Chapter 8
Exploring Interactions Among Multiple Disturbance Agents in Forest Landscapes: Simulating Effects of Fire, Beetles, and Disease Under Climate Change

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Contents

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8.1 Introduction

Global climate varies naturally at millennial time scales, but humans, primarily through combustion of fossil fuels, have now added sufficient greenhouse gases to the atmosphere to cause rapid climate warming at a rate unprecedented in the last 10,000 years (IPCC 2007). In light of its potential adverse effects on natural, political, social, and economic systems, ecologists have been called upon to investigate the consequences of anthropogenic climate change on the world's ecosystems (Bachelet et al. 2001; Schneider et al. 2007). However, questions pertaining to the numerous, complex, and multi-scale interactions among ecological processes, disturbance agents, and climate drivers present intractable challenges with respect to scientific exploration, as traditional field methods used to explore ecosystem responses to environmental change are inadequate to capture complex interactions that occur across large areas and long time periods (Fig. 8.1). Multi-scale ecological interactions often result in nonlinear feedbacks that produce novel and unanticipated landscape responses to changing climates (Lauenroth et al. 1993; Temperli et al. 2013). These can be explored using simulation modeling, in which computer programs are developed to quantitatively simulate complex ecological processes and their interactions over decades or centuries (McKenzie et al. 2014).

In our opinion, most ecological responses to climate change are best evaluated and simulated at landscape scales using landscape models (LMs). Because of their limited spatial extent, finer-scale stand models cannot fully incorporate spatial aspects of disturbance regimes (Bugmann 2001), and coarser-scale Dynamic Global Vegetation Models (DGVMs) are not designed to simulate important species- and plant-level disturbance effects such as successional trajectories and disturbance survival (Flannigan et al. 2009). Spatially explicit simulations using LMs

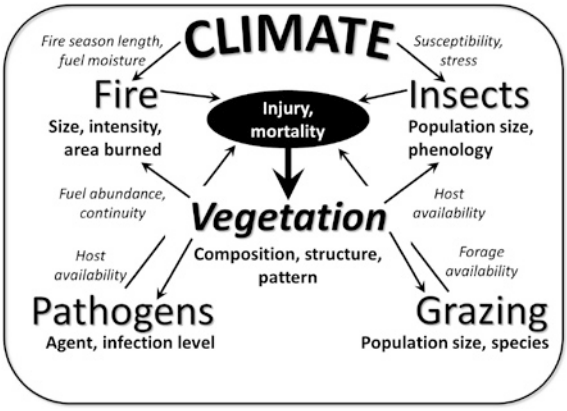

Fig. 8.1 The direct and indirect interactions among disturbances and vegetation that dictate landscape dynamics. Shown are four of the most common disturbances currently affecting landscapes around the world: wildland fire, insects, pathogens (disease), and grazing by native and exotic ungulates

have greatly improved our ability to explore and understand complex interactions (Scheller and Mladenoff 2007; Perry and Millington 2008). Several sources provide details on landscape change modeling (Mladenoff and Baker 1999), ecosystem dynamics (Canham et al. 2004), and spatial fire spread and effects (Gardner et al. 1999). In various reviews, LMs are classified based on their design, structure, detail, resolution, and geographical area (see Keane et al. 2004; He 2008; Baker 1989; Moran and Corcoran 2012; Scheller and Mladenoff 2007, respectively). To realistically predict climate change effects, LMs must be structured to simulate disturbance processes, vegetation growth and mortality, and species composition and distribution as well as their interactions across multiple scales (Bachelet et al. 2000; Purves and Pacala 2008). However, the level of mechanistic detail needed to realistically simulate important interactions among these processes and variables remains a central challenge in landscape modeling (Gustafson 2013).

In this chapter, we explore a unique subset of the many ecological interactions that occur at landscape scales—the interactions among disturbances (Fig. 8.1). Disturbances influence vegetation distribution, structure, and composition, and may indirectly and directly interact with one another and with changing climate to create novel landscapes (Kitzberger et al. 2012). Warming climates have already altered interactions among disturbance regimes resulting in highly visible and rapidly occurring changes in landscape composition and structure, and the importance of these interactions have been shown in studies across the world (Green and Saladin 2005; Parker et al. 2006). In the United States, Bachelet et al. (2000) documented the interactive effects of fire and grazing on vegetation conditions in South Dakota pine forests, while Buma and Wessman (2011) showed that fire, windthrow, and salvage logging interactions dictated vegetation response. Allen (2007) attributed the cause of forest dieback in New Mexico to the interactions of fire, grazing, erosion, and severe drought, and Beh et al. (2014) found that unique interactions between sudden oak death (*Phytophthora ramorum*) and wildfire contributed to the intensity of ambrosia beetle species attacks in California tanoak (*Notholithocarpus densiflorus*) forests. In South America, Matson and Bart (2013) showed that the interaction of fire and grazing dictate shrub encroachment in the Andes mountains. Lewis and Lindgren (2002) found that interactions between tomentosus root disease (*Inonotus tomentosus*) and spruce beetle (*Dendroctonus rufipennis*) controlled tree mortality and wood volume lost in boreal forests of British Columbia, Canada, while the importance of drought, grazing, and fire interactions to the structure and composition of grasslands was documented by Koerner and Collins (2014) in South Africa and Hobbs et al. (2003) in Australia.

To demonstrate the importance of effects of single and interacting disturbances on landscapes, we focused this chapter on a subset of disturbances that are common across many US Rocky Mountain landscapes: wildland fire (any fire that occurs in a non-developed or sparsely developed area), mountain pine beetle (*Dendroctonus ponderosae*), and white pine blister rust (*Cronartium ribicola*). Based on a review of the literature, we discuss the mechanisms of each disturbance type, including possible interactions from each combination of the three disturbances. We then use a landscape simulation model to evaluate how single and interacting disturbances

respond to changes in climate and influence landscapes. Because the magnitude, trend, and type of disturbance interactions differ across ecosystems, our simulation results cannot be wholly extrapolated to other landscapes; however, our goal in this chapter is to demonstrate the general importance of disturbance interactions in influencing future landscape composition and structure.

8.2 The Simulation Model and Application

FireBGCv2 (Fire BioGeoChemical model Version 2) is a bottom-up, mechanistic, individual tree, forest succession model containing stochastic properties implemented in a spatial domain (see Keane et al. 2011 for complete model documentation). It can be categorized as a landscape fire succession model (Keane et al. 2004), a forest landscape model (He 2008), or a landscape dynamics model (Mladenoff and Baker 1999). Versions of the model have been used to address a wide variety of research questions including climate change effects on stream temperatures, wildlife, and vegetation composition (Loehman et al. 2011a); management effectiveness; grazing interactions with fire; landscape structure; fuel-snag dynamics; and carbon emissions (Keane et al. 1997). FireBGCv2 contains five hierarchical levels of spatial organization from coarse, fixed-boundary sites defined by similar topography, weather, soils, and potential vegetation to dynamically created stands that differ by existing vegetation composition and structure; simulation plots on which ecosystem processes are modeled for computational efficiency; species with well-defined physiological parameters; and individual trees, each of which is explicitly represented with attributes, such as age, height, diameter at breast height (DBH), and height to live crown. FireBGCv2 simulates basic processes such as tree growth, organic matter decomposition, and litterfall using detailed physical and biogeochemical relationships (Keane et al. 2011). Long-term daily weather streams drive primary canopy processes (e.g., transpiration, photosynthesis, and respiration), vegetation phenology (e.g., curing, leaf fall), and fire dynamics (e.g., ignition, fuel moisture, spread, intensity) within the simulation landscape.

Weather, tree species and structural traits, and landscape composition determine fire, mountain pine beetle, and white pine blister rust activity within a simulation (Fig. 8.2). In the simulations presented here, fire ignition was based on historical distribution of the Keetch Byram Drought Index, fuel loading, and fuel moisture, while fire spread was modeled on slope and wind vectors, fuel characteristics, and fuel moisture. Blister rust infections for five-needle pines were simulated when site daily relative humidity was above 90 % and daily mean temperature was above 10 °C (Loehman et al. 2011a); and mountain pine beetle epidemics were initiated in the model when lethal temperature thresholds (below −40 °C for a single day, or below −20 °C for 2 weeks) were not met for 40 years, and host pine species comprised more than 30 % of the simulation landscape (Keane et al. 2011).

We simulated all combinations of wildland fire, mountain pine beetle, and white pine blister rust for two forested landscapes that comprise a range of

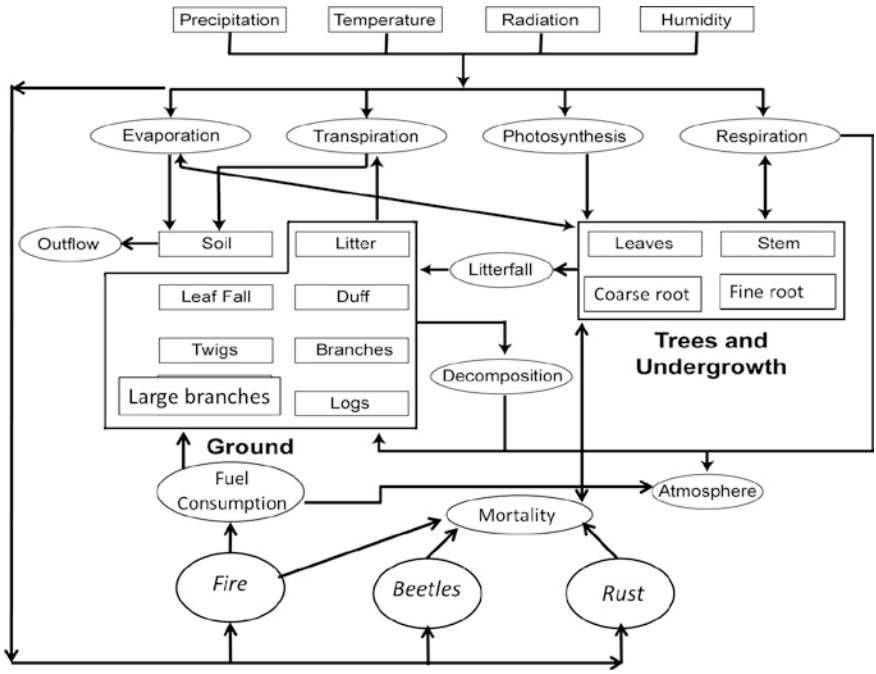

Fig. 8.2 An illustration of the complex linkages among disturbances (bottom) and the ecological processes and components with which they interact to drive landscape behavior. This diagram depicts the interacting ecological processes simulated by the FireBGCv2 landscape model (Keane et al. 2011)

climate, vegetation, and fire regime types common to the US Rocky Mountain region (Fig. 8.3):

- **East Fork of the Bitterroot River (EFBR)**: A 128,000 ha dry mixed-conifer ecosystem in western Montana, USA, with an historical low- to high-frequency, mixed-severity fire regime. Lower-elevation stands comprise primarily ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii)*, and higher elevation stands are dominated by lodgepole pine (*Pinus contorta* var. *latifolia)*, whitebark pine (*Pinus albicaulis*), subalpine fir *(Abies lasiocarpa),* and Engelmann spruce (*Picea engelmannii*).
- **Yellowstone Central Plateau (YCP)**: An 80,000 ha, high-elevation lodgepole pine ecosystem in Yellowstone National Park, USA, with an historical low-frequency, high-severity fire regime. Stands contain minor amounts of Douglas-fir, whitebark pine, subalpine fir, and Engelmann spruce.

We simulated disturbance interactions under two climate scenarios:

- **Current climate**: The recorded daily weather for the last 50+ years collected within or near each of the simulation landscapes, compiled by the National Climatic Data Center. Weather years were used in sequence, repeated for multiple cycles over a 250-year simulation period.

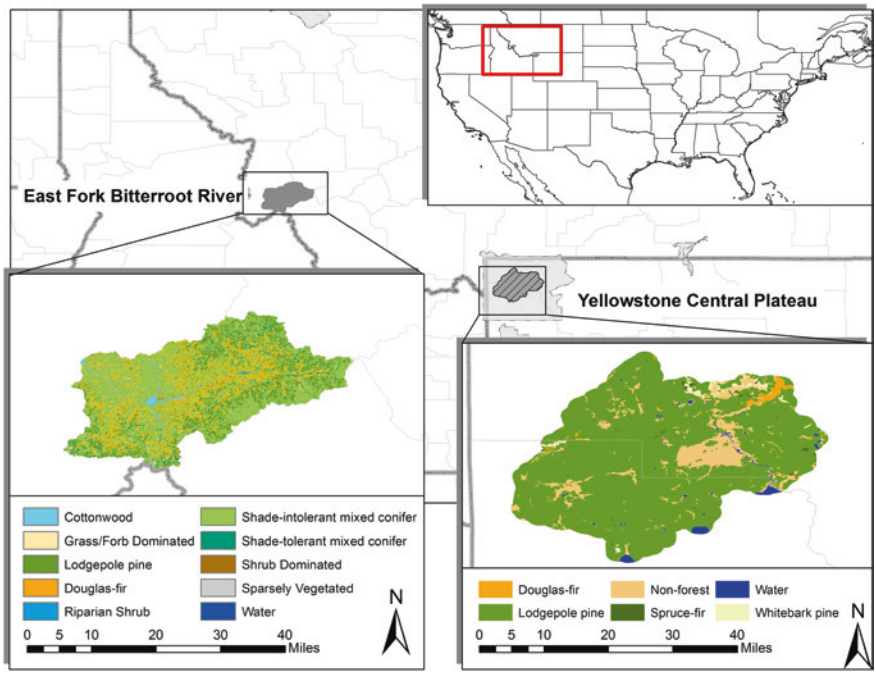

Fig. 8.3 FireBGCv2 simulation landscapes: the East Fork Bitterroot River (EFBR) and Yellowstone Central Plateau (YCP), both within the northern Rocky Mountains, USA

- **Warmer climate**: A climate change scenario in which temperatures increase by an average of 2.8 °C relative to historical weather. Climate offsets for each landscape represent an ensemble average of climate model projections for the A2 emissions scenario (IPCC 2007) downscaled to 12 km for the period 2070 to 2099 (Girvetz et al. 2009).

FireBGCv2 simulations are usually performed with multiple replicates to account for stochastic model elements (e.g., Loehman et al. 2011a), but we did only one run per scenario for the purposes of illustration. For each 250-year simulation, disturbances were implemented beginning in the initial simulation year. We report two response variables sensitive to disturbance interaction effects: species composition (dominant species of each modeled stand) and tree basal area (m^2 ha^{-1}).

8.3 Disturbances

In an ecological context it is not particularly informative to talk about disturbance in terms of a single event because it is the *pattern* of disturbances through time that shapes ecosystems. A disturbance regime defines the spatial arrangement, frequency, intensity, and ecological consequences of disturbance events repeated

Table 8.1 Glossary of terms often used to describe disturbance regimes

Disturbance characteristic	Description	Example
Agent	Factor causing the disturbance	Mountain pine beetle is an 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 tree mortality resulting from mountain pine beetle infestation; 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 areas but weather and fuels can influence fire intensity and therefore the patchwork of tree mortality
Seasonality	Time of year when disturbance occurs	Species phenology can influence wildland fire effects; spring burns when plants are growing can be more damaging than fall burns when plants are dormant
Duration	Length of time that disturbances occur	Mountain pine beetle outbreaks usually last 3–8 years; fires can burn for a day or for an entire summer
Interactions	Disturbances interact with one another, as well as 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 disturbance characteristics listed above	Highly variable weather and mountain pine beetle mortality can cause highly variable burn conditions resulting in patchy burns of various sizes

over space and time. Assessments of a disturbance regime must encompass an area of land that is large enough that the full range of disturbance sizes are manifest, and long enough so that the full range of disturbance characteristics are captured. Disturbance regimes are generally described by 11 characteristics (Table 8.1; Simard 1991; Agee 1993; Skinner and Chang 1996; Keane 2013). These characteristics illustrate the great complexity that confounds any simplistic representation of interacting disturbance regimes in land management. The following is a description of three important disturbances, and their interactions within the US northern Rocky Mountains.

8.3.1 Wildland Fire

Wildland fire is ubiquitous throughout forest ecosystems of the northern Rockies and is arguably the most dominant landscape disturbance in the region. Wildland fire is very responsive to variability in environmental conditions on the landscape, including vegetation type and distribution, climate, weather, and topography. Where rates of vegetation production outpace decomposition, sufficient biomass is available to support fires. Wildland fuels lose moisture and become flammable in the region's typically warm and dry summers, during which 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 well into July. Regionally, widespread fire years are correlated with drought (Heyerdahl et al. 2008; Morgan et al. 2008). At landscape scales, topography can influence the spatial pattern of fire spread. In dissected mountainous areas, topographic features (e.g., barren slopes) can form barriers to fire spread (Grissino-Mayer et al. 2004), but where drainages are aligned with prevailing winds, topography can facilitate the spread of large fires (Sharples 2009).

The composition and structure of forests in the northern Rockies is strongly determined by climate, elevation, topographic position, and fire history. In general, fire regimes vary along environmental gradients, with fire frequency decreasing and fire severity increasing with elevation. For example, at the lowest and driest elevations where forests are dominated by ponderosa pine, frequent surface fires historically consumed litter and dead wood, and killed seedlings and smaller trees. Adaptive traits such as thick bark allowed mature ponderosa pines to survive many repeated fires over time and tree densities were kept low.

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). 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, however, where fires were historically infrequent, fire exclusion has not affected the fire regimes (Romme and Despain 1989; Schoennagel et al. 2004). For example, lodgepole pine forests in Yellowstone National Park historically were subject to large, stand-replacing fires (Romme 1982), and lodgepole pine has the unique ability to regenerate prolifically after these severe fires from seeds released from the tree's serotinous cones (Turner et al. 2003).

Future climate projections for the northern Rocky Mountains have dramatic implications for fire regimes. The fire season is expected to grow longer, allowing more fires to occur and those fires to burn for longer periods and across larger areas (Westerling et al. 2006). Earlier onset of snow melt will reduce fuel moisture during the fire season, making a larger portion of the landscape flammable for longer periods of time (Miller et al. 2011).

8.3.2 Mountain Pine Beetle (MPB)

The principal agent of insect-caused mortality in northern Rocky Mountain pine forests is mountain pine beetle (MPB). The MPB is a native, cambial-feeding bark beetle of several western pines, including ponderosa pine, western white pine (*Pinus monticola*), whitebark pine, limber pine (*Pinus flexilus*), and lodgepole pine (Safranyik and Carroll 2006; Gibson et al. 2009). The entire life cycle is spent beneath the bark of host trees, except when adults emerge from brood trees and fly in search of new host trees. Tree defense against MPB is complex, including both physical (e.g., resin flow) and chemical (e.g., terpenoid compounds) defenses, but these match-head-size beetles can overwhelm host defenses through sheer numbers with a mass attack strategy. The MPB is an integral component of forest ecosystem processes because of its role in stand thinning and redistribution of resources and nutrients important for tree regeneration. It is also recognized as an aggressive and economically important forest insect responsible for tree mortality across large areas (Gibson et al. 2009). Beetle-induced tree mortality influences biogeochemical processes with effects that are nonlinear in time and space and depend on the stage of beetle infestation and rate of ecosystem recovery (Griffin et al. 2011; Edburg et al. 2012). For example, Edburg et al. (2012) found that the timing and amount of snow melt, as well as the quality of water, may be substantially modified following bark beetle outbreaks, and Kurz et al. (2008) report that widespread tree mortality during MPB outbreaks greatly reduced forest carbon uptake and increased carbon emissions from decay of killed trees.

Mountain pine beetle populations are typically innocuous, infesting a few damaged or suppressed trees scattered throughout the forest. However, populations periodically erupt into large-scale outbreaks (Safranyik and Carroll 2006). Such outbreaks can cause dramatic tree mortality over extensive areas in only a few years, often killing the largest host trees in high-density stands. Although some stands may sustain nearly complete mortality (Amman 1977), average mortality in mature lodgepole pine stands across the landscape is usually 30–45 % (Safranyik and Carroll 2006). Mortality of reproductive whitebark pine can exceed 95 % (Schwandt 2006; Logan et al. 2010).

Periodic MPB outbreaks have occurred for millennia (Brunelle et al. 2008) with, for example, pre-twentieth century dates of MPB-caused mortality inferred from whitebark pine tree-ring records (Perkins and Swetnam 1996). From 1990 to 2014, 6.6 million ha of forest in the western United States have been infested by MPB (Jenkins et al. 2012), and the MPB outbreak that has been ongoing in British Columbia over the past decade is the largest recorded in the twentieth century (Sambaraju et al. 2012). Moreover, evidence suggests that the suitable climatic window for MPB is expanding to encompass additional territory, and outbreaks are occurring further north, further south, and at higher elevations than occurred previously (Safranyik et al. 2010; Cullingham et al. 2011; Lynch and O'Connor 2013). For example, MPBs are now found in hybrid lodgepole pine/jack pine (*Pinus banksiana*) stands and are able to infest natural jack pine stands at the leading edge of the Canadian front, which could facilitate a host-range expansion into areas of the boreal forest (Cullingham et al. 2011).

An important focus of current research is the degree to which changes in climate are likely to affect tree host populations and beetle dynamics. Climate is known to govern beetle survival and growth because beetle development and dispersal are sensitive to temperature (Bentz et al. 2010). Recent evidence confirms that MPB activity has been influenced by changes in climate. For example, MPB flight season in the Colorado Front Range now occurs at least one month earlier and for twice as long as recorded historically (Mitton and Ferrenberg 2012). Statistical models based on historical climate and beetle distributions demonstrate that minimum winter temperatures and drought conditions in current and preceding years influence outbreak size (Preisler et al. 2012). Coops et al. (2012) modeled areas of vulnerable host trees and areas of potential beetle expansion under future climate and suggested that timing and location of future outbreaks will depend on complex interactions among climate-driven effects on tree distributions and tree stress, as well as independent effects on MPB phenology and outbreak dynamics.

8.3.3 White Pine Blister Rust (WPBR)

White pine blister rust (WPBR) is an exotic fungus, inadvertently introduced into the United States from Europe around 1910 (Bingham 1983; Tomback and Achuff 2011). Its complex life cycle requires two hosts, with two spore-producing stages on white pine and three separate spore-producing stages on the alternate hosts, *Ribes* spp. The WPBR is a fungus that infects only five-needle pine species, and all nine North American five-needle pine species are susceptible. Infection begins when basidiospores, produced on *Ribes* leaves in late summer, are wind dispersed to pines in the vicinity. The basidiospores germinate on the pine needles and hyphae grow through the stomata into the cell tissues, needles, and stem (Patton and Johnson 1970). Cankers form when the fungus reaches large branches and the main stem, and canker formation and colonization of the phloem by the hyphae, which initially cause branch dieback and top kill, eventually kill the tree. Cankers form blisters that erupt through the bark, releasing aeciospores, the spore stage that infects *Ribes* (see Schwandt et al. (2013) for a detailed description of the WPBR life cycle). Basidiospores are short-lived and disperse relatively short distances, but aeciospores are hardy and can disperse long distances (>100 km; Frank et al. 2008). Basidiospores have a narrow window for production and successful infection of pine needles, requiring warm temperatures (>20 °C) and high humidities (>98 %) (McDonald et al. 1981). The time required for WPBR to kill its host varies by species (5–10 years for western white pine and over 20 years for whitebark pine) (Hoff and Hagle 1990). Native pine populations show some heritable resistance to WPBR but frequency of resistance is low; often less than 1 % of trees show resistant traits (Hoff et al. 1980). Tree mortality affects stand structure and species composition, but the most serious impact of WPBR is long-term effects to white pine regeneration capacity, with direct mortality of the more susceptible seedlings and saplings and the loss of cone and seed production following branch dieback and top kill.

8.4 Disturbance Interactions

8.4.1 Wildland Fire and Mountain Pine Beetle

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). How wildland fire and bark beetles interact has been an important research topic since the early twentieth century (Miller and Patterson 1927; Evenden and Gibson 1940; Weaver 1943) with research primarily focused on the potential for increased fire hazard following outbreaks. Results of multiple studies have indicated changes in fire behavior, extent, and severity result from bark beetle-caused mortality in pine forests, with variability in fire patterns heavily influenced by climate, weather, topography, forest type, and disturbance history (see Hicke et al. 2012 for a summary). Fewer studies have addressed the influence of wildland fires on bark beetle disturbance regimes, and fewer still have examined the reciprocal interactions of beetles and fire through several disturbance cycles (but see Parker et al. 2006). Climate factors, in particular drought and increased temperatures, are recognized as key drivers of both wildland fires and bark beetle outbreaks (Hicke et al. 2012). Anthropogenic climate change has been recognized as 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). Predictions 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 MPB 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 (Fettig et al. 2007; Kurz et al. 2008; Edburg et al. 2012; Falk 2013; Hansen 2014).

Though MPB can be found in fire-damaged trees (McHugh et al. 2003; Schwilk et al. 2006; Six and Skov 2009), it is only weakly attracted to fire-scorched trees (Geiszler et al. 1984; Davis et al. 2012). MPBs rarely contribute significantly to post-fire tree mortality (Geiszler et al. 1984; Powell et al. 2012; Jenkins et al. 2014), and beetle-caused mortality is usually limited to the immediate vicinity of the fire (Ryan and Amman 1996). However, it has been shown that fire injury can increase tree susceptibility to MPB attack, and MPB can kill fire-damaged trees (McHugh et al. 2003; Davis et al. 2012; Jenkins et al. 2014). Although fires can contribute to maintaining local MPB populations (Elkin and Reid 2004; Davis et al. 2012; Powell et al. 2012), fires are not known to initiate MPB outbreaks (Mitchell and Sartwell 1974; Powell et al. 2012).

Fire effects on MPB populations are time-dependent. For example, fire-weakened trees are colonized only when fire occurs near the time when beetles are searching for new host trees, so that beetles encounter the trees before phloem resources become unsuitable (Parker et al. 2006). Although MPB reproduce in

fire-damaged trees, this resource benefit lasts only a few months or years after a fire (Davis et al. 2012; Powell et al. 2012). Wildland fires can affect beetle activity indirectly over longer time periods by altering species composition and structure of forests (e.g., removing fire-intolerant species) and providing increased water, light, and nutrients for surviving trees (i.e., growth release), thus influencing the availability and vigor of suitable host trees (Hessburg et al. 2005; Fettig et al. 2007; Keeling and Sala 2012). In addition, stand-replacing fires can reduce the likelihood of MBP attack until regenerating forests have attained a threshold diameter sufficient to attract beetles, especially when beetle populations are relatively low (Kulakowski et al. 2012).

Mountain pine beetle activity influences wildland fire by altering the quantity, type, vertical and horizontal arrangement, and chemical and moisture properties of dead and live vegetative biomass (fuel) available to burn (Hicke et al. 2012). Thus, a MPB outbreak has the potential to change the probability of fire occurrence, potential for crown fire, rate of fire spread, and burn severity patterns and variability (Table 8.1). Beetle-caused tree mortality can also influence the balance of light, water, and nutrients available for growth of overstory and understory plants, thereby altering species composition and stand structure (i.e., fuel characteristics) for years after an outbreak (Hansen 2014).

Mountain pine beetle impacts in forests occur in three phases important for fire behavior: the endemic phase, in which beetles are restricted to stressed or damaged trees; the epidemic phase, in which large beetle populations attack and kill as many as 80–95 % of susceptible host trees within stands; and the post-epidemic phase, which lasts for approximately five years after an epidemic (Jenkins et al. 2008; Safranyik et al. 2010; Hansen 2014). During the endemic phase, beetle influence on fuels and subsequent fire behavior is fairly limited, as few trees are affected (Page and Jenkins 2007). In the epidemic and post-epidemic phases, fuel and fire characteristics depend on time since attack (Hicke et al. 2012). One to three years after initial attack, when needles are yellowing or red but still attached to branches, attacked trees have lower foliar moisture content, and therefore higher flammability and torching potential, than green trees. Because aerial fuel continuity is maintained, active crown fire potential is high (Page et al. 2012; Jenkins et al. 2014). Four to ten years after attack, standing dead trees have lost their needles and small branches, making active crown fire potential lower than in non-attacked stands, but increased fine surface fuel loads result in higher surface fire rates of spread, flame lengths, and torching potential (Hicke et al. 2012; Schoennagel et al. 2012). The highest fire hazard is assumed to occur in the post-epidemic phase, decades after attack, as a result of accumulation of heavy, large-diameter fuels (snags and large branches), regeneration, and increased wind speeds and drying of fuels resulting from the loss of sheltering vegetation (Jenkins et al. 2008). Fire behaviors and fire effects associated with post-epidemic stands include increased duration of flaming and smoldering, increased fireline intensity, increased potential for crown fire initiation, and increased fire severity (Jenkins et al. 2008; Hicke et al. 2012; Schoennagel et al. 2012).

Consistent with the interactions described above, our modeling results indicate that interactions of wildland fire and MPB activity influence the abundance

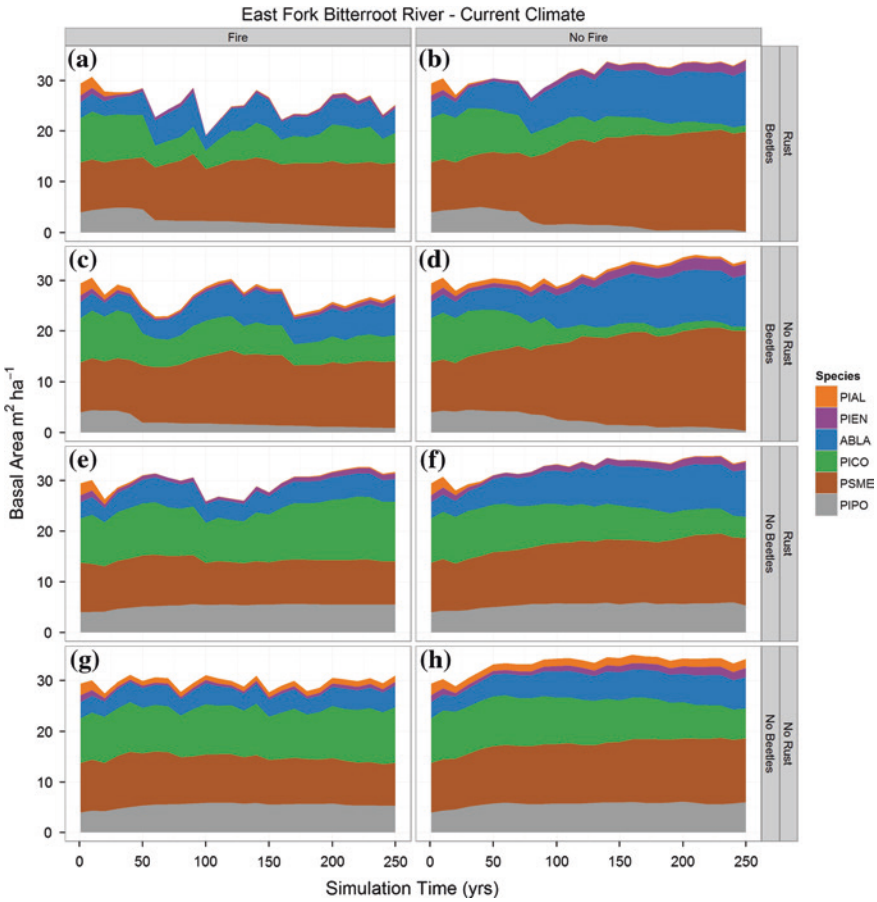

Fig. 8.4 Landscape composition of species cover types mapped using the plurality of basal area for current climate (CC) for the East Fork of the Bitterroot River (EFBR) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **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, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

of individual species on the landscape (Figs. 8.4 and 8.6). Species responses are directly linked to the physiological and life history characteristics that control response to fire and suitability as host species for MPB. As a result of differences in species composition and landscape configuration in each of our simulation landscapes, climate (current vs. projected future) influences fire and beetle interactions in different ways. For example, the EFBR landscape is dominated by low-elevation conifers that are adapted to relatively frequent fire and are MPB hosts, with smaller components of high-elevation, fire-intolerant, and non-host species (Fig. 8.4a). Under current climate and without additional MPB or WPBR disturbance,

simulated fires limit the basal area of fire-intolerant whitebark pine, Engelmann spruce, and subalpine fir and, where their distributions overlap, favor lodgepole pine over Douglas-fir (Fig. 8.4g). Simulated MPB activity in the absence of fire substantially decreases the basal area of host species (lodgepole pine, ponderosa pine, and whitebark pine), allowing for an increase in non-host species such as Douglas-fir, Engelmann spruce, and subalpine fir (Fig. 8.4d). The interaction of MPB and fire produces some of the lowest landscape basal areas. Significantly, we found that fire-mediated MPB effects at the individual species level restrict the abundance of subalpine fir and Engelmann spruce at higher elevations and maintain small but viable populations of lodgepole pine and ponderosa pine at lower elevations. Compared to current climate, the simulated warmer climate has little effect on total basal area in the absence of disturbance, but increases the basal area of Douglas-fir at the expense of lodgepole pine (Fig. 8.5h). Similar to current climate scenarios, in a warmer climate fire reduces the basal area of fire-intolerant trees (Fig. 8.5a, c, e, g), and the interaction of fire and MBP decreases basal area of MPB host tree species and high-elevation conifers, with or without the influence of WPBR (Fig. 8.5a, c). However, the warmer climate decreases fire rotation, increases annual average area burned, and increases the percent of high severity fires for all disturbance scenarios, but these results are more variable across time (Table 8.2).

The vast majority of the YCP landscape is dominated by lodgepole pine, a fire-sensitive and MPB host species, with lesser amounts of high-elevation, non-host species (Engelmann spruce, subalpine fir), and minor populations of Douglas-fir and whitebark pine (Fig. 8.6). Under current climate, simulated wildland fires exert minor and short-term control over species basal area (Fig. 8.6c). Simulated MPB activity, one of the dominant disturbance processes on the YCP landscape, causes periodic and substantial declines in lodgepole pine, allowing for a persistent increase in subalpine fir and Engelmann spruce over initial levels (Fig. 8.6a, b, c, d). The interaction of MPB and fire nearly doubles the percent of high-severity fire as the result of increased surface fuels from MPB-killed trees (Table 8.2) and limits subalpine fir and Engelmann spruce growth, but does not mediate beetle effects on lodgepole pine (Fig. 8.6c, g). Simulated climate change is not a strong enough stressor to alter species or landscape basal area in the absence of disturbance; however, under a warmer climate fires increase in severity and reduce species basal area (Fig. 8.7; Table 8.2). Fires also facilitate increased Douglas-fir representation by freeing resource space previously occupied by lodgepole pine, allowing for the expansion of this more fire-tolerant species, but Douglas-fir representation is also driven by seed source limitations (Fig. 8.7a, c, g).

8.4.2 Wildland Fire and White Pine Blister Rust

Effects of wildland fire on WPBR are minor and primarily indirect, with the exception of the possibility that smoke may kill rust spores produced at the time of the fire (Parmeter and Uhrenholdt 1975). Fire indirectly affects WPBR by

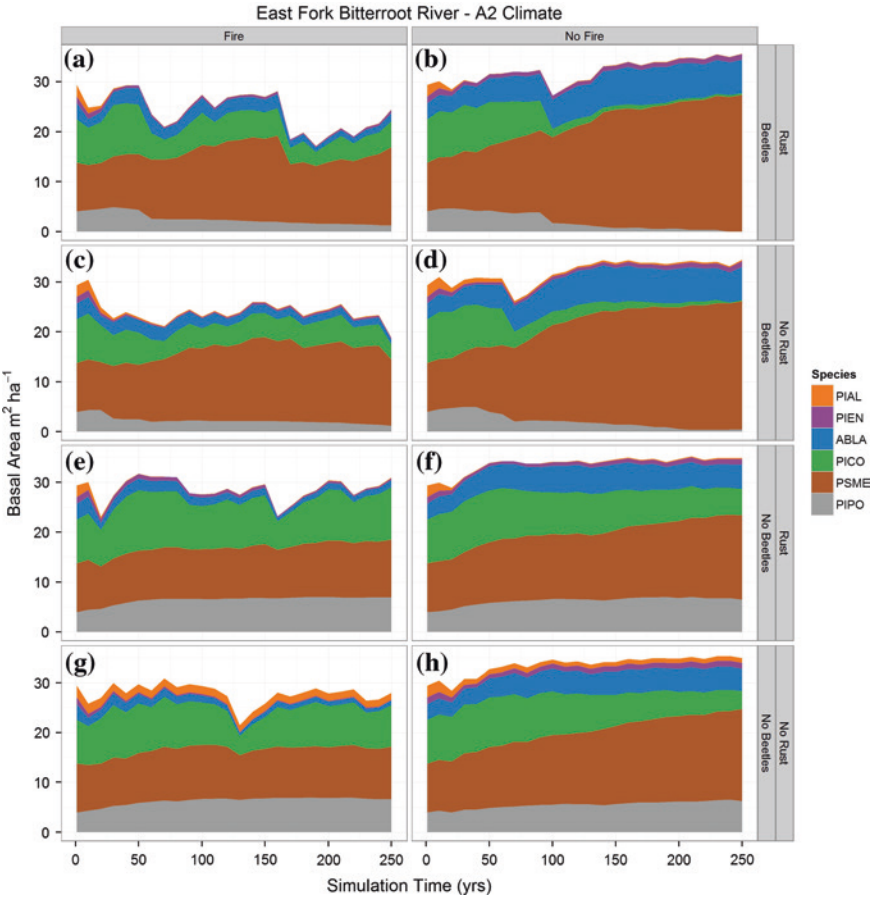

Fig. 8.5 Landscape composition of species cover types mapped using the plurality of basal area for a warmer climate (A2) for the East Fork of the Bitterroot River (EFBR) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **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, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

changing the size, distribution, and abundance of its two hosts—five-needle pines and *Ribes* spp. Most five-needle pines of the western United States are somewhat (whitebark pine, limber pine) to highly (western white pine) fire-adapted, with thick bark, high canopies, and deep roots (Ryan and Reinhardt 1988). Mixed and high severity fires are common in forests where WPBR is present (Arno et al. 2000; Murray 2007). These fires can create favorable conditions for pine regeneration because most five-needle pine seeds are rodent- and bird-dispersed and thus better adapted to spread into post-fire landscapes than seeds of their tree competitors (Lanner 1989; Morgan et al. 1994). Severe fires that kill rust-resistant pine

Table 8.2 Summaries of wildland fire characteristics from the FireBGCv2 model for two simulation landscapes: The East Fork Bitterroot River and Yellowstone Central Plateau for current climate and warmer climate scenarios

Scenario	Fire return interval (years)	Fire rotation (years)	Annual average area burned (%)	High severity fires (%)	Average tree mortality (%)
East Fork Bitterroot River (EFBR)—current climate (CC)					
Fire only	107 (41.64)	119	1.51	4.6	26.8 (0.10)
Fire, WPBR	96 (45.30)	110	1.72	3.9	27.0 (0.08)
Fire, MPB	109 (36.45)	112	1.37	8.6	31.3 (0.13)
Fire, MPB,WPBR	89 (62.06)	98	1.64	3.9	27.7 (0.12)
East Fork Bitterroot River (EFBR)—warmer climate (A2)					
Fire only	31 (30.77)	47	3.22	6.2	24.6 (0.08)
Fire, WPBR	43 (40.88)	56	3.09	6.4	22.3 (0.08)
Fire, MPB	48 (43.73)	36	2.90	5.3	27.1 (0.10)
Fire, MPB,WPBR	89 (61.56)	62	2.81	9.1	27.4 (0.10)
Yellowstone Central Plateau (YCP)—current climate (CC)					
Fire only	145 (43.46)	284	0.47	40.1	46.1 (0.32)
Fire, WPBR	259 (33.95)	310	0.24	52.4	38.6 (0.36)
Fire, MPB	254 (27.34)	518	0.23	77.3	75.1 (0.30)
Fire, MPB,WPBR	238 (32.07)	387	0.33	81.9	58.3 (0.39)
Yellowstone Central Plateau (YCP)—warmer climate (A2)					
Fire only	132 (59.14)	98	0.93	57.9	62.5 (0.22)
Fire, WPBR	215 (13.03)	204	0.48	52.0	58.8 (0.25)
Fire, MPB	214 (12.75)	239	0.46	75.9	64.6 (0.38)
Fire, MPB,WPBR	116 (73.50)	131	0.92	65.9	63.9 (0.33)

Disturbance types implemented are white pine blister rust (WPBR), mountain pine beetle (MPB), and wildland fire (Fire). Results are annual values averaged over the 250-year simulation period, with standard deviations in parentheses

trees ensure continued high rust infection rates and mortality (Keane et al. 2012), however, where rust-resistant five-needle pines survive fire they can provide the seeds for populating future landscapes resilient to both rust infection and fire mortality (Keane et al. 2012). Finally, studies have indicated that fire exclusion has increased competition stress, weakening pine trees and perhaps facilitating rust infection (Parker et al. 2006; Heward et al. 2013).

Stands that are both burned and rust-infected have a higher overall potential for tree mortality. Trees infected with WPBR are weakened, and may be more susceptible to fire-caused damage and mortality (Stephens and Finney 2002). As WPBR kills pine trees slowly, dead foliage and wood added to the fuelbed may increase fire intensity. As occurs after MPB outbreaks, WPBR infection results in

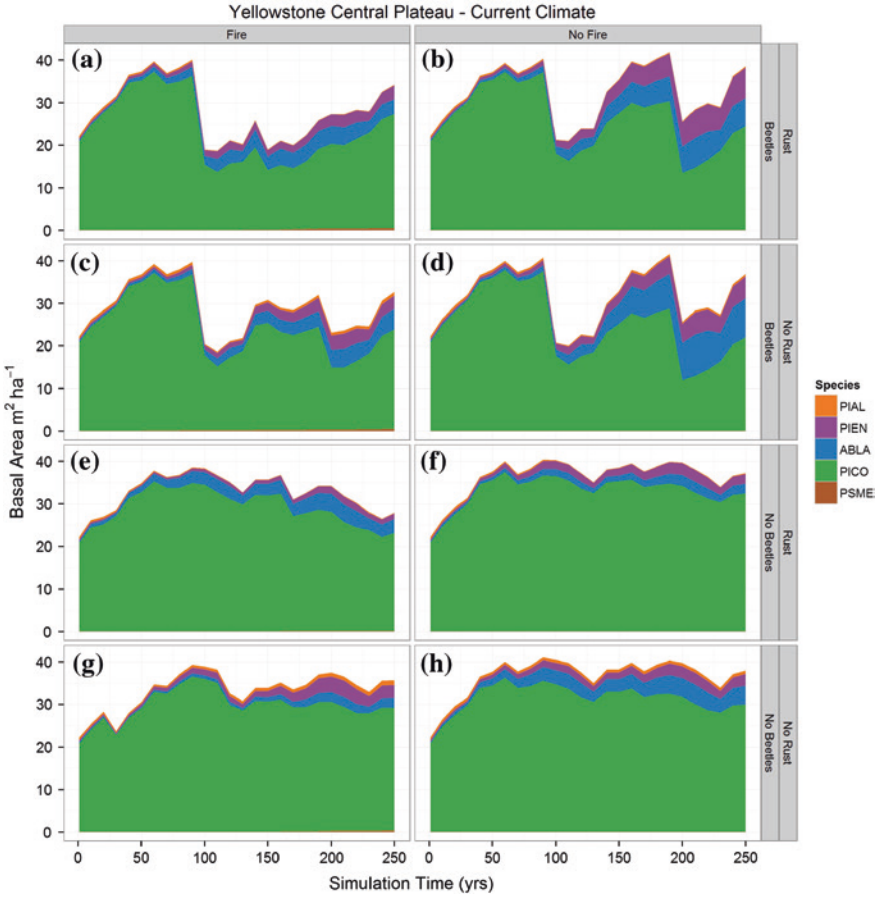

Fig. 8.6 Landscape composition of species cover types mapped using the plurality of basal area for current climate (CC) for the Yellowstone Central Plateau (YCP) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **b** no 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, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

elimination 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 crown fires (Keane et al. 2002; Reinhardt et al. 2010). Shade-tolerant competitors are also more susceptible to fire damage, resulting in high post-fire tree mortality in rust-infected landscapes.

Three five-needle pine species are present on our simulation landscapes: western white pine, whitebark pine, and limber pine. The FireBGCv2 simulations indicate that interactions between fire and rust have a minor influence on landscape

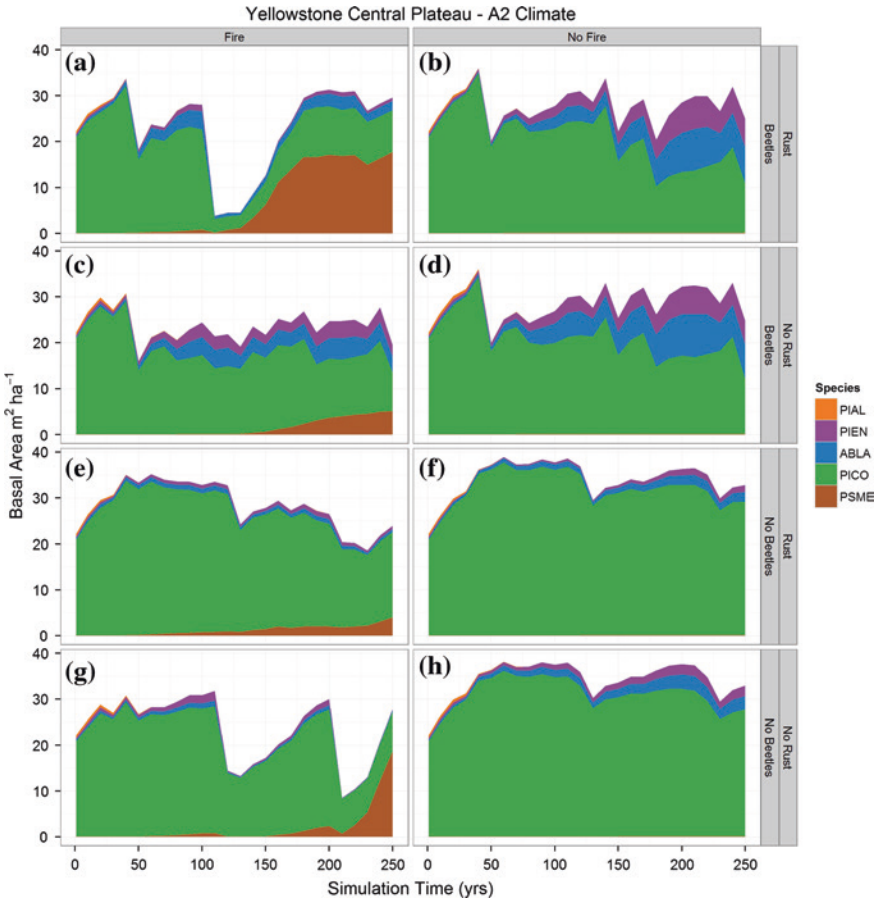

Fig. 8.7 Landscape composition of species cover types mapped using the plurality of basal area for a warmer climate (A2) for the Yellowstone Central Plateau (YCP) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **b** 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, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

composition of host species because our landscapes contain relatively few of these trees. For example, whitebark pine represents only 3.7 % of the EFBR landscape basal area in the absence of simulated WPBR infection, and limber pine is so rare that it is not shown in our modeling results. In WPBR-only simulations, whitebark pine is replaced over time by subalpine fir (Fig. 8.4f), but when fire disturbance is included, whitebark pine remains on the landscape at low levels (1.23 % of landscape basal area; Fig. 8.4e; Table 8.3). In contrast, fire does not buffer WPBR infection effects on whitebark pine at YCP, where it comprises about 2 % of the landscape basal area in simulations with fire and without rust (Fig. 8.6g), but decreases to less than 1 % of basal area when rust is simulated with or without fire (Fig. 8.6e, f).

Table 8.3 Summaries of vegetation and biomass characteristics from the FireBGCv2 model for two simulation landscapes

Scenario	Basal area (m^2 ha^{-1})	Basal area of PIAL (m^2 ha^{-1})	Basal area of pines (m^2 ha^{-1})	Above ground C burned (%)	Basal area killed by WPBR (%)	White pine basal area killed by WPBR (%)	Basal area killed by MPB (%)	Pine basal area killed by MPB (%)
East Fork Bitterroot River (EFBR)—current climate (CC)								
No disturbance	33.37 (1.66)	0.05 (0.01)	0.46 (0.04)	–	–	–	–	–
Only WPBR	32.67 (1.9)	0.01 (0.02)	0.4 (0.06)	–	0.3 (0.6)	24.1 (34.8)	–	–
Only MPB	31.68 (2.18)	0.02 (0.02)	0.23 (0.16)	–	–	–	2.8 (2.9)	11 (9.6)
WPBR, MPB	31.54 (2.19)	0.01 (0.02)	0.23 (0.16)	–	0.4 (0.6)	25.6 (37.2)	2.4 (2.7)	9.5 (8.7)
Fire only	29.81 (1.12)	0.04 (0.01)	0.54 (0.02)	0.1 (0.6)	–	–	–	–
Fire, WPBR	29.97 (2.22)	0.01 (0.02)	0.53 (0.03)	0.1 (0.2)	0.3 (0.5)	21 (33.9)	–	–
Fire, MPB	27.06 (2.38)	0.02 (0.02)	0.33 (0.09)	0.3 (0.5)	–	–	3.3 (3)	9.4 (6.7)
Fire, MPB,WPBR	25.92 (2.75)	0.01 (0.02)	0.35 (0.08)	0 (0.1)	0.3 (0.4)	17.4 (36.1)	3.7 (4.5)	9.9 (10.5)
East Fork Bitterroot River (EFBR)—warm, dry climate (A2)								
No disturbance	33.54 (1.87)	0.03 (0.01)	0.41 (0.06)	–	–	–	–	–
Only WPBR	33.72 (1.72)	0.01 (0.02)	0.43 (0.04)	–	0.6 (1.1)	40 (37.6)	–	–
Only MPB	32.13 (2.32)	0.02 (0.02)	0.19 (0.16)	–	–	–	3.3 (3.9)	14.8 (11.6)
WPBR, MPB	32.26 (2.39)	0.01 (0.02)	0.18 (0.18)	–	0.3 (0.6)	32.4 (35.2)	2.5 (3.3)	12.5 (14.2)
Fire only	27.83 (2.01)	0.06 (0.01)	0.58 (0.03)	0.3 (1.1)	–	–	–	–
Fire, WPBR	28.7 (2.27)	0.01 (0.02)	0.56 (0.04)	0.2 (0.4)	0.2 (0.3)	21.2 (31.7)	–	–
Fire, MPB	24.64 (2.4)	0.02 (0.02)	0.31 (0.07)	0.6 (1.9)	–	–	4.1 (4)	12 (8.5)
Fire, MPB,WPBR	24.24 (3.82)	0.01 (0.02)	0.35 (0.09)	0.7 (2)	0.8 (1.2)	47.1 (36.3)	4 (3.9)	10.7 (8.1)
Yellowstone Central Plateau (YCP)—current climate (CC)								
No disturbance	36.63 (4.54)	0.02 (0)	0.88 (0.05)	–	–	–	–	–

(continued)

Table 8.3 (continued)

Scenario	Basal area (m^2 ha^{-1})	Basal area of PIAL (m^2 ha^{-1})	Basal area of pines (m^2 ha^{-1})	Above ground C burned (%)	Basal area killed by WPBR (%)	White pine basal area killed by WPBR (%)	Basal area killed by MPB (%)	Pine basal area killed by MPB (%)
Only WPBR	36.37 (4.47)	0.01 (0.01)	0.91 (0.03)	–	0.2 (0.2)	22.4 (21.1)	–	–
Only MPB	31.84 (6.86)	0.02 (0)	0.8 (0.17)	–	–	–	7.9 (15.5)	9.7 (19.2)
WPBR, MPB	32.5 (6.76)	0.01 (0.01)	0.81 (0.14)	–	0.2 (0.2)	19.4 (15.7)	7.5 (15)	9.1 (18.4)
Fire only	33.3 (4.54)	0.02 (0.01)	0.91 (0.06)	0 (0.1)	–	–	–	–
Fire, WPBR	32.71 (4.4)	0.01 (0.01)	0.89 (0.05)	0.5 (1.8)	0.2 (0.2)	21.8 (17.2)	–	–
Fire, MPB	29.09 (6.17)	0.02 (0)	0.86 (0.11)	0.1 (0.2)	–	–	7.1 (14.4)	8.2 (16.4)
Fire, MPB,WPBR	28.08 (7.07)	0.01 (0.01)	0.85 (0.1)	0.1 (0.3)	0.3 (0.3)	23.4 (17.1)	5.4 (13.2)	6.3 (14.9)
Yellowstone Central Plateau (YCP)—warm, dry climate (A2)								
No disturbance	34.16 (3.97)	0 (0.01)	0.91 (0.04)	–	–	–	–	–
Only WPBR	34.02 (4.04)	0 (0.01)	0.94 (0.03)	–	0.1 (0.2)	34.8 (36.9)	–	–
Only MPB	28.61 (3.82)	0 (0.01)	0.73 (0.15)	–	–	–	11.9 (12.9)	15.6 (16.1)
WPBR, MPB	27.67 (3.86)	0 (0.01)	0.75 (0.19)	–	0.1 (0.3)	34.1 (35)	13.3 (14.5)	16.9 (18.5)
Fire only	23.46 (7.12)	0 (0.01)	0.86 (0.17)	0.2 (0.6)	–	–	–	–
Fire, WPBR	28.33 (5.02)	0 (0.01)	0.9 (0.05)	1.8 (5.7)	0.1 (0.2)	30.9 (33.1)	–	–
Fire, MPB	23.69 (3.32)	0 (0.01)	0.73 (0.16)	0.6 (1.5)	–	–	10.5 (13)	13.8 (16)
Fire, MPB,WPBR	23.24 (9.01)	0 (0.01)	0.61 (0.26)	0.2 (0.6)	0.1 (0.2)	29 (27.8)	6.3 (10.9)	9.9 (11.8)

The East Fork Bitterroot River and Yellowstone Central Plateau for current climate and warmer climate scenarios. Disturbance types implemented are white pine blister rust (WPBR), mountain pine beetle (MPB), and wildland fire (Fire). Results are annual values averaged over the 250-year simulation period, with standard deviations in parentheses

Although the combination of fire and WPBR implemented for EFBR and YCP affect percent of fires that are high-severity and landscape fire rotation differently than fire-only scenarios, these differences are relatively minor because whitebark pine is a small component of the landscape (Table 8.2). However, as mentioned previously, for both simulation landscapes the warmer climate scenario substantially alters fire rotations, average annual area burned, and percent of fires that are high severity (Table 8.2).

8.4.3 Mountain Pine Beetle and Blister Rust

Few researchers have investigated the interactions between the native MPB and exotic white pine blister rust. In their endemic phase, MPB populations may weaken five-needle 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 low resistance to the disease ensures that most five-needle pines 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 (Campbell and Antos 2000). For example, although whitebark pine stands in the Greater Yellowstone Ecosystem show little WPBR-related mortality, levels of MPB-related mortality are high (Kendall and Keane 2001). 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. 2009).

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 over 90 % 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.

The FireBGCv2 simulations validate the importance of species composition in relation to disturbance interactions, even though effects of MPB and WPBR interactions are minimal because of the scarcity of WPBR host species in our study areas. The EFBR simulations of MPB disturbance under current climate result in a decline in both lodgepole and whitebark pine, with a corresponding increase in subalpine fir and Douglas-fir (Fig. 8.4d; Table 8.3), with little change from the addition of WPBR (Fig. 8.4b). The WPBR-only EFBR simulation (Fig. 8.4f) shows little difference in species composition compared to the no-disturbance scenario (Fig. 8.4h). Similar results are seen for the YCP landscape, except that the decline in lodgepole pine is not countered by increases in subalpine fir because of

dry site conditions (Fig. 8.6b, d, f, h). These trends are enhanced under a warmer climate, where lodgepole pine declines are greater and stands are mainly replaced by Douglas-fir (Fig. 8.7a, g), but WPBR interaction has minor effects on species composition (Fig. 8.7b, d).

8.4.4 Fires, Beetles, and Rust

Real-world studies of the complex interactions among fire, beetles, and rust are rare, but in our simulations the presence of MPB and WPBR reduces the basal area of pine species. Fire, while reducing pines in the short term, appears to ensure their long-term persistence by eliminating competitors, as noted by Keane and Morgan (1994). In previous modeling efforts, decades or centuries were required to re-establish populations of rust–resistant pines after die-off (such as would occur with MPB). Simulated wildland fires killed some trees, but prevented encroachment by shade-tolerant non-pine species and maintained five-needle pines on the landscape (Loehman et al. 2011b). Observationally, the greatest 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 only occur in areas that have the potential to support five-needle pines, which are rare in our simulation landscapes. However, we found that fire rotations in EFBR and YCP under current climate are about 10 % lower when all three disturbances are allowed to interact, and average landscape tree mortality is also lower (Table 8.2). Under a warmer climate, fire rotation decreases (from 98 to 62 years for EFBR, and from 387 to 131 years for YCP), and the percent of high severity fires increases for both landscapes. Landscape basal areas are lower when all three disturbances are included, and the basal area of pines is significantly lower for multiple disturbance scenarios than other disturbance combinations, for both current and warmer climates (Table 8.3). Douglas-fir and subalpine fir dominate the EFBR landscape when all three disturbances are active under current climate without fire (Fig. 8.4a); however, when fires are included, pines are maintained on the simulation landscape (Fig. 8.4b). With a warmer climate Douglas-fir dominates both the EFBR (Fig. 8.5a) and YCP (Fig. 8.7a) landscapes, but both whitebark and lodgepole pines are still present because of continued fire. Thus, interactions among disturbances create different landscapes than when each disturbance acts separately, or in the absence of disturbance.

8.5 Discussion

Interactions among disturbance agents can dramatically influence ecosystems. Our literature review and simulation modeling experiments demonstrate that interactions among various disturbance types may cause easily detectable, direct,

and immediate effects such as differential tree mortality, but at landscape scales, effects of long-term and coupled disturbance regimes can lead to complex feedbacks and nonlinear behaviors causing landscape trajectories to differ significantly (Figs. 8.4, 8.5, 8.6 and 8.7; Tables 8.2 and 8.3). Another finding from this effort is that most of the interaction effects are mediated through vegetation response rather than direct interactions between disturbances, such as a fire killing beetles and fungi. More importantly, we found that the effects of climate change on landscape conditions result mainly from the effects of disturbances and their interactions on vegetation; direct vegetation response to climate change rarely causes significant landscape change.

Many factors determine the magnitude, trend, and direction of interacting disturbance effects. The physical environment is perhaps the most important factor: as shown by our simulations, climate has enormous influence (Figs. 8.4, 8.5, 8.6 and 8.7; Tables 8.2 and 8.3), with a warmer climate allowing for greater MPB activity and more wildland fire, altered landscape composition and structure, and changes in WPBR infection and mortality rates. Topography is also an important influence affecting rate of fire spread, water and radiation balance, and microclimatic conditions that in turn may influence potential for rust infection and host vulnerability. Species composition also influences disturbance interactions. For example, the abundance of host species for both MPB and WPBR may dictate the intensity and magnitude of interactions between these two disturbances, and resulting tree mortality patterns dictate wildland fuel dynamics that then influence fire regimes. The current climate-mediated MPB outbreak in North America might have been less intense and more localized if wildland fires had not been suppressed over the last century, since fire exclusion has increased the abundance of host species of sufficient size and distribution for insect and disease epidemics (Catchpole et al. 2001; Carroll et al. 2003).

Comprehensive simulations of multiple disturbance interactions demand a mechanistic, process-based approach to ensure most effects are appropriately represented (Gustafson 2013). Direct links from climate to both disturbance and vegetation processes are needed to simulate those important ecophysiological interactions that dictate ecosystem response (Keane et al. 2015). In our simulations, for example, wildland fire often killed trees, which increased water availability because of decreased leaf area and evapotranspiration, resulting in increased fitness of surviving trees thereby reducing insect and disease mortality. This result is possible because the model simulated daily the effects of rainfall, snow dynamics, and temperature on soil water, plant phenology, evapotranspiration, photosynthesis, and respiration across an entire landscape (Keane et al. 2011). Phenomenological approaches, such as statistical analysis and modeling, do not incorporate the full suite of ecophysiological responses to climate change into model structure (Gustafson 2013; Keane et al. 2015).

Incorporating the complexity of mechanistic biophysical and biotic drivers for multiple disturbances at landscape scales across decades of simulation is a challenge for even the most comprehensive LMs (Keane et al. 2015). Ecological surprises may emerge due to inadequate model predictive power, particularly for

understanding spatially heterogeneous, scaled, and nonlinear interactions of coupled disturbance processes. Moreover, as disturbance regimes increasingly move beyond historical observations (Westerling et al. 2011), interactions with other disturbance agents become less predictable because modeled relationships cannot be based on observed data. Feedbacks of disturbance-caused ecosystem changes to subsequent disturbance susceptibility are also likely to confound predictive models; for example, MPB epidemics can decrease or increase modeled crown fire susceptibility depending on assumptions about ecosystem productivity and the rate of canopy recovery, which may depend on biophysical setting as well as the severity of the outbreak. Considering that changes in climate can alter disturbance regimes and host vulnerability as well as determine trajectories of ecosystem recovery, potential ecological surprises seem to inhabit an infinite state space.

We must recognize the great need for models that represent coupled systems (e.g., disease and host) to realistically represent complex forest ecosystem dynamics across multiple scales of space and time. In a recent review of climate change effects on plant diseases, Pautasso et al. (2012) identified several key research gaps including the need to (1) focus on mountain and boreal ecosystems, (2) integrate climate drivers other than temperature (e.g., precipitation), and (3) couple long-term observational data sets with climate change scenarios to predict impacts on plant pathogens and their hosts. As in studies of human health, an understanding of coupled systems is needed to fully recognize system vulnerability, resistance, and resilience (Hausermann et al. 2012). Development of such models requires theoretical, field, and modeling work to identify key processes, interactions, and ecological thresholds that cause cascading and nonlinear ecosystem responses. Although there is still a long way to go to represent disturbance interactions in LMs (Keane et al. 2015), newer efforts to couple niche models with more complex ecosystem, population, and disturbance models are promising (see Iverson et al. 2011; Fordham et al. 2013; Tanentzap et al. 2013).

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References

Agee JK (1993) Fire ecology of Pacific Northwest forests. Island Press, Washington

Allen CD (2007) Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. Ecosystems 10:797–808

Amman GD (1977) The role of the mountain pine beetle in lodgepole pine ecosystems: Impact on succession. In: Mattson WJ (ed) The role of arthropods in forest ecosystems. Springer, New York

Archibald S, Lehmann CER, Gómez-Dans JL, Bradstock RA (2013) Defining pyromes and global syndromes of fire regimes. Proc Natl Acad Sci 110(16):6442–6447

Arno SF, Parsons DJ, Keane RE (2000) Mixed-severity fire regimes in the northern Rocky Mountains: consequences of fire exclusion and options for the future, vol 5. In: Wilderness science in a time of change conference: wilderness ecosystems, threat, and management, Missoula, Montana, 23–27 May 1999. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO. RMRS-P-15-VOL-5

Bachelet D, Lenihan JM, Daly C, Neilson RP (2000) Interactions between fire, grazing and climate change at Wind Cave National Park, SD. Ecol Model 134:229–244

Bachelet D, Neilson RP, Lenihan JM, Drapek RJ (2001) Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4:164–185

Baker WL (1989) A review of models of landscape change. Landsc Ecol 2(2):111–133

Beh M, Metz MR, Seybold J, Rizzo DM (2014) The novel interaction between *Phytophthora ramorum* and wildfire elicits elevated ambrosia beetle landing rates on tanoak *Notholithocarpus densiflorus*. For Ecol Manage 318:21–33

Bentz B, Régnière J, Fettig C, Hansen E, Hayes J, Hicke J, Kelsey R, Negrón J, Seybold S (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60(8):602–613

Bingham RT (1983) Blister rust resistant western white pine for the Inland Empire: the story of the first 25 years of the research and development program. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Gen Tech Rep INT-146

Bockino NK, Tinker DB (2012) Interactions of white pine blister rust and Mountain Pine Beetle in whitebark pine ecosystems in the southern Greater Yellowstone area. Nat Area J 32(1):31–40

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

Bugmann H (2001) A review of forest gap models. Clim Change 51(3–4):259–305. doi:10.1023/a:1012525626267

Buma B, Wessman CA (2011) Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2(5):64. doi:10.1890/es11-00038.1

Campbell EM, Antos JA (2000) Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Can J For Res 30(7):1051–1059

Canham CD, Cole JJ, Lauenroth WK (2004) Models in ecosystem science. Princeton University Press, Princeton

Carroll AL, Taylor SW, Régnière J, Safranyik L (2003) Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore T, Brooks JE, Stone JE (eds) Mountain pine beetle symposium: challenges and solutions, Victoria, British Columbia, 2003. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, Inf Rep BC-X-399, Victoria

Catchpole EA, Catchpole WR, Viney NR, McCaw WL, Marsden-Smedley JB (2001) Estimating fuel response time and predicting fuel moisture content from field data. Int J Wildland Fire 10(2):215–222

Coops NC, Wulder MA, Waring RH (2012) Modeling lodgepole and jack pine vulnerability to mountain pine beetle expansion into the western Canadian boreal forest. For Ecol Manage 274:161–171

Cullingham CI, Cooke JEK, Dang S, Davis CS, Cooke BJ, Coltman DW (2011) Mountain pine beetle host-range expansion threatens the boreal forest. Mol Ecol 20:2157–2171

Davis RS, Hood S, Bentz BJ (2012) Fire-injured ponderosa pine provide a pulsed resource for bark beetles. Can J For Res 42(12):2022–2036

Edburg SL, Hicke JA, Brooks PD, Pendall EG, Ewers BE, Norton U, Gochis D, Gutmann ED, Meddens AJH (2012) Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Front Ecol Envir 10:416–424

Elkin CM, Reid ML (2004) Attack and reproductive success of mountain pine beetles (Coleoptera: Scolytidae) in fire-damaged lodgepole pines. Environ Entomol 33(4):1070–1080

Evenden JC, Gibson A (1940) A destructive infestation in lodgepole pine stands by the mountain pine beetle. J For 38(3):271–275

Falk DA (2013) Are Madrean ecosystems approaching tipping points? Anticipating interactions of landscape disturbance and climate change. In: Ffolliott PF, Gottfried G, Gebow B (eds) Biodiversity and management of the Madrean Archipelago III. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Proc RMRS-P-67

Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negrón JF, Nowak JT (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For Ecol Manag 238(1):24–53

Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM, Gowman LM (2009) Implications of changing climate for global wildland fire. Int J Wildland Fire 18(5):483–507. doi:10.1071/WF08187

Fordham DA, Akcakaya HR, Araujo MB (2013) Tools for integrating range change, extinction risk and climate change information into conservation management. Ecography 36(9):956–964

Frank KL, Geils BW, Kalkstein LS, Thistle HW Jr (2008) Synoptic climatology of the long-distance dispersal of white pine blister rust II. Combination of surface and upper-level conditions. Int J Biometeorol 52:653–666

Gardner RH, Romme WH, Turner MG (1999) Predicting forest fire effects at landscape scales. In: Mladenoff DJ, Baker WL (eds) Spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge

Geiszler DR, Gara R, Littke W (1984) Bark beetle infestations of lodgepole pine following a fire in South Central Oregon. Z Angew Entomol 98:389–394

Gibson K, Kegley S, Bentz B (2009) Mountain pine beetle. USDA Forest Service, Forest Insect & Disease Leaflet Number 2. 12p

Girvetz EH, Zganjar C, Raber GT, Maurer EP, Kareiva P, Lawler JJ (2009) Applied climate-change analysis: the climate wizard tool. PLoS ONE 4(12):e8320

Green DG, Sadedin S (2005) Interactions matter—complexity in landscapes and ecosystems. Ecological Complexity 2(2):117–130. doi:10.1016/j.ecocom.2004.11.006

Griffin JM, Turner MG, Simard M (2011) Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For Ecol Manage 261:1077–1089

Grissino-Mayer HD, Romme WH, Floyd ML, Hanna DD (2004) Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. Ecology 85:1708–1724

Gustafson E (2013) When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landsc Ecol 28(8):1429–1437. doi:10.1007/s10980-013-9927-4

Hansen ME (2014) Forest development and carbon dynamics after mountain pine beetle outbreaks. For Sci 60(3):476–488. doi:10.5849/Forsci.13-039

Hausermann H, Tschakert P, Smithwick EH, Ferring D, Amankwah R, Klutse E, Hagarty J, Kromel L (2012) Contours of risk: spatializing human behaviors to understand disease dynamics in changing landscapes. EcoHealth 9(3):251–255. doi:10.1007/s10393-012-0780-8

He HS (2008) Forest landscape models, definition, characterization, and classification. For Ecol Manage 254:484–498

Hessburg PF, Agee JK, Franklin JF (2005) Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For Ecol Manag 211(1):117–139

Heward H, Smith AMS, Roy DP, Tinkham WT, Hoffman CM, Morgan P, Lannom KO (2013) Is burn severity related to fire intensity? Observations from landscape scale remote sensing. Int J Wildland Fire 22(7):910–918. doi:10.1071/WF12087

Heyerdahl EK, McKenzie D, Daniels LD, Hessl AE, Littell JS, Mantua NJ (2008) Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). Int J Wildland Fire 17(1):40–49

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

Hobbs RJ, Abbott I, Burrows N (2003) How fire regimes interact with other forms of ecosystem disturbance and modification. In: Symposium proceedings on fire in ecosystems of south-west Western Australia: impacts and management, vol I, 16–18 Apr 2002, Backhuys Publishers, Perth

Hoff R, Hagle S (1990) Diseases of whitebark pine with special emphasis on white pine blister rust. In: Schmidt WC, McDonald KJ (comp) Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, Ogden, Gen Tech Rep INT-270

Hoff R, Bingham RT, McDonald GI (1980) Relative blister rust resistance of white pines. Eur J For Path 10:307–316

Hoff RJ, Ferguson DE, McDonald GI, Keane RE (2001) Strategies for managing whitebark pine in the presence of white pine blister rust. Whitebark pine communities: ecology and restoration. Island Press, Washington, pp 346–366

IPCC (2007) Climate Change 2007—the Physical Science Basis, vol Working Group I. Climate Change (2007) Working group I contribution to the fourth assessment report of the IPCC. Cambridge University Press, New York

Iverson L, Prasad A, Matthews S, Peters M (2011) Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. Ecosystems 14(6):1005–1020. doi:10.1007/s10021-011-9456-4

Jenkins MJ, Hebertson E, Page W, Jorgensen CA (2008) Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For Ecol Manag 254(1):16–34

Jenkins MJ, Page WG, Hebertson EG, Alexander ME (2012) Fuels and fire behavior dynamics in bark beetle-attacked forests in western North America and implications for fire management. For Ecol Manage 275:23–34

Jenkins MJ, Runyon JB, Fettig CJ, Page WG, Bentz BJ (2014) Interactions among the mountain pine beetle, fires, and fuels. For Sci 60(3):489–501

Keane RE (2013) Disturbance regimes and the historical range of variation in terrestrial ecosystems. In: Simon AL (ed) Encyclopedia of Biodiversity, 2nd edn. Academic Press, Waltham

Keane RE, Morgan P (1994) Landscape processes affecting the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. In: Proceedings of the 12th international conference on fire and forest meteorology, 26–28 Oct Jekyll Island, Georgia. Society of American Foresters, Bethesda

Keane RE, Hardy CC, Ryan KC, Finney MA (1997) Simulating effects of fire on gaseous emissions from future landscape of Glacier National Park, Montana, USA. World Resour Rev 9(2):177–205

Keane RE, Veblen T, Ryan KC, Logan J, Allen C, Hawkes B (2002) The cascading effects of fire exclusion in the Rocky Mountains. In: Baron JS (ed) Rocky Mountain futures: an ecological perspective. Island Press, Washington, pp 133–152

Keane RE, Cary G, Davies ID, Flannigan MD, Gardner RH, Lavorel S, Lennihan JM, Li C, Rupp TS (2004) A classification of landscape fire succession models: spatially explicit models of fire and vegetation dynamic. Ecol Model 256(1):3–27

Keane RE, Loehman RA, Holsinger LM (2011) The FireBGCv2 landscape fire and succession model: A research simulation platform for exploring fire and vegetation dynamics. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-255

Keane RE, Tomback DF, Aubry CA, Bower AD, Campbell EM, Cripps CL, Jenkins MB, Mahalovich MF, Manning M, McKinney ST, Murray MP, Perkins DL, Reinhart DP, Ryan C, Schoettle AW, Smith CM (2012) A range-wide restoration strategy for whitebark pine forests. USDA Forest Service Rocky Mountain Research Station, General Technical Report RMRS-GTR-279

Keane RE, Miller C, Smithwick E, McKenzie D, Falk D, Kellogg L (2015). Representing climate, disturbance, and vegetation interactions in landscape simulation models. Ecol Model 309−310(0):33−47

Keeling EG, Sala A (2012) Changing growth response to wildfire in old-growth ponderosa pine trees in montane forests of north central Idaho. Glob Change Biol 18(3):1117–1126

Kendall K, Keane RE (2001) The decline of whitebark pine. In: Tomback D, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, pp 367–400

Kitzberger T, Aráoz E, Gowda JH, Mermoz M, Morales JM (2012) Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. Ecosystems 15:97–112

Koerner SE, Collins SL (2014) Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. Ecology 95:98–109

Kulakowski D, Jarvis D, Veblen TT, Smith J (2012) Stand-replacing fires reduce susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. J Biogeogr 39(11):2052–2060

Kulhavy DL, Partridge AD, Stark RW (1984) Root diseases and blister rust associated with bark beetles (Coleoptera: Scolytidae) in Western White Pine in Idaho. Environ Entomol 13(3):813–817

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature 452(7190):987–990

Lanner RM (1989) Biology, taxonomy, evolution, and geography of stone pines of the world. In: Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, USDA Forest Service Intermountain Research Station General Technical Report INT-270

Larson ER (2011) Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests. J Biogeogr 38(3):453–470. doi:10.1111/j.1365-2699.2010.02430.x

Lauenroth WK, Urban DL, Coffin DP, Parton WJ, shugart HH, Kirchner TB, Smith TM (1993) Modeling vegetation structure-ecosystem process interactions across sites and ecosystems. Ecol Model 67:49–80

Lewis KJ, Lindgren BS (2002) Relationship between spruce beetle and tomentosus root disease: two natural disturbance agents of spruce. Can J For Res 32:31–37

Littell JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire area burned in western US ecoprovinces, 1916–2003. Ecol Appl 19(4):1003–1021

Loehman RA, Clark JA, Keane RE (2011a) Modeling effects of climate change and fire management on western white pine (*Pinus monticola*) in the Northern Rocky Mountains, USA. Forests 2:832–860

Loehman RA, Corrow A, Keane RE (2011b) Modeling climate changes and wildfire interactions: effects on whitebark pine (*Pinus albicaulis*) and implications for restoration, Glacier National Park, Montana, USA. In: Keane RE, Tomback DF, Murray MP, Smith CM (eds) Proceedings of the high five symposium on the future of high-elevation, five-needle white pines in Western North America Missoula, MT, 2011. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, RMRS-P-063

Logan JA, Macfarlane WW, Willcox L (2009) Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest 2:19–22

Logan JA, MacFarlane WW, Willcox L (2010) Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecol Appl 20:895–902

Lynch AM, O'Connor CD (2013) Mountain pine beetle in Southwestern white pine in the Pinaleño Mountains. In Gottfried GJ, Ffolliott PF, Gebow BS, Eskew LG, Collins LC (comp) Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III and 7th conference on research and resource management in the southwestern deserts; 2012 1–5 May, Tucson, AZ. USDA Forest Service, Rocky Mountain Research Station Proceedings. RMRS-P-67

Matson E, Bart D (2013) Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural páramo. Landsc Ecol 28(9):1829–1840. doi:10.1007/s10980-013-9926-5

McDonald GI, Hoff RJ, Wykoff WR (1981) Computer simulation of white pine blister rust epidemics. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper INT-258

McHugh CW, Kolb TE, Wilson JL (2003) Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environ Entomol 32(3):510–522

McKenzie D, Shankar U, Keane RE, Stavros EN, Heilman WE, Fox DG, Riebau AC (2014) Smoke consequences of new wildfire regimes driven by climate change. Earth's Future 35(2):32–59. doi:10.1002/2013ef000180

Miller J, Patterson J (1927) Preliminary studies on the relation of fire injury to bark-beetle attack in western yellow pine. J Agric Res 34:597–613

Miller C, Abatzoglou J, Brown T, Syphard A (2011) Wilderness fire management in a changing environment. In: McKenzie D, Miller C, Falk D (eds) The landscape ecology of fire. Springer, New York, pp 269–294

Mitchell RG, Sartwell C (1974) Insects and other arthropods. In: Cramer OP (ed) Environmental Effects of forest residues management in the pacific northwest: a state-of-knowledge compendium. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-24

Mitton JB, Ferrenberg SM (2012) Mountain pine beetle develops an unprecedented summer generation in response to climate warming. Am Nat 179(5):E163–E171

Mladenoff DJ, Baker WL (1999) Spatial modeling of forest landscape change. Cambridge University Press, Cambridge

Moran CJ, Corcoran MA (2012) Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecology 93(4):939–950 (comment)

Morgan P, Bunting SC, Keane RE, Arno SF (1994) Fire ecology of whitebark pine (*Pinus albicaulis*) forests in the Rocky Mountains, USA. In: Schmidt W (Compilers), Holtmeier F (eds) Proceedings of the international symposium Subalpine stone pines and their environment: the status of our knowledge. US Forest Service Intermountain Research Station Gen. Tech INT-GTR-309

Morgan P, Heyerdahl EK, Gibson CE (2008) Multi-season climate synchronized forest fires throughout the 20th century, northern Rockies, USA. Ecology 89(3):717–728. doi:10.1890/06-2049.1

Murray M (2007) Fire and Pacific Coast whitebark pine. In: Goheen EM, Sniezko RA (eds) Proceedings of the conference whitebark pine: a Pacific Coast perspective, Ashland, OR, 27–31 August 2006, USDA Forest Service, Ashland, OR. Pacific Northwest Region, R6-NR-FHP-2007-01

Page W, Jenkins MJ (2007) Predicted fire behavior in selected mountain pine beetle infested lodgepole pine. For Sci 53(6):662–674

Page WG, Jenkins MJ, Runyon JB (2012) Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. Can J For Res 42(8):1631–1647

Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric For Entomol 8(3):167–189

Parmeter JR, Uhrenholdt B (1975) Some effects of pine-needle or grass smoke on fungi. Phytopathology 65(1):28–31

Patton RF, Johnson DW (1970) Mode of penetration of needles of eastern white pine by *Cronartium ribicola*. Phyopathology 60:977–982

Pautasso M, Döring T, Garbelotto M, Pellis L, Jeger M (2012) Impacts of climate change on plant diseases—opinions and trends. Eur J Plant Pathol 133(1):295–313. doi:10.1007/s10658-012-9936-1

Perkins DL, Swetnam TW (1996) A dendroecological asessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Can J For Res 26:2123–2133

Perry GLW, Millington JDA (2008) Spatial modelling of succession-disturbance dynamics in forest ecosystems: concepts and examples. Perspect Plant Ecol Evol Syst 9(3–4):191–210

Powell EN, Townsend PA, Raffa KF (2012) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. Ecol Monogr 82(1):69–84

Preisler HK, Hicke JA, Ager AA, Hayes JL (2012) Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. Ecology 93:2421–2434

Purves D, Pacala S (2008) Predictive models of forest dynamics. Science 320(5882):1452–1453
Reinhardt ED, Holsinger L, Keane RE (2010) Effects of biomass removal treatments on stand-level fire characteristics in major forest types of the northern Rocky Mountains. West J Appl For 25(1):34–41
Romme WH (1982) Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol Monogr 52(2):199–221
Romme WH, Despain DG (1989) Historical perspective on the Yellowstone fires of 1988. Bioscience 39(10):695–699
Ryan KC, Amman GD (1996) Bark beetle activity and delayed tree mortality in the Greater Yellowstone Area following the 1988 fires. In: Keane RE, Ryan KC, Running SW (eds) Proceedings, ecological implications of fire in greater yellowstone, International Association Wildland Fire, Fairfield
Ryan KC, Reinhardt ED (1988) Predicting postfire mortality of seven western conifers. Can J For Res 18:1291–1297
Safranyik L, Carroll AL (2006) The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik L, Wilson B (eds) The mountain pine beetle: a synthesis of biology, management and impacts on lodgepole pine forests. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria
Safranyik L, Carroll A, Régnière J, Langor D, Riel W, Shore T, Peter B, Cooke B, Nealis V, Taylor S (2010) Potential for range expansion of mountain pine beetle into the boreal forest of North America. Can Entomol 142(5):415–442
Sambaraju KR, Carroll AL, Zhu L, Stahl K, Moore RD, Aukema BH (2012) Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. Ecography 35:211–223
Scheller R, Mladenoff D (2007) An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. Landscape Ecol 22(4):491–505
Schneider SH, Semenov S, Patwardhan A, Burton I, Magadza CHD, Oppenheimer M, Pittock AB, Rahman A, Smith JB, Suarez A, Yamin F (2007) Assessing key vulnerabilities and the risk from climate change. In: Parry ML, Canziani OF, Palutikof PJ, van der Linden P, Hanson CE (eds) Climate change 2007: impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
Schoennagel TL, Veblen TT, Romme WH (2004) The interaction of fire, fuels, and climate across Rocky Mountain landscapes. Bioscience 54(7):651–672
Schoennagel T, Veblen TT, Negron JF, Smith JM (2012) Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7(1):e30002
Schwandt JW (2006) Whitebark pine in peril: a case for restoration. US Forest Service, Missoula, MT, R1-06-28
Schwandt J, Kearns H, Byler J (2013) White pine blister rust general ecology and management. USDA Forest Service, Forest Health Protection, Insect and Disease Management Series 14.2. www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5415080.pdf
Schwilk DW, Knapp EE, Ferrenberg SM, Keeley JE, Caprio AC (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For Ecol Manage 232:36–45
Sharples JJ (2009) An overview of mountain meteorological effects relevant to fire behaviour and bushfire risk. Int J Wildland Fire 18(7):737–754
Simard A (1991) Fire severity, changing scales, and how things hang together. Int J Wildland Fire 1(1):23–34
Six DL, Adams J (2007) White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). J Ent Sci 42(3):345–353

Six DL, Skov K (2009) Response of bark beetles and their natural enemies to fire and fire surrogate treatments in mixed-conifer forests in western Montana. For Ecol Manage 258:761–772

Skinner CN, Chang C-R (1996) Fire regimes, past and present. University of California at Davis, Davis

Stephens SL, Finney M (2002) Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For Ecol Manage 162(2–3):261–271

Tanentzap AJ, Lee WG, Schulz KAC (2013) Niches drive peaked and positive relationships between diversity and disturbance in natural ecosystems. Ecosphere 4(11):133

Temperli C, Bugmann H, Elkin C (2013) Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. Ecol Mono 83(3):383–402. doi:10.1890/12-1503.1

Tomback DF, Achuff P (2011) Blister rust and western forest biodiversity: ecology, values and outlook for white pines. For Path 40(3–4):186–225. doi:10.1111/j.1439-0329.2010.00655.x

Turner MG, Romme WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. Front Ecol Environ 1(7):351–358

Weaver H (1943) Fire as an ecological and silvicultural factor in the ponderosa-pine region of the pacific slope. J For 41(1):7–15

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

Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proc Nat Acad Sci 108(32):13165–13170

Williams AP, Allen CD, Macalady AD et al (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297