gara 1986). Decay-infected trees then grow at a slower rate than uninfected trees and can be preferentially attacked by MPBs years later (Littke and Gara 1986). In addition, altered stand structure following MPB epidemics may increase dwarf mistletoe in lodgepole pine stands, thereby reducing stand growth and productivity and slowing stand recovery (Agne et al. 2014).

7.6 Nonnative Plants

7.6.1 Overview

Hundreds of nonnative species have been introduced into the Northern Rockies. Not all of these species are abundant, but recent surveys showed that nonnative plants comprise an average of 40% of species present (richness), and 25% of those nonnatives have significant effects on native grassland flora (Ortega and Pearson 2005). Most nonnative invasives 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*]). Nonnative 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 and forage for wildlife.

In this section we explore how climate change might alter current ecosystems and their susceptibility to invasion, and invasiveness of nonnative plants in general. We define the parameters that bound potential community change based on climate projections and discuss how plant communities might be affected across that range of conditions.

7.6.2 Effects of Climate Change on Nonnative Species

Numerous attributes associated with successful invaders suggest nonnatives could flourish under certain climate change scenarios (Dukes and Mooney 1999; Thuiller et al. 2008; but see Bradley et al. 2009). For example, many nonnatives are fast growing, early-seral species that tend to respond favorably to increased resource availability, including temperature, water, sunlight, and CO_2 (Walther et al. 2009). As a result, nonnatives often respond favorably to disturbance because disturbances can increase resource availability (Davis et al. 2000). Successful invaders 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 and ability to expand their populations (Clements and Ditomasso 2011).

Soil moisture often drives species-specific responses to elevated temperatures. For example, 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). 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). This result is consistent with historical observations of spotted knapweed declines following drought conditions (Pearson and Fletcher 2008). In Wyoming sagebrush-steppe systems, 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).

The most susceptible plant communities in the Northern Rockies have low vegetation cover, high bare ground, and unproductive soils; various nonnative plant species exploit these more open sites. As fires and other disturbances increase in intensity and frequency, invasive species may dominate some native plant communities, although numerous factors such as fire resistance of native species, propagule availability, and variation in burn severity can affect establishment (Zouhar et al. 2008). Invasive species are generally adaptable and capable of relatively rapid genetic change, which can enhance their ability to invade new areas in response to ecosystem modifications (Clements and Ditomasso 2011), including short-term disturbance or long-term stressors.

Note Any use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

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