

BARK BEETLE–FIRE–FOREST INTERACTIONS
IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

(Zoology)

at the

UNIVERSITY OF WISCONSIN-MADISON

2010

ACKNOWLEDGEMENTS

This dissertation would not have been possible without the help and support of many people. First and foremost, I would like to thank my advisor and mentor Monica Turner for her support and enthusiasm, and for always pushing me to go beyond my limits intellectually – which was not necessarily always hard. Her insistence to clean up the coffee machine herself has been our only point of disagreement over the last 4½ years. She is a truly amazing person and researcher and it has been a real pleasure to work with her.

This work and the whole experience of my PhD would not be the same without Jake Griffin, with whom I have worked closely over the last 3½ years. Jake and I share the same passion for coffee, dead forests, and chainsaw-wielding maniacs, and some people say that between Madison and Yellowstone, we have spent more time together –sometimes in tents or double beds– than with our wives. Jake has been a fantastic collaborator and friend, and I look forward to continuing to collaborate with him in the future.

I thank the members of my PhD committee, Tony Ives, Volker Radeloff, Ken Raffa, and Phil Townsend, for their insight and for making the whole process so fun and enjoyable. I would like to thank my close collaborators Bill Romme, Dan Tinker, Ken Raffa, Erinn Powell, Phil Townsend, and Roy Renkin, who contributed to a lot of the ideas in this work. I had the chance to work with wonderful labmates during my stay and I thank them for their help and friendship, and for pretending to understand my English. They are (in order of appearance): Erica Smithwick, Dean Anderson, Tom Albright, Tim Kuhman, Jake Griffin, Ann Wieben, Ishi Buffam, Michelle Gooch, and Heather Lumpkin.

The Zoology department staff has been enormously helpful for the different aspects of my research, and I particularly thank Roger Larson for saving us many times when we were out in Yellowstone in need of

some equipment, Dave Hoffman for designing much of our field equipment, and Carol Cooley for being so diligent about making sure our payroll and reimbursement paperwork were in order before leaving and after returning from the field. I had great support from the Yellowstone National Park staff, particularly the permit staff and Roy Renkin, as well as from the Bridger-Teton National Forest staff, especially Andy Norman, Liz Davy, Sarah Alberts, Jacob Somerset, and Marc Dasher.

I thank my friends here in Madison for trying to stop me from working too much by luring me with beer and invitations to go see the roller derby. Special thanks to Jake, Sonya, Ishi, Lena, Erinn, John, Véronique, James, Ann, and Trent.

Thanks to Ishi for helping me realize that tea drinkers are people too.

Finally, I could not be more grateful to any other person than to Valérie, who supported me all along and took the slack during crunch time. She somehow agreed that it would be a good idea to quit our job, move to the US with a 6-month old baby, and earn a third of our previous salary for 4 years. She deserves this PhD as much as I do. And finally, I would like to thank and hug my two boys Zachary and Raphael. They have brought tremendous joy in my life and I thank them for requiring me to step back from my work to change diapers or play Legos. High five!

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ABSTRACT

BARK BEETLE–FIRE–FOREST INTERACTIONS IN THE GREATER YELLOWSTONE ECOSYSTEM

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Bark beetles have affected extensive areas of western North America in the last decade. In this dissertation, the relationships between bark beetle outbreaks, wildfires, and conifer forests were investigated in the Greater Yellowstone Ecosystem (WY, USA). I first investigated the relative importance of plot- and landscape-level variables to explain landscape patterns of tree mortality caused by bark beetle outbreaks. Second, I used remote sensing and a chronosequence approach to quantify the recovery of lodgepole pine (*Pinus contorta* var. *latifolia*) aboveground biomass for 30 years following wildfires and severe mountain pine beetle (*Dendroctonus ponderosae*) outbreaks. Third, I used field surveys and modeling to determine the effects of mountain pine beetle outbreaks on forest fuels and on predicted fire behavior in a 35-year post-outbreak chronosequence that included undisturbed stands.

Bark beetle outbreak severity was generally well predicted by landscape-level variables, especially by beetle pressure, i.e., the amount of and/or proximity to local eruptions at the beginning of the outbreak (3-4 years prior to sampling). Aboveground live biomass was greatly reduced after fire but recovered more rapidly than after bark beetle outbreaks. Recovery of post-disturbance aboveground biomass to pre-disturbance levels was relatively rapid, i.e., about 20-30 years. The major effect of mountain pine beetle outbreak on forest fuels was to reduce canopy bulk density by half compared to

undisturbed stands. As a result, the probability of active crown fire was predicted to decrease for at least 35 years after disturbance. Twenty-five to 35 years after the outbreak, growth of surviving understory trees increased the vertical continuity of fuels between the ground and the tree crowns, and the model predicted an increase in the probability of passive crown fire. Simulated fire behavior was little affected by bark beetle disturbance when wind speed was either below 40 km/h or above 60 km/h, suggesting that fire weather may be a more important driver of fire behavior than fuel abundance and distribution. These results suggest that bark beetle outbreaks do not amplify subsequent fire activity in these forests and that post-disturbance management aimed at reducing the likelihood of active crown fire may not be needed.

Dr. Monica G. Turner, Professor of Zoology

INTRODUCTION

Disturbance interactions have recently received growing interest in ecological research (Veblen et al., 1994; McCullough et al., 1998; Paine et al., 1998; Radeloff et al., 2000; Bigler et al., 2005). Part of that interest stems from the improved understanding of individual disturbances, and the recognition that most ecosystems are affected by different types of natural disturbances that should be studied jointly (Turner, 2005). Interest is also driven by concerns about the effects of climate change and anthropogenic disturbances on natural disturbance regimes (i.e., disturbance frequency, severity, and extent), which might display nonlinear responses and unpredictable feedbacks and interactions that could possibly result in abrupt regime shifts (Paine et al., 1998; Scheffer et al., 2001; Apps and McGuire, 2005; Volney and Hirsch, 2005). However, surprisingly few studies have explicitly targeted interactions between different disturbances.

We distinguish two types of disturbance interactions. *Compound disturbances* (*sensu* Paine et al., 1998) take place when two disturbances occurring in a short period of time have a synergistic effect that cannot be predicted from the sum of the individual disturbances. By definition, compound disturbances have unpredictable effects on ecosystems and may result in regime shifts (Jasinski and Payette 2005). For example, crown fires occurring in black spruce stands that have been either previously logged or attacked by the spruce budworm (*Choristoneura fumiferana*) transform closed-crown forests into open woodlands because the first disturbance greatly reduces the aerial seed bank necessary for postfire regeneration (Payette et al., 2000; Payette and Delwaide, 2003; Simard and Payette, 2005). However these disturbances, if occurring separately, usually result in adequate regeneration of black spruce stands.

In contrast, a disturbance may interact with another by changing its extent, severity, or probability of occurrence (Kulakowski and Veblen 2007, Lynch and Moorcroft 2008), a concept that we call *linked*

disturbances. For instance, the risk of spruce beetle (*Dendroctonus rufipennis*) outbreak in Colorado was reduced in stands that burned 60 years previous to the outbreak compared to stands that originated from older fires (Bebi et al., 2003). Thus, the concept of compound disturbances emphasizes the unpredictable or qualitatively different ecological consequences of successive disturbance events, whereas that of linked disturbances focuses on changes in their probability of occurrence.

Linked disturbances may interact in two ways. One disturbance may amplify the second disturbance by increasing its likelihood or severity through a positive feedback, or alternatively, the first may dampen the second and act as a stabilizing agent. The relationship between linked disturbances may also vary over time, e.g., during succession or in conjunction with changing climate. Predicting when positive or negative feedbacks are most likely to occur between linked disturbances requires understanding the mechanisms underpinning their interactions. In this dissertation, I investigate interactions between two primary disturbance agents in western North America, bark beetle outbreaks and wildfire.

In the western US, most disturbance ecology research has focused on fire, addressing a wide range of topics such as historical fire regimes (Swetnam, 1993; Pierce et al., 2004), climate-fire relationships (Swetnam and Betancourt, 1990; Westerling et al., 2006), fire behavior (Rothermel, 1972, 1983), and fire effects on vegetation and landscape heterogeneity (Romme, 1982; Turner et al., 1994; Turner and Romme, 1994; Turner et al., 1997) (Fig. 1). Forest insects are another key natural disturbance in western forests, and research on bark beetle–forest relationships is also very active. Topics such as population dynamics and pheromone-mediated beetle behavior (Raffa, 2001; Wallin and Raffa, 2004; Raffa et al., 2005), beetle interactions with tree hosts and associated fungi (Paine et al., 1997), host susceptibility to beetles (Bentz et al., 1993; Shore et al., 2000), beetle outbreak effects on vegetation (Roe and Amman, 1970; Cole and Amman, 1980; Safranyik and Wilson, 2006), and

historical outbreak reconstructions (Romme et al., 1986; Veblen et al., 1991) have received considerable attention.

Although there has been a lot of speculation on beetle–fire interactions, few studies exist that are based on empirical data (Simard et al., 2008). The idea that tree mortality resulting from bark beetle outbreaks increases the risk of severe fires has been the dominant point of view since the early 20th century (Hopkins, 1909; Amman and Schmitz, 1988; Parker and Stipe, 1993) and has surprisingly made its way in forest management legislation without any strong supporting evidence (Healthy Forest Restoration Act of 2003 (Public Law 108-148)). The few empirical studies that have addressed this hypothesis have either found no relationship (Bebi et al., 2003; Kulakowski et al., 2003; Kulakowski and Veblen, 2007), or have found slight increases in the probability of crown fire (Bigler et al., 2005; Lynch et al., 2006). Understanding fire–beetle interactions is crucial for ecologically based forest management of beetle-affected landscapes and for better prediction of climate change effects on disturbance regimes. Furthermore, studies of fire–beetle interactions may provide insights into how multiple disturbance regimes affect ecosystem resilience, stability, and equilibrium (Holling, 1973; DeAngelis and Waterhouse, 1987; Turner et al., 1993; Peterson et al., 1998; Gunderson, 2000; Scheffer et al., 2001; Perry, 2002).

In the last 10 years, more than 47 million ha of subalpine and boreal forests have been affected by bark beetle outbreaks in the western US and British Columbia, representing one of the largest outbreaks in recent history (Raffa et al., 2008). Bark beetles are also at outbreak population levels in the Greater Yellowstone Ecosystem (Wyoming, USA), providing a timely opportunity to study their interaction with fire.

The Greater Yellowstone Ecosystem encompasses 80,000 km² and includes Yellowstone and Grand Teton National Parks, and many national forests and adjacent lands. Lodgepole pine (*Pinus contorta* var. *latifolia*) is the dominant forest type in the landscape, and other conifer species include whitebark pine (*Pinus albicaulis*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (Despain, 1990). The climate is cool with cold winters and dry summers, and the average fire return interval is about 100 to 300 years (Romme and Despain 1989; Schoennagel et al. 2003). Native bark beetles and insect defoliators periodically affect the Greater Yellowstone Ecosystem's forests (Furniss and Renkin, 2003), and since 2003, three species of bark beetles have been at high outbreak levels: the mountain pine beetle (MPB - *Dendroctonus ponderosae*), which attacks both lodgepole pine and whitebark pine; the spruce beetle, which feeds on Engelmann spruce; and the Douglas-fir beetle (*Dendroctonus pseudotsugae*), which is found on Douglas-fir.

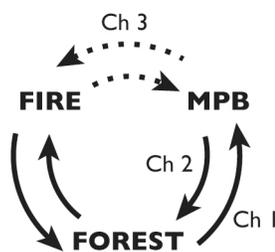


Fig. 1. Current understanding of bark beetle–fire–forest interactions (solid arrows: good understanding; dotted arrows: poor understanding) and contribution of this dissertation to fill knowledge gaps.

Ch = dissertation chapter; MPB = mountain pine beetle.

This dissertation addresses different aspects of the interactions between bark beetles, fire, and vegetation (Fig. 1). In the first chapter, I examine the effects of forest characteristics at different spatial scales on the landscape distribution of three species of bark beetles. I specifically try to determine the

relative importance of stand-level and landscape context (i.e., the characteristics of the landscape surrounding the focal stand) variables to explain why only certain areas of the Greater Yellowstone Ecosystem are currently infested while other seemingly suitable forests are not. Understanding the broad-scale distribution of bark beetles is a necessary step towards the understanding of beetle–fire relationships.

In the second chapter, I combine a chronosequence approach with the analysis of time series of satellite imagery to contrast and compare the recovery of vegetation biomass following stand-replacing fires and severe bark beetle outbreaks in lodgepole pine forests. Post-disturbance recovery of biomass is a critical component of disturbance events because it determines if and how fast ecosystem structure and function may be restored to their pre-disturbance state at the stand level. At a broader scale, biomass recovery rates also influence landscape stability and resilience of landscapes.

The third chapter is the core of this dissertation and focuses on the effects of mountain pine beetle outbreaks on the probability of active crown fire in lodgepole pine forests. I use field sampling of surface and canopy fuels and a fire behavior model to determine the potential fire behavior in a 35-yr post-outbreak chronosequence that includes undisturbed stands. To my knowledge, it is the first chronosequence study that is replicated in both space and time and that has been validated through tree-ring reconstruction of pre-outbreak conditions. The results from this study will contribute to the ongoing debate on bark beetle – fire interactions.

The chapters have been written as independent manuscripts and are therefore self-contained. I will conclude this dissertation with implications and significance of this research.

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CHAPTER 1

What explains landscape patterns of bark beetle outbreaks in Greater Yellowstone?

ABSTRACT

Aim Bark beetle outbreaks have affected extensive areas of western North American forests in the last decade, and factors explaining landscape patterns of infestations are poorly understood. The objective of this study was to determine the relative importance of stand structure, topography, soil characteristics, landscape context (i.e., the characteristics of the landscape surrounding the focal stand), and beetle pressure to explain landscape patterns of recent outbreaks of three species of bark beetles: the mountain pine beetle (*Dendroctonus ponderosae*), the spruce beetle (*D. rufipennis*), and the Douglas-fir beetle (*D. pseudotsugae*). A second objective was to identify common variables that explain tree mortality among bark beetle– tree host pairings.

Location Greater Yellowstone Ecosystem, Wyoming (USA)

Methods We used field surveys to quantify stand structure, soil characteristics, and topography at the plot level in stands of lodgepole pine (*Pinus contorta*), whitebark pine (*P. albicaulis*), Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmannii*) showing different degrees of infestation severity ($n = 129$ sites). We then used forest cover and bark beetle infestation maps derived from remote sensing to develop landscape context and beetle pressure metrics at different spatial scales

for each site. Plot-level and landscape-level variables were used to develop linear models to explain infestation severity for each pair of bark beetle–tree host species.

Results Engelmann spruce and Douglas-fir mortality were best predicted using landscape-level variables alone. Mortality of lodgepole pine was predicted by both landscape-level and plot-level variables and mortality of whitebark pine was best –although poorly– predicted by plot-level variables. Models including landscape context, beetle pressure, and topography variables were much better at predicting outbreak severity compared to models that only included plot-level measures, except for whitebark pine.

Main conclusions Proximity to initial beetle eruptions or amount of beetle-killed forests in the surrounding landscape were the most consistent predictors of subsequent outbreak severity within susceptible stands of all four host species.

Keywords

Bark beetles, Douglas-fir beetle (*Dendroctonus pseudotsugae*), insect outbreak, mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*), subalpine forest, Greater Yellowstone Ecosystem

INTRODUCTION

Bark beetles are ubiquitous disturbance agents of western North American forests. Native bark beetles of the genus *Dendroctonus* (henceforth ‘bark beetles’) are particularly important because they kill live trees over extensive areas during episodic outbreaks. The most extensive bark beetle outbreaks recorded in recent history have occurred in the last 10 years and have affected more than 47 million ha across the Rocky Mountains (Raffa et al., 2008). These outbreaks have had significant ecological effects on forest succession (Klutsch et al., 2009), fuel dynamics (Chapter 3), and carbon cycling (Kurz et al., 2008), as well as substantial socio-economic impacts (Abbott et al., 2009). At the sub-continent and multi-decadal scales, beetle outbreak recurrence is driven by climate (Fauria & Johnson, 2009). Over the course of an outbreak however, local and landscape factors influence the amount and distribution of tree mortality, resulting in a mosaic of undisturbed and beetle-killed forest stands across the landscape. Understanding the factors that explain landscape patterns of bark beetle outbreaks is critical to assess the consequences of current and future outbreaks on landscape structure and function.

Many susceptibility and risk-rating systems have been developed to predict the likelihood of bark beetle damage at the stand scale (reviewed in Shore et al., 2000). Risk of insect-caused mortality is the product of stand susceptibility, i.e., the attributes of a stand that increase the probability of tree mortality, and of beetle pressure, i.e., the abundance of beetle populations near the focal stand (Shore & Safranyik, 1992; Bentz et al., 1993). The most common variables explaining susceptibility to bark beetles are related to the quantity (stand basal area, abundance of large-diameter trees, etc.) and quality (e.g., Site Index) of host trees, and to their level of physiological stress (stem density, soil characteristics, etc.; Negron, 1998; Perkins & Roberts, 2003; Reynolds & Holsten, 1994; Shore & Safranyik, 1992). These empirical models typically have good predictive power at the stand scale once beetle density is known, but have had less success when applied to the landscape ($>10^3$ km²; Nelson et al., 2006; Robertson et al., 2008;

Dymond et al., 2006), suggesting that additional factors may drive bark beetle population dynamics at that scale.

Between outbreak episodes, bark beetles are present at low densities across the landscape, so in the absence of stand-level factors the probability of outbreak is theoretically constant across susceptible forests. During an outbreak, infestations are concentrated in some areas of the landscape and show a high spatial and temporal autocorrelation pattern typical of contagious processes (Aukema et al., 2006; Aukema et al., 2008). Not all stands of the suitable host species and age categories are heavily infested and this suggests that some landscape characteristics may facilitate eruptions of local beetle populations. Landscape composition (i.e., the proportion of different cover types) and configuration (i.e., the spatial arrangement of the different cover types) can affect the severity and frequency of insect outbreaks (Roland, 1993; Cappuccino et al., 1998). This is particularly true for bark beetles, which interact with their tree hosts across multiple spatial scales (Raffa et al., 2008). For example, initial mortality of host trees in a stand is first driven by stand and tree characteristics, but may be later influenced by landscape context (i.e., the characteristics of the landscape surrounding the focal stand). Therefore, although stand-level factors might be important to explain initiation of local eruptions, landscape factors are possibly more important once a regional outbreak has begun (Raffa et al., 2008).

In this study, we performed field sampling to measure variables within plots, and GIS analyses to measure characteristics of the landscape surrounding each plot to explain the patterns of mortality of susceptible host trees caused by outbreaks of three species of bark beetles across the Greater Yellowstone Ecosystem (Wyoming, USA). Despite the fact that the outbreaks occurred concurrently across the landscape, the bark beetle species are host-specific at the level of plant genus: the mountain pine beetle (*Dendroctonus ponderosae*) feeds on lodgepole pine (*Pinus contorta* var. *latifolia*) and whitebark pine (*P. albicaulis*), the spruce beetle (*D. rufipennis*) attacks Engelmann spruce (*Picea*

engelmannii), and the Douglas-fir beetle (*D. pseudotsugae*) feeds on Douglas-fir (*Pseudotsuga menziesii*). All beetles are native and have been historically associated with their current host, but whitebark pine, a high-elevation species previously less exposed to the mountain pine beetle because of low temperature, has recently been infested to unprecedented levels, a likely consequence of global warming (Logan & Powell, 2001). Risk rating systems have been developed for each of these host tree species individually, but to our knowledge no study has yet compared multiple bark beetle–host tree systems in the same landscape and at the same time.

Here we capitalize on the co-occurrence of outbreak populations of all three species of beetles, thereby controlling for differences between places and time, to address the following questions: What is the relative importance of stand structure, topography, soil, landscape context, and beetle pressure variables in explaining tree mortality patterns? Are there common variables that explain tree mortality across the different species of bark beetles and host trees? If outbreak-level population dynamics dominated, we expected that landscape context and beetle pressure variables would have greater explanatory power than plot-level variables because once beetle populations are at epidemic levels across the landscape, stand and tree characteristics exert less influence on population dynamics (Wallin & Raffa, 2004). Specific expectations for measured variables are summarized in Table 1. In particular, we expected that proximity to local eruptions in previous years would be positively related to current mortality and that this effect would be the same across tree hosts because all three beetle species are closely related biologically (Table 1). We also expected that the stand-level abundance of large-diameter host trees would be positively related to tree mortality for all species but whitebark pine, which would show heavy mortality irrespective of its abundance because of its lower defense capacity against the mountain pine beetle.

METHODS

Study area

The Greater Yellowstone Ecosystem covers an 80,000-km² area in Wyoming, Idaho and Montana, and includes Yellowstone and Grand Teton National Parks and several national forests (Fig. 1). Conifer forests dominate the landscape and show distinct zonation of forest types with elevation (Despain, 1990). Lodgepole pine grows on most xeric and nutrient-poor substrates at mid-elevation (between 2000 and 2600 m) where it forms both pioneer and late-successional stages. On more mesic sites, pioneer cohorts of lodgepole pine are succeeded by Engelmann spruce and subalpine fir (*Abies lasiocarpa*), and also by whitebark pine which also forms monospecific stands at treeline (about 3000 m in elevation). Douglas-fir is typically found at lower elevation (< 2300 m) and on slopes. The climate is characterized by cold, long winters and dry summers. Mean annual temperature (Old Faithful weather station, 1971-2000) is 0.9°C (mean monthly temperatures for January and July are respectively -10.7°C and 13.7°C) and mean annual precipitation is 620 mm (Western Regional Climate Center, 2007).

Fire is a major natural disturbance in the conifer forests of Greater Yellowstone. Lodgepole pine and Engelmann spruce forests are under a stand-replacing crown fire regime with an average fire return interval of 100-300 years (Romme & Despain, 1989; Schoennagel et al., 2003), whereas Douglas-fir and whitebark pine forests are characterized by mixed-severity fire regimes (Veblen et al., 2000; Larson et al., 2009). Native bark beetles are also an important component of subalpine forest dynamics and undergo episodic outbreaks every 20-40 years (Raffa et al., 2008). In the Greater Yellowstone Ecosystem, mountain pine beetle outbreaks have been documented in the 1920s-30s and in the late 1960s to early 1980s (Furniss & Renkin, 2003; Lynch et al., 2006), and the current outbreak started in the early 2000s (USDA Forest Service, 2008a; 2008b).

Site selection and field sampling

We used US Forest Service Insect and Disease Aerial Detection Survey maps (USDA Forest Service, 2008a; 2008b), vegetation maps, and field reconnaissance to select stands of varying degrees of beetle infestation throughout Greater Yellowstone, including undisturbed stands. Because only relatively large-diameter trees are suitable for bark beetle development (Shore & Safranyik, 1992; Schmid & Frye, 1977), and because our objective was to identify the measured variables that explain tree mortality in susceptible stands, we only selected stands dominated by host trees older than 100-yr-old and with a diameter at breast height (dbh) >20 cm. In addition, beetle-infested stands had to show recent signs (i.e., about 1-5 yr post-infestation) of beetle activity, i.e., red-needle or bare trees with fine twigs still attached to dead branches, along with presence of pitch tubes, boring dust, and J-shaped ovipositional galleries. Semivariance analysis of Landsat satellite imagery determined that pixel reflectance values were independent at distance greater than 500 m (results not shown). We thus located the sampling sites at least 500 m from each other to limit spatial autocorrelation in our data.

Field sampling was conducted during the summers of 2006 and 2007 using slightly different designs (Table 1). In 2006, we selected 8 forest stands with low beetle damage (<30% basal area beetle-killed) and 8 stands with severe damage (>40% basal area beetle-killed) for each tree host species (lodgepole pine, whitebark pine, Engelmann spruce, and Douglas-fir; $n = 16$ stands per tree host species, total $n = 64$ stands). At each stand, we randomly determined the center of the plot and recorded its location using a Trimble GeoExplorer 3 GPS (50-400 readings), slope (on a 50-m basis), and aspect. The GPS coordinates were later differentially corrected, yielding a horizontal precision <2 m for 97% of the plots. At each plot, two 100-m long and 4-m wide transects (total area: 800 m²) placed in a cross pattern oriented in the cardinal directions were used to describe tree attributes. For each standing tree rooted in the transects that had a dbh >7.5 cm, we recorded its species, dbh, and status (live, dead beetle-killed [using the criteria described above], or dead of other causes). We recorded the same information (except

tree dbh) in five prism points (metric, basal area factor 2), one at the center of the plot and one at each end of the transects. Increment cores were taken at 30 cm from the ground on 10 dominant host trees and were then brought to the laboratory, mounted, polished (320 grit), and cross-dated under a dissecting microscope (40x magnification) using standard dendrochronological techniques (Stokes & Smiley, 1968). Samples of the mineral soil (to 15 cm depth) were collected at each of the five prism points and composited. Soil samples were sent to the University of Wisconsin Soil and Plant Analysis Lab (Madison, WI) to determine their pH (McLean, 1982), total N (Bremner & Mulvaney, 1982), exchangeable Ca, Mg, and K (Thomas, 1982), available P (Bray & Kurtz, 1945), and organic matter content (loss-on-ignition at 360°C; Schulte & Hopkins, 1996). Exchangeable cation capacity was calculated as the sum of the exchangeable cations. Finally, soil texture was determined using the Bouyoucos hydrometer technique (McKeague, 1976).

After the 2006 season it was clear that a greater sample size would be needed. Therefore, in 2007 we used data from lodgepole pine stands that were sampled for a different study, and we sampled additional stands of whitebark pine, Engelmann spruce, and Douglas-fir. All stands sampled in 2007 represented a continuum of tree mortality, in contrast with the 2006 sampling that was concentrated on low- and high-severity mortality. In the lodgepole pine sites ($n = 23$), all the variables that were sampled in 2006 were also collected, but in three 200-m² plots co-located in a 0.25-ha area (total area: 600 m²). The other three stand cover types were sampled less intensively than the 2006 stands because of time constraints. In these stands (whitebark pine, $n = 14$; Engelmann spruce, $n = 15$; Douglas-fir, $n = 13$), only site conditions (slope, aspect, and elevation) and tree characteristics were recorded (Table 1). At each site, tree characteristics (same variables than in 2006 prism points) were recorded in three prism points arranged in a triangular fashion and separated by 30 m.

From these field data, we computed the live and beetle-killed basal area for each plot using the prism point data. *Pre-outbreak basal area* was computed as the sum of live and beetle-killed basal area. *Pre-outbreak host relative basal area* was calculated as the proportion of pre-outbreak host basal area relative to total pre-outbreak basal area $\times 100$ and thus represents the relative abundance of host trees before the outbreak. *Percent basal area in large trees* was calculated from the transect data as the pre-outbreak basal area of host trees above a certain dbh threshold relative to the pre-outbreak basal area of all trees in the plot with a dbh >7.5 cm $\times 100$. Dbh threshold values were 20 cm for lodgepole pine (Amman et al., 1977) and whitebark pine (Perkins & Roberts, 2003), 30 cm for Engelmann spruce (Holsten et al., 1999), and 25 cm for Douglas-fir (Negron, 1998). *Percent host basal area beetle-killed* was calculated as the proportion of host tree basal area beetle-killed relative to pre-outbreak basal area of host trees $\times 100$.

Aspect was transformed to a southwest-ness index by taking the cosine of the difference between the aspect measured in the field and 225° . This index ranges from -1 (north-east) and 1 (south-west) and expresses the contrast in sun exposure and dryness between these two aspects. Postfire stand age was estimated by using the age of the oldest tree sampled.

Landscape context and bark beetle pressure variables

Bark beetles are relatively poor dispersers (Turchin & Thoeny, 1993), and therefore the abundance of host trees in neighboring stands and the connectivity of surrounding suitable habitat are important for local eruptions to contribute to outbreaks across the landscape (Robertson et al., 2009; Aukema et al., 2006; Raffa et al., 2008). To characterize the landscape at multiple spatial scales around each plot ($n = 129$), we computed two landscape context indices and two variables related to proximity to beetle infestation in 250-m, 500-m, 1-km, and 2-km radius buffers around each plot (Table 1). The 250-m to 2-km radius buffers represent the range of effective dispersal radius of the beetles (Safranyik et al., 1992;

Safranyik et al., 1995; Turchin & Thoeny, 1993). For each plot and buffer size, we computed the proportion of evergreen forest, and the forest-nonforest edge density using the 2001 National Land Cover Database (Homer et al., 2004). Edge density is a measure of fragmentation of a cover type and is calculated by dividing the total length of edge between two or more cover types (here, evergreen forest vs. all other cover types) by the sampled area (McGarigal & Marks, 1995).

For beetle pressure variables, we used a bark beetle outbreak map that was developed for the study area (Jin et al., in prep.). Briefly, the map was generated using a change detection approach (Rogan et al., 2002), differencing pre-outbreak (1999) and outbreak (2003 to 2007) Landsat imagery after transforming the images' reflectance values to the Moisture Stress Index, a vegetation index sensitive to vegetation biomass (Rock et al., 1986). The 2007 map was validated with field data and yielded an R^2 of 0.77 with a root-mean-square error of prediction of 14% basal area beetle-killed. To characterize tree mortality patterns in the earlier stages of the outbreak, we only used the maps for 2003 and 2004. From these maps, we first calculated the percentage of pixels with >10% basal area beetle-killed for each buffer size in each site. Second, we determined distance to the closest outbreak by identifying the smallest buffer size that contained at least 4 pixels (0.36 hectare) with >10% basal area beetle-killed. Therefore, three of the landscape-level variables were calculated for different buffer sizes whereas the fourth one yielded a single value per site (Table 1).

Statistical analyses

To compare the relative importance of plot-level and landscape-level variables, we analyzed the data in three ways. First, we used all measured variables, therefore using only a subset of the stands (Table 1). Second, we analyzed the effect of landscape context, beetle pressure, and topography using the data from all sampled stands. Third, we only used the plot-level variables, i.e., stand structure and soil. This approach resulted in three regression models for each stand type.

To identify and remove intercorrelated explanatory variables, we first calculated a correlation matrix between all pairs of variables. For each pair of correlated variables ($r > 0.4$), we deleted the one that had the lowest correlation with percent host basal area beetle-killed, and repeated the process until all intercorrelated explanatory variables were removed. To reduce the number of variables used in model selection, we also removed all explanatory variables that were weakly correlated ($r < 0.25$) with percent host basal area beetle-killed. For landscape context variables that were calculated at multiple spatial scales, we first selected the scale (buffer size) that was best correlated with percent host basal area beetle-killed before entering the variable in the correlation matrix.

Model selection was done in two steps. First, the best 10 models with up to 5 variables were identified, based on the models' R^2_{adj} (PROC REG, BEST option; SAS Institute Inc., 2003). Because this model selection option only takes into account the overall fit of the model and not the significance level of individual variables in the models, we performed a second step where we tested each model individually using a linear model approach (PROC GLM; SAS Institute Inc., 2003). Non-significant ($\alpha > 0.05$) variables were removed from each model in a backward selection process. When necessary, variables were transformed to meet the assumptions of normality and homoscedasticity of the residuals. Finally, we calculated the Akaike information criterion (AICc) and $\Delta AICc$ for all models (Burnham & Anderson, 2002), and since none of the competing models were within 2 $\Delta AICc$ of the best model, the results of the AICc analysis are not further discussed. Finally, we tested for the presence of spatial autocorrelation in the residuals of the regression models using correlograms and the software GS+ (Gamma Design Software, 2004). None of the regression model residuals were spatially autocorrelated (results not shown and not discussed hereafter).

RESULTS

In total, 129 sites were sampled in 2006 and 2007 across the whole Greater Yellowstone Ecosystem (Fig. 1), representing a range of bark beetle-caused mortality of tree host basal area of 0% - 79% in lodgepole pine, 0% - 90% in whitebark pine, 0% - 98% in Engelmann Spruce, and 0% - 89% in Douglas-fir. Sampling year was not a significant variable in any of the regression models, suggesting that the differences in sampling designs between sampling years were inconsequential.

Lodgepole pine mortality

Using all measured variables (Table 1), lodgepole pine mortality decreased with distance from the nearest outbreak in 2004 and increased with percent basal area in large trees ($R^2_{adj} = 0.63$; Table 2). With only the landscape context, beetle pressure, and topography variables, lodgepole pine mortality also decreased with distance from the nearest outbreak in 2004 but increased with elevation ($R^2_{adj} = 0.59$; Table 3). When only plot-level variables (stand structure and soil characteristics) were used, lodgepole pine mortality increased with percent basal area in large trees ($R^2_{adj} = 0.40$; Table 4).

Whitebark pine mortality

In the model using all variables, whitebark pine mortality increased with pre-outbreak host relative basal area ($R^2_{adj} = 0.25$; Table 2). Percent forest beetle-killed in 2004 within a radius of 1 km was only marginally significant ($P = 0.0683$) in this model, but was positively related to tree mortality in the model based on landscape context, beetle pressure, and topography variables ($R^2_{adj} = 0.12$; Table 3). In the model using plot-level measurements (stand structure and soil characteristics) alone, whitebark pine mortality increased with pre-outbreak host relative basal area ($R^2_{adj} = 0.25$; Table 4).

Engelmann spruce mortality

In the all-variable model, spruce mortality increased with percent forest beetle-killed in 2003 within a radius of 500 m (Table 2; $R^2_{adj} = 0.66$). In the model using landscape context, beetle pressure, and topography variables, spruce mortality increased with percent forest beetle-killed in 2003 within a radius of 500 m and decreased with elevation (Table 3; $R^2_{adj} = 0.62$). In the model that used stand structure and soil characteristics variables, tree mortality increased with total nitrogen ($R^2_{adj} = 0.22$; Table 4).

Douglas-fir mortality

For the model using all measured variables ($R^2_{adj} = 0.52$; Table 2), and the one using landscape-level (landscape context, beetle pressure, and topography) variables ($R^2_{adj} = 0.67$; Table 3), Douglas-fir mortality increased with percent forest cover within a radius of 500 m and with percent forest beetle-killed in 2003 within a radius of 2 km. Using stand structure and soil characteristics variables only, tree mortality increased with pre-outbreak host relative basal area ($R^2_{adj} = 0.28$; Table 4).

DISCUSSION

For three of the four tree host-bark beetle pairings (lodgepole pine, Engelmann spruce, and Douglas-fir), either proximity to initial eruptions or the amount of beetle-killed forests in the surrounding landscape was a key predictor of subsequent mortality when all variables were used — for whitebark pine, the amount of beetle-killed forests in the surrounding landscape was only marginally significant ($P = 0.0683$). The same was true for the models based on landscape context, beetle pressure, and topography variables only (Table 3), where the mortality of all host tree species included a measure of beetle pressure. For Douglas-fir, the percentage of coniferous forest surrounding the stands also predicted tree mortality, which suggests that the abundance of forest habitat in the landscape was important for supporting bark beetle outbreak and perhaps facilitating dispersal. However edge density was not

significant in any of the models that included landscape context variables, suggesting that this measure of habitat configuration and connectivity was relatively unimportant.

In general, models that included landscape context, beetle pressure, and topography variables (Tables 2 and 3) were much better at predicting bark beetle outbreak severity ($R^2_{adj}=0.52-0.67$ for lodgepole pine, Engelmann spruce, and Douglas-fir) than the models that only included the plot-level variables (stand structure and soil characteristics; $R^2_{adj}=0.22-0.40$), except for whitebark pine (see discussion below). Models that used plot-level variables usually included descriptors of the abundance (pre-outbreak host basal area for whitebark pine and Douglas-fir) or average size (percent basal area in large trees for lodgepole pine) of host trees (Tables 2 and 3). The absence of many stand structure variables in the models that used all measured variables (Table 2) may result in part from sampling only susceptible stands, i.e., stands with an abundance of large-diameter host trees. Stands dominated by younger, smaller-diameter host trees are known to be less susceptible to bark beetles (Safranyik & Carroll, 2006), but such stands were not included in this study.

These results are in agreement with current understanding of bark beetle population dynamics. Because these three species typically feed and reproduce in live trees, successful reproduction of bark beetles at endemic (i.e., non-epidemic) levels is contingent on the presence of weakened or stressed host trees, which have compromised defense mechanisms. Successful colonization of a tree by bark beetles depends on the interplay between beetle attack rate and tree defense, and subsequent reproduction is largely influenced by predation, competition with other insects, and weather (Raffa et al., 2008). Under endemic conditions, tree and stand attributes such as tree vigor, size, and density are critical for determining the outcome of bark beetle attack (Raffa & Berryman, 1983). However, when favorable environmental conditions (e.g., warm temperature, drought, etc.) increase the success rate of beetle attacks and that populations reach a critical size, bark beetles can successfully mass attack host trees

irrespective of their vigor, age, or size, and local infestations may develop (Wallin & Raffa, 2004; Raffa et al., 2008). The transition from local eruptions to regional outbreaks may then be significantly affected by the connectivity of surrounding forests.

In this study, beetle-killed stands were sampled when the outbreaks were well underway (2006-07), i.e., at a time when landscape factors may have had a greater influence on beetle activity than local factors. This is particularly true for the spruce beetle and the Douglas-fir beetle, which began to erupt one year earlier (2003) than the mountain pine beetle (2004), and whose damage was only explained by variables characterizing the surrounding landscape (Table 2). However beetle pressure in the first years of the outbreak was a significant variable explaining tree mortality across all beetle species, suggesting that the best predictor of beetle activity in one place is the presence of local outbreaks in previous years (Aukema et al., 2006; Aukema et al., 2008).

Models for whitebark pine generally had the least explanatory power and included pre-outbreak host basal area. This variable was the only significant one when all measured variables were used (Table 2). Whitebark pine is a high-elevation species that historically has not been continually exposed to mountain pine beetle outbreaks because low winter temperature can kill overwintering larvae (Regniere & Bentz, 2007). This tree species is thus relatively naïve to the beetle and may have less elaborate defense mechanisms because of relatively lower evolutionary pressure. However, contrary to our hypothesis, whitebark pine mortality increased with its pre-outbreak relative basal area, suggesting that not all whitebark pine trees are killed when bark beetles are present in a stand. With climate warming, mountain pine beetle outbreaks are now occurring more frequently and continually in high-elevation whitebark stands, which sustain high mortality levels (Logan & Powell, 2001). It is unclear if bark beetle outbreaks in these stands are mainly supported by immigration from low elevation populations, or if resident populations are established locally (Logan & Powell, 2001). In this study, whitebark pine

mortality increased with increasing amount of area beetle-killed in 2004 within a 1-km radius (Table 3), and we speculate that this may suggest that resident populations may be established in these ecosystems. However, the relationship was very weak (R^2_{adj} of 0.12), which suggests that these populations may be strongly affected by an external stochastic driver such as winter temperature, which may regularly cause high mortality to beetle populations and create high interannual variability in population size.

CONCLUSION

The fortuitous co-occurrence of outbreaks of three species of bark beetles on four host tree species in Greater Yellowstone allowed us to study the effects of landscape- and plot-level variables on the distribution of bark beetle damage while controlling for differences between places and time. We conclude that variables describing forest habitat and beetle pressure in the surrounding landscape (radii of 500-2000 m) were much better than the selected plot-level measurements at explaining spatial patterns of beetle-caused tree mortality in susceptible stands of lodgepole pine, Engelmann spruce, and Douglas-fir. Furthermore, proximity to the initial eruptions or the amount of beetle-killed forests in the surrounding landscape was a key predictor of subsequent mortality for these three conifer species and is a marginal predictor of whitebark pine mortality.

ACKNOWLEDGMENTS

We would like to thank Joel and Jesse Charles, Jaclyn Entringer, J. Griffin, Lucille Marescot, Ryan Peaslee, and Greg Skupien for their help with field sampling, Kevin Tita for laboratory work, and Jake Griffin, Dan Tinker, Bill Romme, and Roy Renkin for fruitful discussions. We would also like to thank Roy Renkin for giving us the opportunity to observe bark beetle damage patterns from the air. This study was funded by the Joint Fire Science Program, the Andrew W. Mellon Foundation, and through a fellowship to M. Simard from the Fonds Quebecois pour la Nature et les Technologies.

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TABLES

Table 1. List of explanatory variables available for the 2006 and 2007 sampling years and for the different stand types. Variables that are underlined were evaluated at different spatial scales (see text for further explanations). The rationale for including these variables in the analysis are provided.

Variables	Scale of measurement	2006 dataset (PICO, PIAL, PIEN, PSME)*	2007 dataset (PICO)	2007 dataset (PIAL, PIEN, PSME)	Expected relationship
Stand structure					
Pre-outbreak host relative basal area (%) †	Plot	yes	yes	yes	Stands with a greater proportion of host species may be more susceptible to bark beetles
Percent basal area in large trees (%) ‡		yes	yes	—	Stands with a greater proportion of large trees may be more susceptible because larger trees have thicker phloem and are preferred by bark beetles
Stand postfire age		yes	yes	—	Older stands may be more susceptible to beetles
Topography					
Elevation (m)	Plot	yes	yes	yes	Tree mortality may decrease with elevation because colder temperatures at higher elevation may reduce development rate of bark beetles; alternatively, trees growing in lower-elevation sites may be more water-stressed and therefore more susceptible to bark beetles
Slope (%)		yes	yes	yes	Trees may be more water-stressed on steep slopes and therefore more susceptible to bark beetles
Southwest-ness		yes	yes	yes	Trees may be more water-stressed on southwest-facing slopes and therefore more susceptible to bark beetles
Mineral soil					
Texture (sand-silt-clay) (%)	Plot	yes	yes	—	Trees growing on coarse-textured soils may be more water-stressed and therefore more susceptible

Organic matter content (%)	yes	yes	—	to bark beetles Trees growing on soils with low organic matter content may be more water-stressed and therefore more susceptible to bark beetles
pH (pH units)	yes	yes	—	Trees growing on acidic soils may have reduced growth rates because of lower nutrient availability and may be more susceptible to bark beetles
Total nitrogen (%)	yes	yes	—	Trees growing on nitrogen-poor soils may be less vigorous and therefore more susceptible to bark beetles
Exchangeable cations (ppm)	yes	yes	—	Trees growing on nutrient-poor soils may be less vigorous and therefore more susceptible to bark beetles
Landscape context				
<u>Forest cover (%)</u>	Landscape	yes	yes	A greater amount of suitable habitat may increase survival and probability of mass attack
<u>Edge density (m/ha)</u>	Landscape	yes	yes	More connected forest habitat may facilitate beetle coalescence and spread
Bark beetle pressure				
<u>Percent forest beetle-killed (%)</u>	Landscape	yes	yes	A greater amount of local eruptions early in the outbreak may increase probability of attack in later stages of the outbreak
<u>Distance to closest local eruption (m)</u>	Landscape	yes	yes	A stand that is closer to local eruptions early in the outbreak may be more likely to be attacked in the later stages of the outbreak

* PICO, lodgepole pine; PIAL, whitebark pine; PIEN, Engelmann spruce; PSME, Douglas-fir;

† Sum of the basal area of live trees at time of sampling and of dead trees with bark beetle galleries;

‡ Pre-outbreak basal area of host trees with a diameter at breast height (dbh) > threshold dbh relative to pre-outbreak basal area of all trees with a dbh > 7.5 cm. Threshold dbh is species-specific: lodgepole pine and whitebark pine: 20 cm; Engelmann spruce: 30 cm; Douglas-fir: 25 cm.

Table 2. Results of the best linear models explaining percent host basal area beetle-killed in a subset of sites for which all variables were available (see Table 1).

Bark beetle – host tree	Model statistics			Explanatory variables				
	<i>N</i>	R^2_{adj}	<i>F</i>	<i>P</i>	Source	d.f.	<i>F</i>	<i>P</i>
Mountain pine beetle – lodgepole pine	38	0.63	32.82	<0.0001	– Distance to BB 2004 *	1	22.71	<0.0001
					+ % BA in large trees	1	27.71	<0.0001
Mountain pine beetle – whitebark pine	16	0.25	5.94	0.0287	+ Pre-outbreak host BA	1	5.94	0.0287
Spruce beetle – Engelmann spruce	16	0.66	29.99	<0.0001	+ % BK 2003 – 500 m †	1	29.99	<0.0001
Douglas-fir beetle – Douglas-fir	16	0.52	9.23	0.0032	+ Forest cover – 500 m ‡	1	7.34	0.0179
					+ % BK 2003 – 2 km †	1	5.00	0.0435

* Distance to closest local bark beetle eruption in 2004;

† Proportion of area beetle-killed in 2003 within a radius of 500 m or 2 km;

‡ Forest cover within a radius of 500 m.

Table 3. Results of the best linear models explaining percent host basal area beetle-killed using landscape context, beetle pressure, and topography variables.

Bark beetle – host tree	Model statistics			Explanatory variables				
	<i>N</i>	<i>R</i> ² _{adj}	<i>F</i>	<i>P</i>	Source	d.f.	<i>F</i>	<i>P</i>
Mountain pine beetle – lodgepole pine	38	0.59	27.93	<0.0001	– Distance to BB 2004 *	1	25.24	<0.0001
					+ Elevation		1	21.62
Mountain pine beetle – whitebark pine	30	0.12	4.96	0.0342	+ % BK 2004 – 1 km †	1	4.96	0.0342
Spruce beetle – Engelmann spruce	31	0.62	25.44	<0.0001	+ % BK 2003 – 500 m †	1	15.66	0.0005
					– Elevation		1	22.30
Douglas-fir beetle – Douglas-fir	29	0.67	29.51	<0.0001	+ Forest cover – 500 m ‡	1	21.21	<0.0001
					+ % BK 2003 – 2 km †		1	18.85

* Distance to closest local bark beetle eruption in 2004;

† Proportion of area beetle-killed in 2003 or 2004 within a radius of 500 m, 1 km, or 2 km;

‡ Percent forest cover within a radius of 500 m.

Table 4. Results of the best linear models explaining percent host basal area beetle-killed using stand structure and soil variables in a subset of sites for which these variables were available (see Table 1).

Bark beetle – host tree	Model statistics			Explanatory variables				
	<i>N</i>	R^2_{adj}	<i>F</i>	<i>P</i>	Source	d.f.	<i>F</i>	<i>P</i>
Mountain pine beetle – lodgepole pine	39	0.40	26.84	<0.0001	+ % BA in large trees	1	26.84	<0.0001
Mountain pine beetle – whitebark pine	16	0.25	5.94	0.0287	+ Pre-outbreak host BA	1	5.94	0.0287
Spruce beetle – Engelmann spruce	16	0.22	5.28	0.0375	+ Total nitrogen	1	5.28	0.0375
Douglas-fir beetle – Douglas-fir	16	0.28	6.96	0.0195	+ Pre-outbreak host BA	1	6.96	0.0195

FIGURES

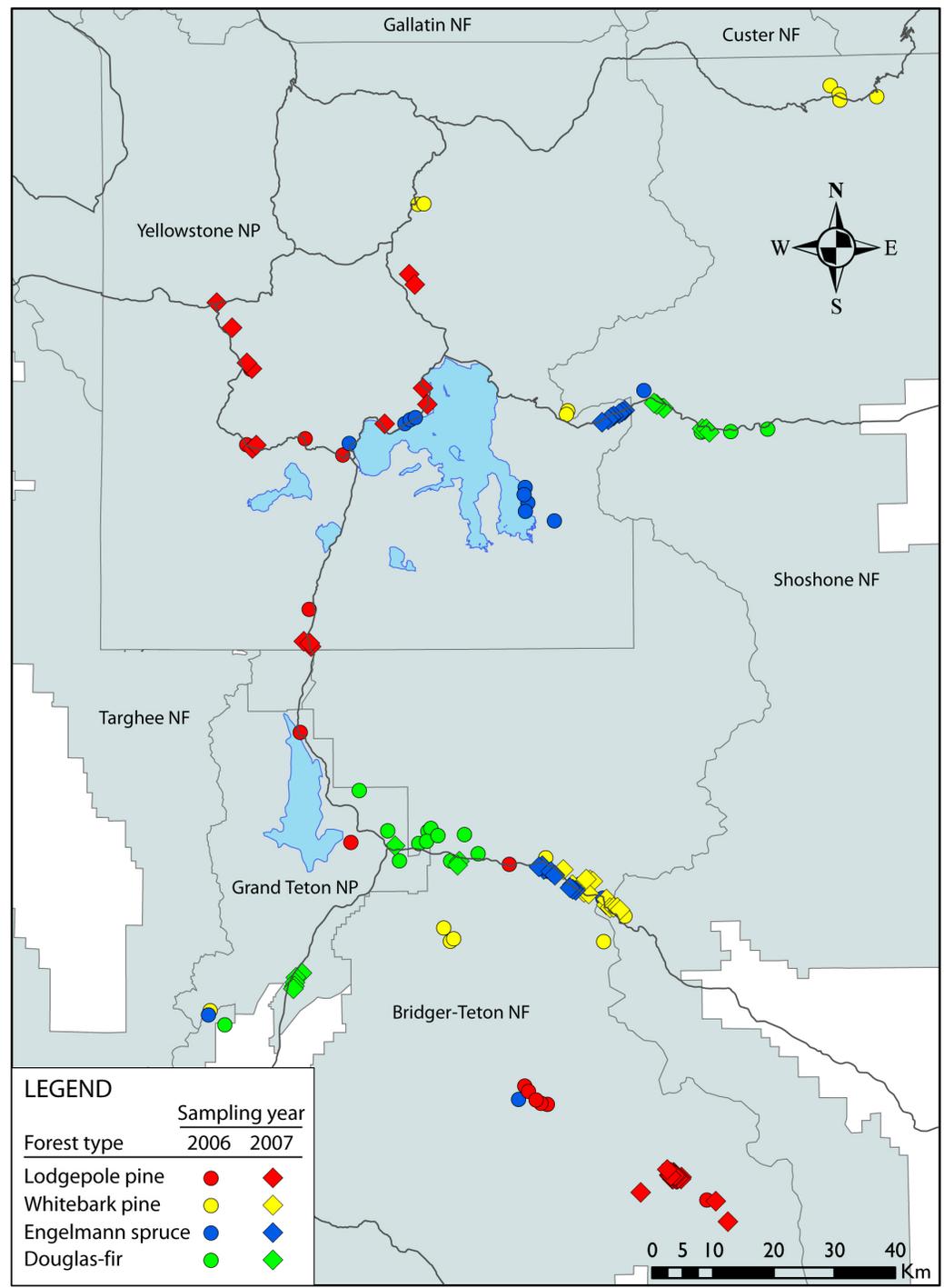


Figure 1. Location of sampling sites in Greater Yellowstone.

CHAPTER 2

Quantifying biomass recovery rates of lodgepole pine forests following fire and bark beetle outbreaks using a combined time series and chronosequence approach

Abstract

Forested landscapes throughout the West are periodically affected by fires and bark beetle outbreaks of different severity, extent, and spatial configuration. Rates of vegetation biomass recovery can influence important ecological processes like ecosystem carbon balance but are typically difficult to assess because of a lack of long-term data over large areas. We analyzed remote sensing data in a chronosequence framework to address the following question: how does disturbance type (stand-replacing fire vs. severe bark beetle outbreak) influence post-disturbance recovery rates of vegetation biomass in lodgepole pine forests of the Greater Yellowstone Ecosystem (Wyoming, USA)? From knowledge of disturbance effects on forest components and post-disturbance recovery mechanisms, we hypothesized that biomass recovery rates would be higher following mountain pine beetle outbreak than after stand-replacing fire. We used historical fire maps and aerial surveys of bark beetle outbreaks to identify forest polygons of different post-fire and post-beetle ages and create a post-disturbance chronosequence for fire and mountain pine beetle. Sampling locations were then randomly distributed within each polygon and were used to sample Moisture Stress Index (MSI) values from a time series (1987-2006) of satellite imagery. Finally, 39 lodgepole pine stands were sampled to determine tree basal area and estimate foliar biomass using allometric equations.

Lodgepole pine basal area and foliar biomass were negatively related to MSI ($R^2 = 0.60$ for both regressions). Using the 19-year time series of satellite imagery, we were able to infer changes in vegetation biomass over 27 (post-fire) to 34 (post-beetle) years. After a strong increase (reduced biomass) following fire, and a somewhat moderate increase following beetle outbreak, MSI rapidly returned to pre-outbreak values after about 20-30 years for both disturbance types. Post-disturbance MSI trajectories followed a logarithmic trend, suggesting a diminishing rate of biomass accumulation with time. Contrary to our hypothesis, post-fire recovery rates of MSI were greater than that of post-beetle stands, which may be caused by a greater availability of resources and/or by a higher density of tree seedlings. The concurrent return to pre-disturbance MSI values following fire and bark beetle outbreaks suggest that lodgepole pine stands may be equally resilient to both disturbance types, for at least some aspects of ecosystem structure and function. The combination of a chronosequence approach and a time series analysis reduced the limitations and built on the strengths of both methods, and allowed a robust estimation of post-disturbance biomass recovery rate over long time periods and broad spatial scales.

Keywords: bark beetles; chronosequence; Greater Yellowstone Ecosystem; Landsat; Moisture Stress Index; natural disturbances; remote sensing; wildfire;

1. Introduction

Natural disturbances have a significant impact on global ecological and biogeochemical processes by altering the stocks and flows of energy and matter in terrestrial biomes (Lovett et al. 2002; Bond-Lamberty et al. 2007; Turner et al. 2007; Kurz et al. 2008). The short-term effects of natural disturbances on terrestrial ecosystems are often to reduce live vegetation biomass, which then gradually recovers over time. Post-disturbance recovery is a critical component of the disturbance event because it determines if and how fast ecosystem structure and function may be restored to their pre-disturbance state. At a broader scale, biomass recovery rates influence landscape stability and resilience (Turner et al. 1993). For example, forest fires release large amounts of carbon to the atmosphere in the short term, and vegetation biomass recovery rates determine when the burned forests transition from a carbon source to a carbon sink, and they determine the strength of that sink (Kashian et al. 2006). Although there have been many studies documenting post-disturbance forest succession (e.g., Christensen and Peet 1984; Glitzenstein et al. 1986; Bergeron 2000), fewer have quantified post-disturbance recovery of vegetation biomass over long periods of time and across broad spatial scales (Frelich and Reich 1995). Because field-based studies are resource-consuming, few sites can usually be sampled (Pearson et al. 1987; Ryan and Waring 1992; Smith and Resh 1999), and therefore the results are not necessarily representative of the whole landscape. Disturbance regimes are changing rapidly in many parts of the globe and many ecosystems are subjected to more frequent, intense, or extensive disturbances (Westerling et al. 2006; Raffa et al. 2008). Quantifying the rates of vegetation biomass recovery following disturbance over broad spatial scales and long time scales is essential to understand and predict the effects of future disturbance regimes on ecosystem resilience and biogeochemical cycles.

A major challenge to quantifying post-disturbance recovery rates of vegetation biomass is the lack of long-term (> 100 yr) field data over broad scales. To circumvent this, researchers have used two approaches. First, the space-for-time substitution, or chronosequence approach, has been used

extensively in studies of post-disturbance succession (Pickett 1989; Kashian et al. 2005a; Simard et al. 2007). In this method, sites that have different post-disturbance age are sampled and used to infer changes that may occur over time in a single site. Although this method allows the study of ecosystems over long time scales, it is based on the critical assumption that all sites are similar in every aspect except for their post-disturbance age, a condition that is seldom verified (Johnson and Miyanishi 2008). A second method is to use time series of remotely sensed data to monitor the same areas over broad spatial scales. Repeat aerial photography and multispectral satellite remote sensing have been used to quantify post-disturbance changes in vegetation cover and biomass, respectively (Viedma et al. 1997; Yang et al. 2005; Hope et al. 2007), but are limited in their temporal scope. In this study, we use a method that combines chronosequence and time series approaches to quantify and compare the recovery rate of vegetation biomass following two major disturbances of western subalpine forests, fire and insect outbreaks.

Crown fires and bark beetle outbreaks are the two most important natural disturbance factors of subalpine coniferous forests in western North America. During recent decades, the frequency of large fires, the total area burned, and the length of the fire season have significantly increased (Westerling et al. 2006; Littell et al. 2009), and the extent and severity of bark beetle outbreaks have exceeded historical levels (Logan et al. 2003; Raffa et al. 2008). In the Greater Yellowstone Ecosystem (Wyoming, USA) lodgepole pine (*Pinus contorta* var. *latifolia*) forests are subjected to recurrent stand-replacing fires and mountain pine beetle (*Dendroctonus ponderosae*) outbreaks. In the last 40 years (1968-2007), close to 90% of the coniferous forest in Yellowstone National Park has been affected by mountain pine beetle infestations (30%), fire (20%), or both (40%) (National Park Service 2007; USDA Forest Service 2008b, a). These two disturbance types differ in their severity, i.e. their effect on vegetation and soils.

Stand-replacing crown fires kill most vegetation and consume most of the litter layer on the ground. Although fire severity can be very heterogeneous across the landscape and even within burns (Turner et al. 1997; Turner et al. 1999), canopy and understory vegetation mortality is generally high. In high-severity burns, forest recovery is provided by seeds that are released from serotinous cones, which open from the heat of the fire. After the 1988 fires in Yellowstone National Park, post-fire seedling density spanned six orders of magnitude (5 – 500,000 seedlings/ha), creating multiple regeneration pathways of varying tree density that have important implications for ecosystem processes (Turner et al. 2004; Kashian et al. 2006; Turner et al. 2007).

The mountain pine beetle attacks mature stands of lodgepole pine but kills only large-diameter trees, leaving intact the smaller trees, the understory vegetation, and the litter layer (Safranyik and Carroll 2006). Post-outbreak recovery is mainly provided by accelerated growth of surviving vegetation. These differences in the severity and mechanism of vegetation recovery likely result in different biomass recovery rates following fire and mountain pine beetle disturbance. Although some studies have quantified post-fire vegetation biomass recovery in lodgepole pine systems (Pearson et al. 1987; Kashian et al. 2005a), few have documented recovery following mountain pine beetle outbreak (Romme et al. 1986), and to our knowledge, none has compared it between these two types of disturbances. More importantly, few if any studies have been able to capture broad-scale variability of biomass recovery by sampling a large number of stands (but see Kashian et al. 2005a). Here, we analyzed multi-year remote sensing data in a chronosequence framework to address the following question: how does disturbance type (stand-replacing fire vs. severe bark beetle outbreak) influence post-disturbance recovery rates of vegetation biomass in lodgepole pine forests of the Greater Yellowstone Ecosystem? Because post-beetle stands have more residual vegetation than post-fire sites, we hypothesized that biomass recovery rates would be higher following mountain pine beetle outbreak than after stand-replacing fire.

2. Methods

2.1. Study area

The Greater Yellowstone Ecosystem, in Northwestern Wyoming, is an 80,000-km² region whose forests are dominated by lodgepole pine. Pure lodgepole pine stands establish following fire and either self-replace over time (usually on dryer sites), or are replaced by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) over time on wetter sites. The average fire return interval is about 100 to 300 years (Romme and Despain 1989; Schoennagel et al. 2003), and mountain pine beetle outbreaks have occurred periodically at 10-40 year intervals (Furniss and Renkin 2003). The climate is characterized by cold, long winters and dry summers. Mean annual temperature (Old Faithful weather station, 1971-2000) is 0.9°C (mean monthly temperatures for January and July are respectively -10.7°C and 13.7°C) and mean annual precipitation is 620 mm (Western Regional Climate Center 2007).

2.2. General approach

To determine post-disturbance recovery rates of vegetation biomass across the landscape, we analyzed time series of satellite imagery in a chronosequence framework (Figure 1). We first identified forest polygons of different post-fire and post-beetle ages using historical maps to create a post-disturbance chronosequence for fire and mountain pine beetle outbreaks. Sampling locations were then randomly distributed within each polygon and were used to sample a time series of satellite imagery.

2.3. Satellite imagery

We selected for the study area (WRS-2 path 38, rows 29 and 30) the best (i.e., cloud-free and snow-free) Landsat TM and ETM scenes acquired in late summer or early fall of 1987, 1989, 1994, 1999, and 2006 (Table 1). For each year, we selected scenes that were acquired the same day to facilitate their mosaicking. Raw images were converted to top of atmosphere reflectance, mosaicked in their original projection (Albers Conical Equal Area projection, GRS 1980 spheroid, and NAD 1983 datum), and

manually masked for clouds. To correct for between-year variations in reflectance caused by changes in atmospheric conditions at the time of image acquisition, we normalized the images to the 1999 scene using bright (treeless geothermal areas) and dark (small dark lakes) pseudo-invariant features (Schott et al. 1988). Moisture Stress Index (MSI) was calculated for each scene as a proxy for live vegetation biomass (TM5/TM4 - Rock et al. 1986; Hunt and Rock 1989) because preliminary tests showed this index to be the best predictor of live biomass in the study area (Tinker et al. 2009).

2.4. Post-fire chronosequence

To identify lodgepole pine stands that sustained high severity crown fires, we first inspected a historical fire map of Yellowstone National Park covering the period 1881-2007 (National Park Service 2007) and identified large burned areas that could potentially be used for sampling. Areas that were disturbed (by fire or insects) twice within a period of 30 years were rejected, as well as fires that occurred in non-lodgepole pine forest types (using a forest cover map; Mattson et al. 2003). We identified three fire years that met these conditions and had relatively large burned areas: 1979, 1988, and 1994. For the 1988 fires, we mapped fire severity with the differenced normalized burn ratio (dNBR - Key and Benson 2006), using the 1987 and 1989 Landsat images for pre- and post-fire conditions. We subsetted the map to only include high-severity canopy burns (dNBR > 660). For the 1979 and 1994 fire years, for which we had no pre-fire image, we used the most recent post-fire images (1985 and 1994, respectively) and rejected pixels within the burned polygons that had low MSI (< 20th percentile) after the fire, to reject low-severity burns. For each fire year, we then masked out the non-lodgepole pine forest types using a forest cover map (Mattson et al. 2003) and we randomly placed within the burned polygons 50 windows of 3 x 3 pixels (90 m x 90 m, averaged) that were used to sample the satellite imagery.

2.5. Post-beetle chronosequence

Aerial detection survey data that covered the whole study area from 2000 to 2006 were obtained online from the US Forest Service (USDA Forest Service 2008a, b), and were supplemented by historical insect survey data available for Yellowstone National Park since 1962 (Lynch et al. 2006). Both datasets were subsetted, keeping only polygons that represented very heavy mountain pine beetle damage (> 50 beetle-killed trees/ha) in lodgepole pine-dominated stands. Yearly layers of bark beetle damage were then combined into a single vector layer, keeping only the most recent attack when polygons of multiple attack years overlapped over a given area. A historical map of fire perimeters in Yellowstone (see section 2.4) was then used to mask out areas that subsequently burned. In the resulting map, only the years 1972, 1974, 1979, 2002, and 2003 had infested areas that were relatively large enough for further analyses. For each infestation year, 50 windows of 3 x 3 pixels were randomly placed in the infested polygons and used to sample the satellite imagery.

2.6. Field sampling

To determine the relationship between MSI and lodgepole pine stand biomass, we used data from 39 survey plots that were sampled in 2007 for another study (Chapter 2) and that were located in the area covered by the satellite imagery. Each plot was within a homogeneous area (> 1 ha) dominated by lodgepole pine and was at least 100 m from the nearest road. The location of each sample plot was recorded with a Trimble GeoExplorer 3 GPS (50-400 readings) and differentially corrected, yielding a horizontal precision < 2 m for 97% of the plots. Live basal area was computed from measurements of tree diameter at breast height (dbh) in three 200-m² quadrats co-located in a 0.25-h plot. Live foliar biomass was estimated from the dbh data and allometric equations developed for lodgepole pine (Brown 1978).

2.7. Statistical analyses

We used reduced major axis regression (Cohen et al. 2003) to relate tree basal area and foliar biomass to MSI values of the 2006 Landsat scene obtained from the pixel centered on each field plot. To compare recovery rates between disturbance types, we modeled post-disturbance MSI using a mixed effect model (PROC MIXED - SAS Institute Inc. 2003) with $\ln(\text{MSI})$ as the response variable, time since disturbance, disturbance type, and their interaction as fixed effects, and pixel ID nested within disturbance type as a random effect. The nested random effect acted as a repeated measure term for the pixel locations (more specifically, the 3x3 pixel windows), which were used to sample repeatedly across the time series of Landsat scenes (Littell et al. 1991). Variables were transformed if needed to meet the assumptions of normality and homoscedasticity of the residuals.

3. Results

Moisture Stress Index (MSI) decreased linearly with increasing live tree basal area ($R^2 = 0.60$; $F = 56.53$; $P < 0.0001$) and with increasing foliar biomass ($R^2 = 0.60$; $F = 54.56$; $P < 0.0001$), suggesting that this index can represent post-disturbance recovery of vegetation biomass (Fig. 2).

Post-disturbance trends of MSI were quantified for 30 years following fire and severe bark beetle outbreak (Fig. 3a). Pre-disturbance MSI values were comparable between disturbance types and disturbance years, suggesting that all stands had a somewhat similar live biomass before disturbance. The initial increase in MSI (i.e., reduced vegetation biomass) was much greater following fire disturbance than bark beetle outbreak. For both disturbance types, the best regression model that predicted the change in MSI with time was a logarithmic function, suggesting a diminishing rate of vegetation biomass accumulation, as estimated by MSI, with time since disturbance (Fig. 3b). Rate of vegetation biomass recovery (i.e., $\Delta\text{MSI}/\text{time}$) was greater in post-fire than in post-beetle stands, as indicated by the significant interaction between time since disturbance and disturbance type (Table 2).

However post-beetle biomass, as estimated with MSI, was always greater than post-fire biomass for the first 20 years or so following disturbance, after which time the two MSI trajectories converged.

4. Discussion

In this study, we reconstructed recovery of vegetation biomass for 30 years following stand-replacing crown fire and severe mountain pine beetle outbreak by combining a chronosequence approach with the analysis of time series of satellite imagery. Not surprisingly, the post-fire increase in MSI was greater than that following beetle outbreak, but contrary to our hypothesis, the recovery rate of post-fire stands was much greater than that of post-beetle stands. This result could be due to increased resource availability, greater tree seedling density, or both.

4.1. Resource availability

After severe fires, most of the vegetation has been killed, reducing competition for light and nutrients for the newly established tree seedlings. Although nutrients such as nitrogen are volatilized during severe fires (MacLean 1983; Smithwick et al. 2005), post-fire soil pools of inorganic N are usually elevated compared to pre-fire conditions (Turner et al. 2007) and may not be limiting for lodgepole pine seedlings (Romme et al. 2009). In contrast, bark beetle outbreaks can kill most of the large trees in a stand but some mature trees remain and the understory vegetation is not disturbed. As a result, tree seedlings and saplings in the understory are competing with mature trees and other plants for nutrients and light, which are only moderately increased after the outbreak (Morehouse et al. 2008).

4.2. Tree and seedling density

Biomass accumulation declines with tree and stand age (Gower et al. 1996; Ryan et al. 1997; Ryan et al. 2004), so stands that have a greater proportion of young trees should have greater rates of biomass accumulation. Lodgepole pine seedling density is highly variable following fire (Kashian et al. 2004;

Turner et al. 2004) but can reach values that are much higher than those of undisturbed or beetle-killed stands (Kashian et al. 2005b; Simard et al. in review). In 17-year old post-fire lodgepole pine stands, accumulation of biomass is proportional to seedling density up to a certain point (Turner et al. 2009). Consequently, the greater abundance of seedling and saplings in post-fire stands contributes to greater rates of biomass accumulation compared to post-beetle stands.

4.3. Rapid biomass recovery and convergence between disturbance types

Vegetation biomass was considerably lower following fire than after beetle outbreak, but recovered at a higher rate (Fig. 3). As a consequence, vegetation biomass of both disturbance types (as indicated by MSI) converged and reached pre-disturbance values between 20 and 30 years after disturbance, which is surprisingly rapid for post-fire stands. Because MSI is primarily influenced by the water content of the vegetation, it is highly sensitive to foliar biomass (Rock et al. 1986; Hunt and Rock 1989). Therefore, although 30-year-old post-fire stands may not be composed of mature trees, all but the very low-density stands have developed a closed canopy by then, and may have canopy biomass values that are comparable to that of the older, and typically more open, pre-disturbance stands (Smith and Resh 1999). The fact that post-fire and post-beetle stands reach pre-disturbance MSI values at the same time suggests that lodgepole pine may be equally resilient to both disturbance types, for at least some aspects of ecosystem structure and function.

4.4. Time series – chronosequence approach

The merging of chronosequence and time series approaches revealed recovery trends that were consistent between disturbance events within each disturbance type, even though the disturbance events studied were separated in time by up to 7 years for beetle outbreaks and to 15 years for wildfire. This consistency, added to the fact that 50 samples were taken for each disturbance event, suggests that the trends may be representative of the whole landscape and is promising for future studies of post-

disturbance recovery of vegetation biomass. We found only a few other studies that have used a combined chronosequence – time series approach (Hicke et al. 2003; McMichael et al. 2004; Goetz et al. 2006). However only one took our approach of including disturbance events that occurred before the date of the earliest satellite image (McMichael et al. 2004), a method that allows the time period studied to be extended beyond that of the imagery time series. The time series that we used in this study was relatively short because we relied on the TM sensor first launched in 1985 aboard Landsat 4. Using this 19-year-long time series, we were nevertheless able to infer biomass trajectories over 27 (post-fire) to 34 years (post-beetle). This approach, if used with longer time series (e.g., Landsat MSS, since 1972, or AVHRR, since 1979), could considerably extend the period over which post-disturbance dynamics can be studied.

5. Conclusion

The frequency, extent, and severity of bark beetle outbreaks and fire have increased in recent decades and are predicted to increase further (Logan et al. 2003; Flannigan et al. 2005; Hicke et al. 2006; Westerling et al. 2006). Prediction of the long-term effects of these disturbances over broad scales requires an understanding of the spatial and temporal variability of past disturbance events, and of the resilience of impacted vegetation types. In this study, we have presented an approach that allows the quantification of post-disturbance recovery of vegetation biomass over broad spatial scales, long time periods, and across different disturbance events. We have found that lodgepole pine forests may be equally resilient to bark beetle and fire disturbances, for at least some aspects of ecosystem structure and function.

Acknowledgements

We would like to thank Clayton Kingdon for technical support, We would like to thank Jaclyn Entringer, Lucille Marescot, Ryan Peaslee, and Greg Skupien for their help with field sampling, Hank

Harlow and the University of Wyoming – National Park Service staff for logistic support in the field, and the Yellowstone National Park and Bridger-Teton National Forest staff for their support. This study was funded by the Joint Fire Science Program, the Andrew W. Mellon Foundation, and through a fellowship to M. Simard from the Fonds Quebecois pour la Nature et les Technologies.

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Tables

Table 1. Acquisition dates for Landsat TM and ETM+ imagery.

Date	Satellite & sensor	Path / Rows (WRS-2)
09/22/1987	Landsat 5 TM	038 / 029-030
08/02/1989	Landsat 4 TM	038 / 029-030
09/25/1994	Landsat 5 TM	038 / 029-030
09/15/1999	Landsat 7 ETM+	038 / 029-030
08/09/2006	Landsat 5 TM	038 / 029-030

Table 2. Results of the mixed linear model relating $\ln(\text{Moisture Stress Index})$ to time since disturbance (TSD) and disturbance type (TYPE; fire vs. mountain pine beetle) for the post-fire chronosequence ($R^2 = 0.94$; $n = 1050$; $F_{(301, 748)} = 39.78$; $P < 0.0001$). Note: the R^2 and F -value for the model were computed with a fixed-effect linear model.

Covariance parameters			
Source	Ratio	Z	P
Pixel ID (TYPE)	2.1696	10.56	< 0.0001
Fixed effects			
Source	d.d.f.*	F	P
TSD	792	3547.10	< 0.0001
TYPE	684	804.00	< 0.0001
TSD * TYPE	792	1503.02	< 0.0001

* denominator degrees of freedom; numerator degrees of freedom are all equal to 1.

Figure captions

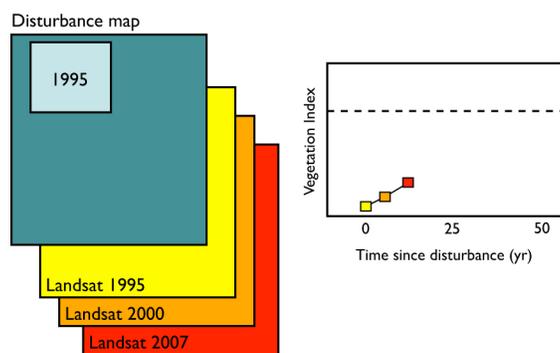
Figure 1. Schematic representation of the chronosequence – time series approach. A) Time series of satellite imagery allow to follow stand development of the same locations over time but are typically short. B) Space-for-time substitution, or chronosequence studies allow to extend considerably the temporal scope of ecological studies but may not represent real time sequences of stand development unless some critical assumptions are met. C) The analysis of time series of satellite imagery in a chronosequence framework builds on the strengths and reduce the limitations of both methods, allowing robust estimation of stand development over long time periods and broad spatial scales.

Figure 2. Relationship between A) live tree basal area and Moisture Stress Index and between B) live foliar biomass and MSI.

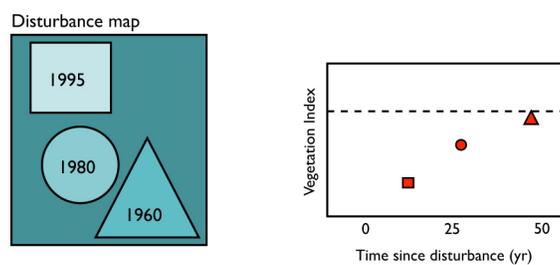
Figure 3. A) Data points and B) regression curves of the change in Moisture Stress Index with time since stand-replacing fire and severe mountain pine beetle outbreak. In A), each line represents a different disturbance year, and symbols linked by a line represent time series for the same locations. Each symbol represents 50 samples \pm 1 standard error. The gray area represents the pre-disturbance state. Note that the y axis has been reversed to facilitate interpretation of the Moisture Stress Index.

Figures

A. Time series



B. Chronosequence



C. Combined approach

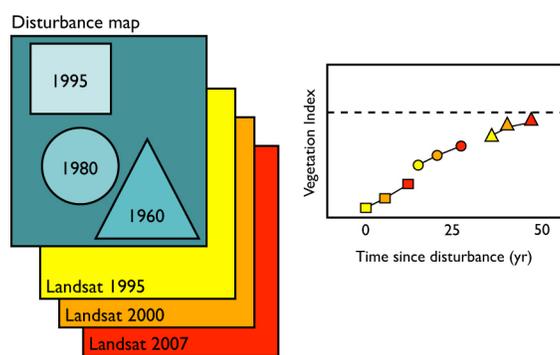


Figure 1.

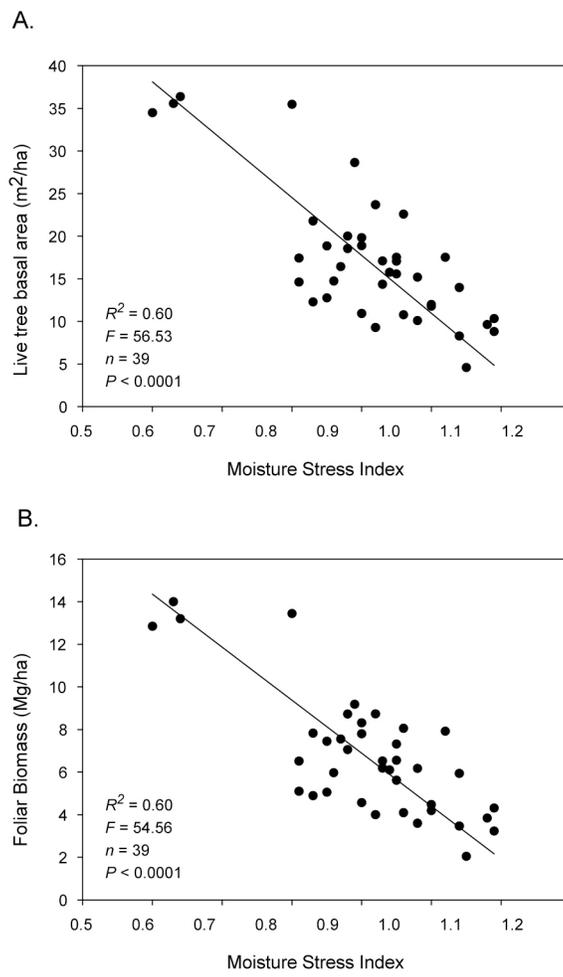


Figure 2.

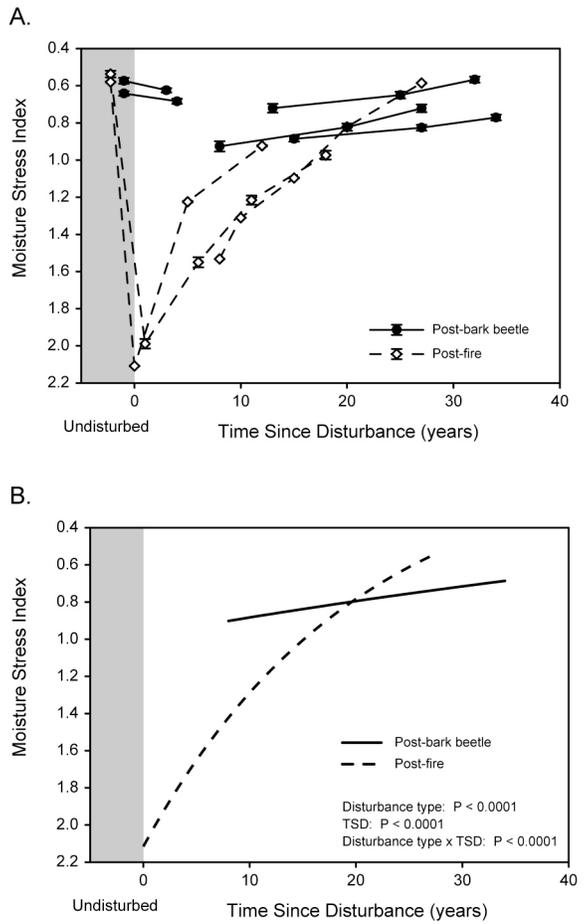


Fig. 3.

CHAPTER 3

Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests?

ABSTRACT

Disturbance interactions have received growing interest in ecological research in the last decade. Fire and bark beetle outbreaks have recently increased in severity and extent across western North America, raising concerns about their possible interactions. Although it is often presumed that bark beetle outbreaks increase probability of active crown fire by producing high loads of surface and canopy dead fuels, empirical data are scarce and results are ambivalent. We combined field measurements and modeling to address the following question: How do fuel characteristics, microclimate, and potential fire behavior change with time since severe bark beetle outbreak in lodgepole pine forests of Greater Yellowstone (Wyoming, USA)? We measured surface and canopy fuels, and soil surface temperature in a time-since-beetle outbreak chronosequence ($n = 35$ sites) from undisturbed to 36-yr post-outbreak, including stands in red- and gray-needle stages (respectively 1-2 and 3-5 yrs post-outbreak). Field data were used to parameterize the fire behavior model NEXUS and predict potential fire behavior at each site.

Dead surface woody fuel loads of all size categories did not differ among undisturbed, red, and gray-stage stands. Compared to undisturbed sites, red and gray-stage sites had on average 53% lower canopy bulk density, 42% lower canopy fuel load, and 29% lower canopy moisture content, but had a similar canopy base height (3.1 m). In subsequent decades, coarse wood loads doubled and canopy base height declined to 0 m. Modeling results suggested that undisturbed, red, and gray-stage stands were unlikely to exhibit transition of surface fires to tree crowns (torching), and that the likelihood of sustaining an

active crown fire (crowning) decreased from undisturbed to gray-stage stands. Simulated fire behavior was little affected by beetle disturbance when wind speed was either below 40 km/h or above 60 km/h, but at intermediate wind speeds, probability of active crown fire in the red and gray-stage stands was lower than in undisturbed stands, and old post-outbreak stands were predicted to have passive crown fires. Our results suggest that mountain pine beetle outbreaks in Greater Yellowstone may reduce the probability of active crown fire in the short term by thinning lodgepole pine canopies.

Key words: bark beetles; chronosequence; compound disturbances; disturbance interactions; fire behavior modeling; fuel loads; Greater Yellowstone Ecosystem; insect-fire interactions; linked disturbances; lodgepole pine (*Pinus contorta*); mountain pine beetle (*Dendroctonus ponderosae*); Rocky Mountains.

INTRODUCTION

Disturbance interactions have received growing interest in ecological research (Paine et al. 1998, Kulakowski and Veblen 2007). Understanding of individual disturbances has greatly improved, and ecologists now recognize that many ecosystems are affected by different types of natural disturbances that may interact in surprising but important ways (Turner 2005). Interest in disturbance interactions is also driven by concerns about the effects of climate change and human impact on natural disturbance regimes, which might display nonlinear responses and unpredictable feedbacks that could possibly result in abrupt regime shifts (Paine et al. 1998, Scheffer et al. 2001, Apps and McGuire 2005). However, surprisingly few studies have explicitly targeted interactions between disturbances.

We distinguish two types of disturbance interactions. *Compound disturbances* (*sensu* Paine et al., 1998) take place when two disturbances occurring in a short period of time have a synergistic effect that cannot be predicted from the sum of the individual disturbances. By definition, compound disturbances have unpredictable effects on ecosystems and may result in regime shifts (Jasinski and Payette 2005). In contrast, a disturbance may interact with another by changing its extent, severity, or probability of occurrence (Kulakowski and Veblen 2007, Lynch and Moorcroft 2008), a concept that we call *linked disturbances*. Thus, the concept of compound disturbances emphasizes the unpredictable or qualitatively different ecological consequences of successive disturbance events, whereas that of linked disturbances focuses on changes in their probability of occurrence.

Linked disturbances may interact in two ways. One disturbance may amplify the second disturbance by increasing its likelihood or severity through a positive feedback, or alternatively, the first may dampen the second and act as a stabilizing agent. The relationship between linked disturbances may also vary over time, e.g., during succession or in conjunction with changing climate. Predicting when positive or negative feedbacks are most likely to occur between linked disturbances requires understanding the mechanisms underpinning their interactions. In this study, we investigate interactions between two primary disturbance agents in western North America, bark beetle outbreaks and wildfire.

Bark beetle outbreaks and forest fires have both increased in extent and severity during recent decades (Westerling et al. 2006, Raffa et al. 2008), raising concerns about their possible interactions (Negrón et al. 2008). Native bark beetles of the genus *Dendroctonus* undergo episodic population outbreaks that result in widespread mortality of host trees through pheromone-mediated mass attacks (Wallin and Raffa 2004, Raffa et al. 2005). In the last 10 years, more than 47 million ha of subalpine and boreal forests have been affected by bark beetle outbreaks in the western US and British Columbia, representing one of the largest outbreaks in recent history (Raffa et al. 2008). It is often presumed that bark beetle outbreaks increase the probability of active crown fire because they create great quantities of dead and ladder fuels (Hopkins 1909, Brown 1975, Amman and Schmitz 1988, McCullough et al. 1998). On the other hand, it has also been proposed that beetle outbreaks may reduce the probability of active crown fire by thinning the forests and reducing canopy fuel loads (Despain 1990, Schmid and Amman 1992). If bark beetle outbreaks amplify subsequent probability of active crown fire, then extensive regions of western North America could be at risk of high-severity fires, and carbon losses to the atmosphere, which are already substantial following beetle outbreak (Kurz et al. 2008), would be further increased. However, if fire disturbance is dampened, carbon losses may not accelerate so rapidly and the probability of high-severity fires at the wildland-urban interface may be lessened. Given the extent of the forests affected by the recent bark beetle outbreak, understanding whether the probability of subsequent high-severity fire is elevated is increasingly important.

Previous empirical studies on linked bark beetle and fire disturbances have either used a retrospective approach, i.e., by comparing observed to expected patterns of area burned in a landscape that was previously affected by bark beetle outbreaks, or a prospective approach, by predicting potential fire behavior with fire behavior models and fuel data sampled in beetle-killed and undisturbed forests. These studies have yielded ambivalent results (Simard et al. 2008), with some analyses suggesting slightly increased probability or severity of fire following beetle outbreak (Turner et al. 1999, Bigler et al. 2005, Lynch et al. 2006), and others showing no evidence for such a relationship (Bebi et al. 2003,

Kulakowski and Veblen 2007, Jenkins et al. 2008). In this study, we employ a prospective approach to quantify fuel dynamics and predict potential fire behavior during and for several decades after beetle outbreak. A few prospective studies have explored the relationship between beetle-caused changes in fuels and fire behavior, yet, to our knowledge, this is the first study to include detailed fuels, microclimate, and fire behavior data in a 35-yr post-outbreak chronosequence replicated in space ($n = 35$ sites) and time (1981 and 2007) and validated using extensive dendrochronological reconstruction of pre-outbreak stand conditions.

Bark beetle outbreaks potentially may amplify or dampen different components of fire behavior, including fire intensity, rate of spread and fire type (e.g., surface vs. crown fire). Active crown fires are especially threatening to human values because of their high intensity and rate of spread. Active crown fires develop when weather and fuel conditions allow both *torching* (when surface fire transitions to tree crowns when the vertical continuity of canopy fuels (ladder fuels) permits; Pyne et al. 1996) and *crowning* (when fire then spreads to nearby tree crowns). If canopy fuels are sparse or weather conditions are moderate, crown fires do not spread to nearby tree crowns, resulting in passive crown fires. Conditional crowning is predicted when conditions allow crowning but not torching. In this case, active crown fire could potentially occur if the canopy was ignited by a firebrand or by a crown fire from an adjacent stand (Scott and Reinhardt 2001). Thus, weather conditions can constrain the effects of stand structure (i.e., fuels) on fire behavior (Renkin and Despain 1992).

A linkage between bark beetle outbreaks and fire behavior could occur through several mechanisms related to the quantity and arrangement of live and dead fuels and to microclimate (Fig. 1). In the short term (1-2 yrs post-beetle, 'red-needle stage'), probability of torching and crowning may be increased because foliar moisture is reduced but dead needles are retained in the canopy. When dead needles fall to the ground (3-5 yrs post-beetle, 'gray-needle stage'), the reduction in canopy fuels may decrease probability of crowning, but inputs of fine fuels from the canopy to the surface, and increased understory live fuel loads resulting from accelerated growth of grasses and shrubs might increase

surface fire intensity and possibly torching. At longer time periods (10 to 40 years post-outbreak), understory tree growth may create ladder fuels that promote torching, and the opening of the stand could result in higher wind speeds and temperatures, and lower moisture content of surface fuels, which may increase surface fire intensity and possibly also increase torching, crowning, and overall fire intensity. Given the complexity of changes in stand structure and microclimate, the net effect of beetle outbreak on fire behavior is also complex and likely varies through time since beetle outbreak (TSB).

We combined field studies and fire behavior modeling to determine whether bark beetle outbreaks and wildfire are linked disturbances and whether this linkage results in amplification or dampening of post-beetle fire severity in Greater Yellowstone (Wyoming, USA). Specifically, we addressed the following question: How do fuel characteristics, microclimate, and likely fire behavior under a range of fire weather conditions change with time since severe bark beetle outbreak in lodgepole pine (*Pinus contorta* var. *latifolia*) forests? We hypothesized that the disturbances would be linked, but that the nature of the linkage would change over time in response to changes in fuel characteristics and microclimate (Fig. 1), such that bark beetle outbreak would: (1) amplify probability of active crown fire in red-needle stands 1-2 yrs post-outbreak; (2) amplify intensity and rate of spread of surface fire but dampen probability of active crown fire in gray-needle stands 3-5 yrs post-outbreak; (3) amplify probability of torching and passive crown fires but dampen probability of active crown fire in stands 10-40 yrs post-outbreak as small surviving trees grow in the canopy. In this study, ‘lower probability’ means that higher wind speeds and/or lower fuel moisture content are required to propagate fire, and ‘higher probability’ means that the fire behavior component (torching, crowning, passive crown fire, etc.) could happen at lower wind speeds and/or at higher fuel moisture content. Both terms are used to qualify fire behavior of a TSB class relative to the undisturbed stands.

STUDY REGION

Lodgepole pine forests of Greater Yellowstone are ideal for studying bark beetle-fire interactions because it is a crown fire-driven ecosystem that is also prone to periodic outbreaks of the mountain pine beetle (MPB; *Dendroctonus ponderosae*), for which long-term (1960-present) records of activity are available (Lynch et al. 2006). The Greater Yellowstone Ecosystem, a 80,000 km² area straddling the states of Wyoming, Montana, and Idaho, represents one of the largest tracts of unmanaged forest in the conterminous United States. Yellowstone and Grand Teton National Parks form the core of this landscape and are surrounded by National Forests and other federal lands. Lodgepole pine is a dominant forest type in the region and grows on most xeric and nutrient-poor substrates, where they form both pioneer and late-successional stages (Despain 1990). On more mesic sites, post-fire cohorts of lodgepole pine are succeeded by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), and also by whitebark pine (*Pinus albicaulis*) which can form monospecific stands at treeline. Douglas-fir (*Pseudotsuga menziesii*) is typically found at lower elevations and on slopes. The climate is cool with cold winters and dry summers. Mean annual temperature (Old Faithful weather station, 1971-2000) is 0.9°C (mean monthly temperatures for January and July are respectively -10.7°C and 13.7°C) and mean annual precipitation is 620 mm (Western Regional Climate Center 2007).

Fire reconstruction studies in Yellowstone National Park have documented a mean fire return interval ranging from about 160 years at low elevation (2100 – 2500 m) to more than 300 years at high elevation (2300 – 2600 m) (Romme and Despain 1989, Schoennagel et al. 2003). The mountain pine beetle (MPB – *Dendroctonus ponderosae*) is an important biotic disturbance in the region, affecting mature stands of both lodgepole pine and whitebark pine across their distribution range (Raffa et al. 2008). Bark beetle colonization occurs during the summer, when female beetles excavate vertical J-shaped galleries in the phloem of the trees to lay eggs, a process that induces abundant production of tree resin that accumulates at the entrance of the galleries (i.e., ‘pitch tubes’). The developing larvae feed in horizontal galleries that girdle and kill the trees within weeks, although beetle-killed trees keep

their green foliage until the end of the summer of the attack (also called ‘green attack stage’). One year after the initial attack, all the needles of the beetle-killed trees have turned red (‘red-needle stage’) and will remain on the trees for a few years, after which they will fall to the ground (about 3+ years post-beetle; ‘gray-needle stage’). The last previous major MPB outbreak in Greater Yellowstone occurred during the 1960s through early 1980s (Furniss and Renkin 2003, Lynch et al. 2006), and a current outbreak has been ongoing since about 2003 (USDA Forest Service 2008b, a).

METHODS

We measured forest fuels in a time-since-beetle outbreak (TSB) chronosequence from undisturbed to 36-yr post-outbreak stands and used the field data to parameterize the fire behavior model NEXUS (Scott and Reinhardt 2001) and predict potential fire behavior at each site under similar abiotic conditions. Two different sets of field data were used. The first is a chronosequence of 25 sites that we established in 2007, where all components (canopy, understory, and surface) of fuels were measured. This chronosequence, which comprised undisturbed to 36-yr-old post-outbreak stands, was supplemented by another chronosequence sampled in 1981 that included undisturbed to 18-yr-old post-outbreak stands ($n = 10$) but only included surface fuel measurements. These two chronosequences did not share common stands and were selected, sampled, and validated using slightly different criteria, which are explained below. Combining these two independent datasets provided a way to cross-validate the chronosequences and verify that the trends observed were independent of sampling time. To our knowledge, this is the first post-beetle chronosequence study that is replicated in both space and time. Addition of the 1981 dataset also helped fill a gap in the 2007 chronosequence between 4 and 26 yr post-beetle.

*2007 chronosequence**Site selection*

Based on aerial detection survey maps (US Forest Service, 1999-2006; National Park Service, 1960-1986) and current forest composition and successional stage maps, we identified potential sites that were either undisturbed or severely impacted by the MPB. All potential sites were visited and inspected for evidence of MPB activity from current (pitch tubes, J-shaped galleries, exit holes, and boring dust) or past (J-shaped galleries and pupation chambers on large downed logs) outbreaks. Pitch tubes, which are accumulations of tree resin at the entrance of boring holes, are a diagnostic sign of *Dendroctonus* bark beetle attack and persist for several years until the bark sloughs off the trees (Safranyik and Carroll 2006). J-shaped galleries and pupation chambers are also specific to *Dendroctonus* beetle feeding but can persist for decades because tree xylem is damaged. Final selection of sites was based on strict criteria to minimize variability in factors other than MPB activity. All sites were homogeneous lodgepole pine-dominated (> 90% basal area) stands (> 1 ha in extent) growing on coarse-textured soils, and showed similar understory composition (mainly sedges, grasses, and shrubs such as *Vaccinium scoparium* and *Shepherdia canadensis*). In addition, all post-outbreak stands had high outbreak severity (> 40% beetle-killed basal area), showed no evidence of other disturbances (including other outbreaks of the MPB) before or after the targeted MPB outbreak, and had approximately the same post-fire stand age at the time of the outbreak (based on increment cores taken on-site and post-outbreak age from aerial detection survey maps). To avoid pseudoreplication due to spatial autocorrelation, selected sites were separated by a minimum of 350 m, a distance at which variance was stabilized according to semivariance analysis of Landsat imagery (results not shown).

Recently infested sites were classified in the red (TSB set at 2 yr) or gray stage (TSB set at 4 yr) if the proportion of gray tree basal area (relative to total beetle-killed basal area) was below or above 30%, respectively (Appendix B). In total, 25 sites were selected, with five replicates of each of the following TSB classes: undisturbed, red stage (1-2 yrs post-outbreak), gray stage (3-5 yrs post-outbreak), 25-yr

post-outbreak, and 35-yr post-outbreak. All sites were selected and sampled during the summer of 2007.

Field sampling

Trees and canopy fuels.—At each site, we established a 50 m × 50 m plot and noted its slope, aspect, and location (Trimble GeoExplorer 3 GPS; > 500 readings differentially corrected, yielding a horizontal precision < 2 m). Within each plot, we recorded canopy trees (i.e., > 1.4 m in height) in three 200 m² subplots: a circular subplot in the center, and two 50 m × 4 m subplots at the West and East sides of the plot (total area sampled = 600 m²). For each tree rooted in the subplots, we recorded tree species, diameter at breast height (dbh; 1.4 m from the ground), status (live, dead standing, or dead downed), foliage condition (green, 0-50% red needles, 51-100% red needles, no needles), and signs of MPB presence (pitch tubes, J-shaped galleries, exit holes, and boring dust for recent outbreaks, and J-shaped galleries and pupation chambers for old outbreaks). In ¼ of each subplot, tree saplings and seedlings (< 1.4 m in height) were described using the same variables used for canopy trees, except that height (nearest 10 cm) was noted instead of dbh. In the West and East subplots, we recorded crown base height for each tree as the distance between the ground and the lowest green or red needles. Crown base height was recorded at a 0.25-m precision from 0 to 1 m, a 0.5-m precision from 1 to 6 m, and a 1-m precision above 6 m.

Surface fuels.—Surface fuels were sampled in ten 10-m long transects (preliminary tests showed no difference in mean or coefficient of variation in the amount of fuels between 10 and 20 transects) using Brown's planar intersect method (Brown 1974). We recorded dead surface fuels that intersected a 2-m high plane in the following diameter classes: 0 - 0.64 cm (1-hour timelag fuels; tallied over the first 2 m of the transect), 0.64 - 2.54 cm (10-hour timelag fuels; tallied over the first 2 m of the transect), 2.54 - 7.62 cm (100-hour timelag fuels; tallied over the first 3 m of the transect), and > 7.62 cm (1000-hour

timelag fuels; diameter measured and decay class recorded over the whole 10-m transect). Duff (organic layer between the mineral soil surface and the litter layer, composed of the fermentation and humus layers) depth and dead fuel depth (distance between bottom of litter layer to top of highest particle in plane) were recorded at two and three locations, respectively, within the first two meters of each transect. Fuel load per area was calculated for each diameter class following Brown (1974).

Understory vegetation.—Understory cover was visually estimated (0-5%, 5-10%, 10-20%, 20-30%, etc.) in 20 circular microplots (0.25-m²) using the following cover classes: grass, sedge, forb, shrub, tree seedling/sapling, tree trunk, litter, bare soil, and rock. When grass, sedge, or shrub cover was greater than 5%, mean height of these plant groups was also recorded in 10-cm classes.

Tree-ring sampling.—We used dendrochronology to determine precise time since beetle outbreak (TSB) and time since stand-replacing fire, and to reconstruct stand conditions at time of outbreak in all chronosequence stands (Appendix A). In each undisturbed, red-, and gray-stage stand, an increment core was taken at 30 cm from the ground on 10 dominant live trees (Kipfmüller and Baker 1998), whereas in the 25- to 35-year post-outbreak stands, increment cores were sampled on 50 live trees and cross-sections were sampled on 20 downed trees showing MPB galleries. Tree cores were mounted on wood sticks, and all cores and cross-sections were finely sanded (400 grit), scanned (1200 dpi) and measured (OSM 3, SCIEM, Brunn am Gebirge, Austria).

To determine year of beetle attack in the 25- and 35-year post-outbreak stands, we cross-dated the 200 cross-sections taken from beetle-killed trees using master chronologies developed from live trees in each stand (chronologies had 6 to 20 tree-ring series, were 115- to 268-yr long, and had an intercorrelation coefficient of 0.35 to 0.56) and the program COFECHA (Holmes 1983). Bark beetle outbreak was identified at each site by a pulse of mortality within a 2-4 yr window period that corresponded with published aerial survey data, and year of outbreak was defined as the year where

cumulative basal area killed of sampled trees exceeded 50% (Appendix A). Post-fire stand age was estimated using the earliest pith date of all tree cores and cross sections in each site. All sites showed a pulse of tree establishment in a relatively narrow time window (~10 years) during which tree growth was not suppressed, indicating synchronous establishment of a post-fire cohort following a stand-replacing fire (Appendix A).

To verify the assumption that all chronosequence sites had similar stand conditions before the outbreak and sustained similar levels of insect damage (Johnson and Miyanishi 2008), we reconstructed pre-outbreak basal area by adding up the basal area of surviving trees minus the basal area grown since the outbreak, and the basal area of beetle-killed trees after adjusting for loss of bark and for shrinking due to loss of water content (Appendix C). Outbreak severity was calculated as the percentage of bark beetle-killed basal area relative to pre-outbreak basal area (see Appendix C for details).

Microscale meteorology.—To quantify the influence of MPB outbreak on microscale meteorology, we deployed temperature and relative humidity probes (iButton, Maxim Integrated Products Inc., Dallas Semiconductor, Sunnyvale, CA) in three sites of each TSB class ($n = 15$ stands in total). At each site, one air temperature and moisture probe encased in a well-ventilated white PVC tube was installed on a tree at 1.5 m from the ground. In addition, temperature probes were installed at the litter-duff interface at three locations within each site. Temperature and relative humidity were recorded every hour with a resolution of 0.5°C and 0.6%, respectively, between June 20 and August 3, 2008. Data from the three litter-duff probes were averaged for each site, and then both air and litter-duff temperature time series were averaged to get average air and litter-duff temperature per site. To highlight the difference in temperature between air and the litter-duff interface, and to account for differences in local temperature between sites, we calculated the difference between litter-duff and air temperature.

*1981 chronosequence**Site selection*

During the summer of 1981, potential chronosequence sites that were either undisturbed or severely affected by the MPB were identified using field surveys and annual reports of the National Park and Forest Service. As for the 2007 chronosequence, all sites were visited and carefully examined for evidence (or lack thereof) of MPB attack (see *2007 chronosequence* above). Each site had to be located within a relatively homogeneous (> 0.5 ha in extent), even-aged, lodgepole pine-dominated ($> 75\%$ of stand basal area in lodgepole pine) forest between 50 and 250 years old and show either low ($< 10\%$ of total basal area affected) or high ($> 30\%$) mortality due to MPB for the undisturbed and post-outbreak stands, respectively. In total, two undisturbed stands and eight post-outbreak stands ranging in TSB from 0 to 18 years were selected and sampled in the summer of 1981. Time since stand-replacing fire was determined from tree-ring dating of synchronous establishment dates of dominant trees, and TSB was determined from growth releases in tree rings of sub-canopy trees that survived the outbreak (Romme et al. 1986, Veblen et al. 1991).

Field sampling

Trees and canopy fuels.—At each site, three belt transects (one in the center and one on either side) were established within a ~ 0.5 -ha plot to survey canopy and sub-canopy trees. Transects were 3 m wide and had a variable length (30 m to 120 m), depending on tree density. Within each belt transect, every canopy tree (dbh > 2.5 cm) was tallied, recording species, dbh, status (live, dead standing, dead downed), presence of MPB pitch tubes, and presence of red needles. Saplings (dbh < 2.5 cm and height > 0.3 m) were measured (to the nearest 30 cm) and described (same variables as above), and seedlings (< 30 cm high) were counted in only one or in all three belt transects, depending on their density. At each site, average cover (%) and height (to the nearest 3 cm) of live ground fuels were noted, and two values of average canopy base height were recorded to the nearest 30 cm: live canopy base height and

dead canopy base height, defined as the vertical distance between surface fuels and the lowest live or dead branch, respectively.

Surface fuels.—Dead surface fuels were described using the same method as outlined above, except that the number and length of transects varied between sites to account for variability in fuel loads. Twenty transects were established in all but one site where 30 transects were sampled. Across all sites, 1-hour and 10-hour timelag fuels were sampled in the first 1.8 to 4.6 m of each transect; 100-hour fuels were sampled in the first 3.7 to 15.2 m; and 1000-hour fuels were sampled in the whole transects, which measured between 12.2 and 24.4 m. In all transects, duff depth and needle depth were noted to the nearest 0.5 cm at two to three locations.

Data pre-processing

Canopy fuel calculations

Crown weight and the proportions of foliage, 1-hour, 10-hour, and 100-hour timelag fuels in the crown were estimated for individual stems using tree dbh measured in the field and allometric equations developed for Rocky Mountain conifers (Brown 1978). To account for loss of foliage in recently killed trees (red and gray stages), foliage weight was multiplied by 0.25 and 0.75 for trees in the 0-50% and 51-100% red needle classes, respectively. Available canopy fuel load was computed for each stand as the sum of foliar biomass plus 50% of the 1-hour timelag fuels, which are generally thought to be consumed during a crown fire (Reinhardt and Crookston 2003, Reinhardt et al. 2006).

Tree height was estimated from dbh using allometrics developed for lodgepole pine (Schlieter 1986, cited in Koch 1996, p. 450) and used to calculate crown length (here and for the rest of the paper, crown is a tree-level attribute and canopy is a stand-level attribute). Vertical profiles of canopy bulk density were then developed for each stand by distributing available crown fuel along the crown of each tree in 0.25-m bins, and summing across trees; the vertical profiles were then smoothed with a 3-m

running mean (Scott and Reinhardt 2001, Reinhardt et al. 2006). This method, which is implemented in the Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS; Reinhardt and Crookston 2003), assumes that canopy fuels are uniformly distributed along tree crowns. Unlike other methods however, it provides an unbiased estimate of canopy bulk density and results in vertical profiles that accurately represent the observed profiles (Reinhardt et al. 2006). For each stand, effective canopy bulk density was calculated as the maximum value of available canopy bulk density, and effective canopy base height was defined as the lowest height in the profile where canopy bulk density exceeded 0.011 kg/m^3 .

Although recently killed (gray stage) trees have less canopy fuels than live trees, their fine twigs (1-hour fuels) contribute to canopy bulk density. However because these trees did not bear foliage, their crown base height was not recorded. To circumvent this shortcoming and incorporate gray-attacked trees in the calculation of canopy bulk density, we developed regression equations between dbh and crown base height for all trees for which both variables were available ($n = 2438$). We used a linear model (PROC GLM, SAS Institute Inc. 2003) with $\ln(\text{crown base height} + 1)$ as the response variable, and $\ln(\text{dbh} + 1)$ and its interaction with site as explanatory variables ($R^2 = 0.69$, $F_{25, 2413} = 543.05$, $P < 0.0001$). The resulting site-specific equations were then used to estimate missing crown base heights ($n = 101$ trees).

Understory fuel calculations

Dry biomass of herbaceous and woody fuels were computed using percent cover data in each site and previously published (Turner et al. 2004) or new (*Shepherdia canadensis*) allometric equations. Equations for the dominant understory species were used to estimate biomass of each of the broad categories: *Calamagrostis canadensis* for grasses, *Carex geyeri* for sedges, *Arnica cordifolia* for forbs, and *Vaccinium scoparium* for shrubs smaller than 20 cm. Cover of shrubs taller than 20 cm were converted to biomass using new allometrics developed for *S. canadensis* ($R^2 = 0.97$). Biomass of

grasses, sedges, and forbs was then summed to obtain live herbaceous fuel load, and that of *Vaccinium* and *Shepherdia* to obtain live woody fuel load.

Fire behavior modeling

We used the fuel data sampled in the field to parameterize the fire behavior model NEXUS and predict potential fire behavior at each site under similar abiotic conditions (wind, slope, fuel moisture, etc.).

NEXUS

NEXUS is a non-spatial deterministic fire modeling system that uses fuel, weather, and topographic inputs to predict stand-level fire behavior and assist in decision-making for fire management (Scott 1999, Scott and Reinhardt 2001). Its basic structure, which is shared among many other models (e.g., BehavePlus, FARSITE, etc.; Scott 2006), includes (1) a surface fire spread module (Rothermel 1972), driven by surface fuel characteristics, slope, and wind speed; (2) a crown fire initiation module (Van Wagner 1977), which depends on surface fire intensity, canopy base height (ladder fuels), and foliar moisture; and (3) a crown fire spread module (Van Wagner 1977, Rothermel 1991a), which depends primarily on surface fire rate of spread, canopy bulk density, and wind speed. In these models, predictions are greatly influenced by fuel type and loads, in contrast with other models such as the Canadian Forest Fire Behavior Prediction System (Forestry Canada Fire Danger Group 1992), which are primarily driven by weather conditions. NEXUS assumes that fuels are homogeneously distributed horizontally, but uses simple metrics to describe their vertical distribution.

Outputs

NEXUS predicts fire type, i.e., surface, passive crown, active crown, and conditional crown fire. Crown fraction burned represents the degree of crowning, i.e., the proportion of canopy fuels consumed

in a fire. It ranges from 0 (surface fire) to 1 (crown fire or conditional fire), with intermediate values characterizing passive crown fires. Rate of spread (km/h) is the speed at which the flaming front moves forward in a direction perpendicular to the perimeter, and heat per unit area (kJ/m^2) is the total amount of energy released per area. Fireline intensity (kW/m), which is the rate of heat release in the flaming front per unit length of fire front, is the product of rate of spread and heat per unit area, and is related to flame length. In NEXUS, the overall rate of spread of the headfire is the average of the surface and crown fire rates of spread, scaled with the crown fraction burned. Since wind speed is highly variable and is a major driver of fire behavior, it can be used as a metric to evaluate thresholds for crown fire initiation and active crown fire spread, all other things being equal. NEXUS computes the Torching Index and the Crowning Index, which are the open wind speed at which torching and crowning respectively occur under a given set of fuel and moisture parameters.

Model parameterization and simulation experiments

We used field data to construct custom fuel models and canopy fuel profiles for each site. Parameters derived from field data included surface fuel loads, fuel bed depth, canopy fuel characteristics, and wind adjustment factor (Table 1). To focus specifically on the effects of stand structure on fire behavior, we kept the slope constant (0%) and set the moisture content of live and dead fuels to conditions characteristic of a dry summer. Although moisture content of dead and live canopy fuels was constant, stand-level canopy moisture content was site-specific, depending on the proportion of live and dead canopy biomass in a stand. Because wind speed is highly variable and can qualitatively change fire behavior, we studied a range of wind speed values (0 to 100 km/h). Finally, to determine the effects of surface fuels on surface fire behavior only, we performed simulation runs in a surface fire-only mode, using data from both datasets. This was necessary because in NEXUS, the overall rate of spread of the headfire (and thus also overall fireline intensity) is the average of the surface and crown fire rates of spread, scaled with the crown fraction burned.

Statistical analyses

To test among-stand differences in stand conditions at time of sampling (live and beetle-killed basal area) and at time of beetle outbreak (pre-outbreak basal area, outbreak severity, and stand age at time of outbreak), we used analysis of variance (ANOVA) on TSB class (undisturbed, red stage, gray stage, 8- to 18-yr post-beetle stands, and 25- to 35-yr post-beetle stands), data source (1981 vs. 2007 data) and their interaction.

We used two statistical approaches to analyze the fuels data. First, to test the short-term effects of beetle outbreak, we used ANOVA to compare the undisturbed, red, and gray stages of beetle outbreak. Because of the significant difference in stand age at time of beetle outbreak between the two chronosequences (see above), we also tested for the effect of data source and its interaction with TSB class. Second, for a longer-term analysis, we used regression to relate fuel characteristics to TSB (as a continuous variable) in beetle-killed stands, while still accounting for data source and its interaction with TSB. We used a similar approach to analyze canopy fuel characteristics and fire behavior indices (Torching Index and Crowning Index) except that data source was not included because canopy data was only available for 2007. Because fire behavior response variables (crown fraction burned, headfire rate of spread, heat per unit area, and fireline intensity) were analyzed with a range of wind speed, we tested differences among TSB classes using ANOVA at four different wind speeds: 20, 40, 60, and 80 km/h. For all statistical analyses, we used a significance level of 5% and log-transformed the data when needed to meet the assumptions of statistical tests. For all ANOVAs, we used Duncan's multiple range test to identify differences among class means, but relied on the P-value of the ANOVA to determine if these differences were significant (Sokal and Rohlf 1995).

RESULTS

Time Since Beetle chronosequence

In total, 10 and 25 sites were sampled in 1981 and 2007, respectively, representing a time-since-beetle (TSB) chronosequence from undisturbed (7 sites) to 36-yr post-outbreak. Tree-ring dating of downed logs bearing beetle galleries confirmed timing of beetle attack in the 25- to 35-yr post-beetle sites, which was evidenced by a pulse of mortality within a narrow time window of 1-4 years (Appendix A). Three sites that were initially selected to represent the 35-yr post-beetle class (based on historical aerial surveys) were in fact attacked in the early 1980s and were re-classified as such, resulting in a slightly unbalanced chronosequence (Appendix B).

At time of sampling, live basal area of beetle-killed stands did not differ among beetle disturbance classes (average = 15 m²/ha) but was about 60% lower on average than in undisturbed sites (average = 35 m²/ha; $R^2 = 0.54$; $F_{4,30} = 9.16$; $P < 0.0001$; Fig. 2, Appendix B). Beetle-killed basal area showed an opposite trend, with significantly lower values in undisturbed stands (average = 1 m²/ha) than in post-outbreak stands (average = 16 m²/ha; $R^2 = 0.87$; $F_{4,30} = 50.62$; $P < 0.0001$). Tree-ring reconstruction of stand structure however indicated that pre-outbreak basal area of all sites was similar, averaging 31 m²/ha ($P > 0.1$; Fig. 3A, Appendix C). Outbreak severity (percent basal area killed relative to reconstructed pre-outbreak basal area) did not differ among beetle-killed stands, where it ranged from 36% to 82%, but was significantly lower in undisturbed sites (average = 3%; $R^2 = 0.87$; $F_{4,30} = 52.05$; $P < 0.0001$; Fig. 3B, Appendix C). Stand age (time since stand-replacing fire) at time of beetle outbreak did not significantly vary with TSB within each chronosequence, but the sites sampled in 1981 were 63 years younger on average than those sampled in 2007 (171 yrs; $F_{1,33} = 12.8$; $P = 0.011$; $n = 35$; Fig. 3C, Appendix A).

Fuel characteristics

Dead surface fuels.—In the first five years following bark beetle outbreak (i.e., red and gray stages), there was no significant change in the load of any of the dead surface fuel categories (1-h to 1000-h timelag fuels) compared to the undisturbed stands (Fig. 4A-D). Needle litter depth in the red stands (average = 2.6 cm) was 60% thicker than in the undisturbed stands and had intermediate values in the gray stands (Fig. 4F). Fuel bed depth and duff depth did not vary between the undisturbed, red stage, and gray stage (Fig. 4E, G). Fuel loads of the generally younger stands sampled in 1981 were about 60% lower than that of the 2007 data for the 1-hr, 10-hr, and 1000-hr fuel categories (Appendix D).

Over the entire post-outbreak chronosequence, the 1-hr fuels decreased from about 1.5 Mg/ha in the red and gray stages to about 1 Mg/ha at 35 yrs post-outbreak (Fig. 4A). The 10-h fuels increased from year 1 to year 18 in the 1981 data, but by 35 years had fallen below the 1-year values (2007 chronosequence). The 100-hr fuels and fuel bed depth showed no trend with time since beetle outbreak. During the same period, coarse fuel loads (1000-hr, diameter > 7.62 cm) tripled, from about 20 Mg/ha in the red stage to about 60 Mg/ha by 35 yrs after outbreak (Fig. 4D), and both litter and duff depth declined by 45-50% between 2 and 35 yrs post-beetle (Fig. 4F, G). Surface fuel loads in the 1-h and 100-h categories were about 55% lower, and litter layer depth was 23% lower in the younger stands of the 1981 dataset than in the 2007 dataset, but the opposite was true for the duff layer, which was about 25% deeper in the 1981 chronosequence.

Canopy fuels and live understory fuels.—Vertical profiles of available canopy bulk density, which were constructed for each stand in the 2007 chronosequence, showed important changes in maximum bulk density (i.e., effective bulk density), total fuel load (i.e., available canopy fuel load), and vertical distribution (effective canopy base height) through the post-beetle sequence of stands (Fig. 5). Canopy base height (average = 3.1m) and sapling density (average = 467 stems/ha) did not change in the first few years following the outbreak, but canopy bulk density and canopy fuel load decreased by 50% from

the undisturbed to the red and gray stages (Fig. 5 and 6). Canopy moisture content dropped from 100% in the undisturbed stands to 63% in the red-stage sites and was 78% in the gray stands. Live herbaceous fuels doubled in the first few post-outbreak years, from 0.8 Mg/ha to about 1.6 Mg/ha, and live woody fuel load was significantly higher in red-stage stands (average = 1.2 Mg/ha) than in the undisturbed stands (average = 0.2 Mg/ha), with gray-stage stands having intermediate values (Fig. 6F, G).

In the longer term, canopy base height decreased substantially from about 3 meters in the red stage to 0 m at 35 yrs post-outbreak whereas sapling density showed the opposite trend, with a ten-fold increase from about 400 to more than 4000 stems/ha (Fig. 5, 6A, B). Canopy bulk density, canopy fuel load, and live woody fuel load did not change between 2 and 35 yrs post-beetle (Fig. 6D, E, G), but remained below the values in the undisturbed stands. During this period, live herbaceous fuels continued to increase (Fig. 6F) and canopy moisture content returned to pre-outbreak values (Fig. 6C).

Microclimate

Temperature differed little between air and the litter-duff interface at the undisturbed sites, whereas in red and gray sites, the litter and duff layers were about 2°C cooler than air (Fig. 7). In contrast, the litter-duff interface was 2.5°C warmer than air in sites that were infested 25 years ago. When only mid-afternoon temperatures were considered, the overall pattern remained but temperature differences were amplified in the old attacks, where litter and duff were more than 10°C warmer than air (Fig. 7B).

Fire behavior

Simulation results suggested that in the short term, undisturbed, red, and gray stands were unlikely to torch, with Torching Index values (wind speed needed to initiate torching) well above 100 km/h (Fig. 8). In the long term (2 to 36 yrs post-outbreak), Torching Index was reduced to zero at 35 yrs post-beetle, indicating that in these stands, passive crown fires may be initiated even without wind. Crowning

Index (the wind speed needed to sustain an active crown fire) was higher in gray-stage sites (71 km/h) than in undisturbed sites (39 km/h), with intermediate values in the red-stage sites (61 km/h), suggesting that the immediate effect of MPB outbreak was to greatly reduce the probability of active crown fire, because wind speeds above 60 km/h are rarely observed (Rothermel 1991b). In subsequent decades, Crowning Index did not change, with an average value of 71 km/h (Fig. 8B).

Simulated fire behavior was qualitatively different among the TSB classes but these differences were sometimes overridden by the effect of wind speed. At wind speeds below 40 km/h, the undisturbed, red and gray stages, and 25-yr post-beetle stands were all predicted to have surface fires whereas for the 35-yr post-beetle stands, passive crown fires were predicted (Fig. 9A). At these wind speeds, simulated fire rate of spread and fireline intensity were low (< 0.25 km/h and < 1000 kW/m, respectively) in all TSB classes and heat per unit area was not different among classes, with an average value of 7000 kJ/m².

For wind speeds between about 40 and 60 km/h, the overall effect of bark beetle outbreak was to reduce the predicted probability of crown fire in the short term compared to the undisturbed stands (Fig. 9). Striking differences in simulated fire behavior were observed between the undisturbed and the red- and gray-stage sites, which were respectively predicted to have conditional vs. surface fire, crown fraction burned of 0.58 vs. 0.06 (-90%), headfire rate of spread of 0.89 vs. 0.13 km/h (-85%), heat per unit area of 22,300 vs. 7,300 kJ/m² (-67%), and fireline intensity of 8300 vs. 600 kW/m (-93%) at 40 km/h (Fig. 9). The 25- and 35-yr post-beetle stands were predicted to have passive crown fires and had values of crown fraction burned, rate of spread, heat per unit area, and fireline intensity that were intermediate between the undisturbed and the red and gray classes. Consequently, for all fire behavior metrics, the predicted long-term trend from undisturbed to 35-yr post-outbreak stands suggested a sharp decline in fire activity in the red and sometimes gray stages followed by a gradual return toward pre-outbreak values.

At very high wind speeds (> 60 km/h), most predicted differences among TSB classes disappeared, with all classes having either conditional (undisturbed, red, and gray stands) or active (25- and 35-yr-old attacks) crown fires, and having a similar crown fraction burned and headfire rate of spread. Simulated heat per unit area and fireline intensity showed a trend similar to that observed between 40 and 60 km/h, with a decline in the red and gray stands followed by a return toward pre-outbreak values.

When the fire behavior model was run in a surface fire-only mode, there was no significant difference between TSB classes or datasets for predicted headfire rate of spread, heat per unit area, and fireline intensity at any of the four simulated wind speeds (Appendix D).

DISCUSSION

Bark beetles and fire as linked disturbances

The results of this study indicate that mountain pine beetle (MPB) and fire are linked disturbances in Greater Yellowstone, and that the interaction was a negative feedback in which probability of active crown fire appeared to be reduced. Over the short term (1-2 yrs post-outbreak), we had hypothesized that MPB outbreak would increase probability of active crown fire because dead foliage is still in the canopy and is very dry (Fig. 1 and 10). Estimated canopy moisture content was indeed reduced to about 63% of its pre-outbreak value, but neither torching nor crowning was predicted to increase, probably because canopy moisture in fire behavior models has a relatively small effect compared to other variables. The primary driver of crowning is canopy bulk density (Van Wagner 1977), and post-outbreak reduction of canopy fuels is the most likely mechanism of reduced probability of active crown fire in both red and gray-stage sites. Our field data revealed a 50% reduction in canopy bulk density in these stands compared to undisturbed stands, and simulation modeling predicted a reduced probability of active crown fire. Dead needle fall is already occurring in the red-needle stage, consistent with our field observations of mortality occurring over a number of years. Although individual trees are clearly in the green, red, and gray stage, whole stands cannot be classified as neatly in these stages and usually

have a mixture of green, red, and gray trees in different proportions. Contrary to canopy bulk density, canopy base height did not change in the short term because of the lagged response of understory tree growth. Consequently, predicted probability of torching also did not differ between the undisturbed, red, and gray-stage stands because torching is directly, although not exclusively, related to canopy base height.

Contrary to our hypothesis (Fig. 1 and 10) and to the findings of other studies (Page and Jenkins 2007a, Jenkins et al. 2008) but consistent with Klutsch et al. (2009), we did not observe a short-term increase in dead surface fine fuels or fuel bed depth in the gray-stage stands (3-5 yrs post-outbreak). Dead surface fuel loads were highly variable among stands of the same TSB class and throughout the chronosequence, even though all stands were similar in age and pre-outbreak conditions, and sustained a comparable disturbance severity. This variability is typically observed in the field and suggests that our chronosequence adequately captured the natural heterogeneity in stands of the same TSB class. Despite this variability, we detected strong trends in crown fire behavior, which suggests that our overall conclusions are robust. Live understory fuel loads, particularly herbaceous fuels, and needle litter depth increased in the short term as hypothesized. However, predicted surface fire intensity and rate of spread (for simulations run in surface fire-only mode) did not differ between TSB classes, suggesting that these changes in live understory fuels were inconsequential for surface fire behavior. Significantly deeper needle litter found in the red stands could produce somewhat different fire behavior in real forests, but did not affect our results because this variable does not contribute to surface fire spread in fire behavior models (Rothermel 1972, Scott and Reinhardt 2001). Our hypothesis of predicted increased surface fire intensity in the gray stage was thus not supported (Fig. 10). However probability of active crown fire was predicted to decrease in gray-stage stands, as hypothesized, because canopy bulk density was still low.

Predicted fire behavior in the decades that followed the outbreak (25-35 yrs post-outbreak) was qualitatively different than at the early stages of the outbreak. As hypothesized (Fig. 1 and 10), passive

crown fires were predicted to be the norm in the 25- and 35-yr post-outbreak stands because post-disturbance release of understory saplings provided ladder fuels that greatly reduced canopy base height. However, canopy bulk density was still low and thus model simulations did not predict crowning – only passive crown fires were predicted. Because of the lower mass and density of canopy fuels in the old stands, predicted fire intensity and energy released (heat per unit area) were lower than in undisturbed stands.

In light of these results, we revise our hypothesized trends in potential fire behavior (Fig. 10) as follows. Following MPB outbreak, (1) probability of active crown fire is reduced in the short-term and for up to 35 years after outbreak; (2) probability of passive crown fire does not change in the short term but greatly increases in the decades following the outbreak; and (3) probability of surface fire remains unaffected.

Effects of bark beetle outbreaks on microclimate

In addition to their direct effect on forest fuels, beetle outbreaks modify the microclimate of affected stands by opening the canopy, which may indirectly affect fire behavior. Compared to undisturbed stands, the litter-duff interface in the red- and gray-stage stands was much cooler than air, a difference likely caused by the insulating effect of the thick needle litter layer from dead needle fall. In contrast, the litter-duff interface in stands 25-35 yrs post-outbreak was warmer than air, likely as a consequence of two related mechanisms. First, because beetle-killed trees in these stands have fallen to the ground, solar radiation may be higher than in the red or gray stages, although we did not measure this variable. Second, the shallower litter and duff layers in these stands provide less insulation. The warmer temperatures in these stands may lead to reduced moisture content in surface fuels. The extent to which these modifications to stand and surface fuel microclimate affect fire behavior is not clear because we purposefully did not use the temperature data as inputs in our simulations, in order to be able to focus specifically on the effects of stand structure on fire behavior. However, we speculate that

moister surface fuels in the red and gray-stage stands may reduce surface fire intensity and rate of spread, and that dryer fuels in the old attacks would have the opposite effect. This would contribute to reduced probability of surface fire in the red and gray stands and higher probability of torching and passive crown fires in the old stands.

Relationship to other studies

Our results are generally in line with those of the few other prospective studies on the effects of bark beetle outbreaks on potential fire behavior, which have found reduced probability of crowning in all post-outbreak stands and increased probability of torching in older post-outbreak stands of lodgepole pine, Douglas-fir, and Engelmann spruce (Page and Jenkins 2007a, b, Jenkins et al. 2008, Deroose and Long 2009). Contrary to our findings, some of these studies also found a consistent increase in surface fine fuels in the red and gray stages of beetle outbreak, and associated this change with a potential for increased surface fire intensity and rate of spread (Page and Jenkins 2007a, b, Jenkins et al. 2008). It is impossible to determine whether this increase in surface fire intensity would have resulted in a change in fire type because the probabilities of torching and crowning were not examined.

Our prospective fire modeling results also agree with some long-term retrospective studies in spruce-fir forests of Colorado, which generally do not support the hypothesis of increased probability of stand-replacing crown fire following bark beetle outbreak (Bebi et al. 2003, Kulakowski et al. 2003, Kulakowski and Veblen 2007). Similarly, in lodgepole pine forests, Kulakowski and Veblen (2007) did not find higher occurrence or severity of fire in 5-yr post-beetle stands. At first glance, our results may appear to disagree with those of Bigler et al. (2005), who found a slightly elevated probability of high-severity burns 60 years after beetle outbreak, and Lynch et al. (2006), who found that the 1988 fires in Yellowstone National Park were slightly more likely to occur in areas that were disturbed by the MPB in the 1970s (about 15 yrs post-beetle) but not in the 1980s (about 7 yrs post-beetle). However, these seemingly contradictory results may agree with our modeling results when time since beetle outbreak

and fire behavior are both considered. In Bigler et al. (2005) and Lynch et al. (2006), elevated probability of fire occurrence was observed at post-beetle periods (60 and 15 yrs, respectively) characterized, according to our simulations, by higher probability of torching and passive crown fire. Furthermore, Lynch et al. found no effect of beetle outbreak on fire incidence in 7 yrs post-outbreak stands, in agreement with our simulation results (Fig. 10B). On the other hand, Turner et al. (1999) found that 7 to 15 yrs following MPB outbreak, probability of severe fire increased with severe MPB damage and in late-successional stands. However because beetle damage and successional stage are intercorrelated and were analyzed independently, it is not possible to untangle the respective effects of each. Given the paucity and mixed results of studies in lodgepole pine forests, there is a need for further bark beetle-fire interaction research in this forest type, which represents one of the most dynamic crown fire-dominated ecosystems in North America.

Assumptions, limitations, and uncertainties

Both retrospective and prospective approaches have their advantages and shortcomings. Retrospective analysis of past fires describes actual fire events but does not allow control of weather or of most pre-fire conditions, and the fire events represent only one realization of multiple possible outcomes. Furthermore, retrospective analysis of fire events generally does not allow the discrimination of active and passive crown fires. Fire behavior modeling parameterized with field data has the advantages of allowing control of weather conditions and incorporating the mechanisms that link beetle-caused changes in forest structure with fire behavior. However, predictions are influenced by the quality of input data. In this study, we validated our chronosequence in multiple ways to and ensure that it adequately represented the time sequence that each beetle-killed stand would follow. A central (but often unverified) assumption in chronosequence studies is that stands only differ by time since disturbance, and therefore should have similar pre-disturbance conditions and disturbance severity (Johnson and Miyanishi 2008). Contrary to previous bark beetle prospective studies, we were able to

determine timing of beetle attack and post-fire stand age accurately, and to reconstruct pre-outbreak conditions using dendrochronology. This analysis confirmed that stands in different TSB classes had similar pre-outbreak basal area, sustained a similar outbreak severity, and within each chronosequence had the same post-fire age at time of beetle outbreak (Fig. 3, Appendix A, C). In addition, our chronosequence was replicated in space (many replicates per TSB class) and time (two independent sampling campaigns: 1981 and 2007), which to our knowledge has never been done in post-disturbance chronosequence studies. Although the stands in the 1981 dataset were younger (post-fire age at time of beetle outbreak) and consequently had lower fuel loads than those sampled in 2007, both series generally displayed consistent trends with time since beetle outbreak. These multiple lines of evidence suggest that the chronosequence and the results derived from it are robust.

An important assumption in current fire behavior models is that all foliage and half of the fine (1-hour) canopy fuels are consumed during a crown fire (Reinhardt and Crookston 2003). While this may be a reasonable assumption for live trees, these values may underestimate canopy consumption in dead trees, which would in turn underestimate heat per unit area and fireline intensity in the red and gray-stage stands. However, our own calculations indicated that predictions of fire indices (Torching and Crowning Index) and fire type were fairly robust to these assumptions, and that the trends observed here did not change even when assuming that all 1-hour and 10-hour fuels are available for consumption (Appendix E).

Another uncertainty about bark beetle effects on fire behavior is how soil heating is affected by large-diameter downed wood in old beetle kills. It is often thought that the abundance of these fallen snags may increase soil heating by smoldering, therefore increasing potential damages to soil biota. However, very little is known about the effects of large fuels on the duration of post-frontal combustion, and current models do not consider either the load or moisture content of 1000-hr fuels to calculate soil heating when duff is present (Reinhardt et al. 1997). Field measurements of soil heating in several different crown fires suggest that excessive soil heating ($> 60^{\circ}\text{C}$) may be uncommon in subalpine and

boreal ecosystems (J. Reardon, *pers. comm.*). In these forests, the mineral soil may be insulated from heat by the unburned duff layer, and sometimes by the ash created by the fire itself and consequently, only a few centimeters at the surface of the mineral horizon may have substantial heating. Additionally, coarse fuel loads in old post-outbreak stands are high but cover a relatively small surface area (< 10% cover in our plots), so even if substantial heating occurs, it may have a relatively small impact at the stand scale. Clearly, this area of research needs more attention.

When does bark beetle-caused mortality matter for fire behavior?

Fire behavior in this study was little affected by beetle disturbance when wind speed was either below 40 km/h or above 60 km/h. Under low wind speed conditions, most stands were predicted to have surface fires, whereas at very high wind speeds, all stand types eventually achieved crowning. This suggests that beetle outbreaks may influence fire behavior only under certain intermediate weather conditions, or at least under intermediate wind speeds. This scenario is somewhat analogous to the situation that occurred during the 1988 fires in Yellowstone National Park, when forest type influenced the spread of early season crown fires when fire weather was moderate to severe but had little effect during the late-summer fires that burned under extreme conditions (Renkin and Despain 1992, Turner et al. 1994). So when does stand structure in general, and bark beetle-caused mortality in particular, really matter? The relative importance of fuels and weather in explaining fire activity has been debated for some time, but evidence in coniferous subalpine forests points toward climatic control of wildfire area burned at broad scales and control of fire behavior by weather at finer scales (Bessie and Johnson 1995, Schoennagel et al. 2004, Littell et al. 2009). Our study supports this idea with its finding that variability in wind speed had a greater effect on fire behavior than beetle-caused changes in stand structure for the fuel moisture conditions used in this study. Fire behavior models based on Rothermel's (1991a) equations, including the one that was used in this study, can only predict fire behavior of wind-driven fires, and not of the more intense plume-dominated fires, during which forest structure attributes appear

to have even less influence on fire behavior. Consequently, predictions from these models represent only a portion of the whole range of fire behavior observed in nature. Future research on bark beetle-fire interactions should concentrate on the actual probability within a given fire year that the structure of beetle-killed stands has an influence on fire behavior, and on the potential consequences of these interactions on wildfire area burned.

This study has shown that a linked disturbance interaction likely exists between MPB outbreaks and wildfire in lodgepole pine forests of the Greater Yellowstone Ecosystem. The direction of the interaction is opposite to what is widely presumed by the public, in that our study predicts a reduction in most measures of fire intensity for up to 35 years after a beetle outbreak, including a reduced probability of active crown fire. Our results also underscore the fact that weather conditions during a burn may have a greater influence than fuel characteristics on fire behavior and effects. This study combined a replicated and validated chronosequence, which provided an empirical characterization of changes in surface and canopy fuels during 35 years after MPB outbreak, with simulations of potential fire behavior under a range of fire weather conditions. Our overall conclusion was that the linkage of prior MPB disturbance to future fire disturbance generally results in a dampening rather than an amplification of fire behavior and intensity. Explicit consideration of time since disturbance (e.g., TSB), environmental context (e.g., weather conditions), and underpinning mechanisms (e.g., fire behavior) is essential to understand and predict linked disturbances.

ACKNOWLEDGEMENTS

We wish to thank our field crew J. Entringer, L. Marescot, S. Nikiforov, R. Peaslee, and G. Skupien (U. of Wisconsin) for their tireless work in the field, E. Mellenthin, M. Fork, and R. Peaslee for laboratory work, and J. Klaptosky (Yellowstone NP) for his assistance in collecting tree-ring samples. We also thank D. Tinker, K. Raffa, P. Townsend, R. Renkin, B. Hawkes, T. Schoennagel, T. Veblen, M. Rocca, and H. Lynch for fruitful discussions on bark beetle – fire interactions, Yellowstone National

Park and Bridger-Teton National Forest staff for their support and assistance, Roy Renkin (Yellowstone NP) for logistic support and for the opportunity to see the extent of bark beetle outbreaks from the air, and Hank Harlow and the University of Wyoming-National Park Service Research Station for logistical support during the field season.. Funding for this study was provided by the Joint Fire Science Program, the Andrew W. Mellon Foundation, the USFS Western Wildland Environmental Threat Assessment Center (WWETAC), Le Fonds Quebecois de Recherche sur la Nature et les Technologies (FQRNT) and the University of Wisconsin-Madison. Finally, we thank K. Raffa and S. Gauthier for constructive reviews that improved this paper.

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TABLES

Table 1. Parameters used for fire behavior modeling

Parameter	Units	Value
Surface Fuels (Custom Fuel Models)		
1-hour timelag fuel load	Mg/ha	field
10-hour timelag fuel load	Mg/ha	field
100-hour timelag fuel load	Mg/ha	field
Live herbaceous fuel load	Mg/ha	field
Live woody fuel load	Mg/ha	field
1-hour fuel surface area to volume ratio	m ² /m ³	6562 ^a
Live herbaceous surface area to volume ratio	m ² /m ³	4921 ^a
Live woody surface area to volume ratio	m ² /m ³	4921 ^a
Fuel bed depth	m	field
Dead fuel moisture of extinction	%	25 ^a
Dead fuel heat content	kJ/kg	18 622 ^a
Live fuel heat content	kJ/kg	18 622 ^a
Canopy Fuel Characteristics		
Canopy base height	m	field
Available canopy bulk density	kg/m ³	field
Available canopy fuel load	Mg/ha	field
Fuel moisture		
1-hour timelag fuel moisture	%	5
10-hour timelag fuel moisture	%	6
100-hour timelag fuel moisture	%	7
Live herbaceous moisture	%	70
Live woody moisture	%	100
Foliar moisture	%	5 (red foliage) 100 (green foliage) ^b
Weather		
Open wind speed	km/h	0-100
Wind adjustment factor	-	0.1 to 0.2 (field) ^c
Terrain		
Slope steepness	%	0

^a From fuel model 10 (timber litter and understory, Anderson 1982);

^b Calculated as the average of red (5%) and green (100%) canopy moisture content, weighted by their respective biomass;

^c Calculated from field-based measurements of canopy cover and lookup tables in NEXUS, which are based on Albini and Baughman (1979), Rothermel (1983), and Finney (1998).

FIGURE CAPTIONS

Figure 1. Description of hypothesized mechanisms through which bark beetle outbreak could affect fuel characteristics and potential fire behavior compared to undisturbed stands. MC, moisture content; RoS, rate of spread; temp., temperature.

Figure 2. (A) Live and (B) beetle-killed basal area (± 1 standard error) at time of sampling in the 2007 and 1981 chronosequence sites ($n = 35$). Uppercase letters above each bar indicate ANOVA results testing differences in means among classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 5\%$).

Figure 3. (A) Reconstructed pre-outbreak basal area, (B) outbreak severity, and post-fire stand age at time of beetle outbreak in the chronosequence sites sampled in 2007 ($n = 25$) and 1981 ($n = 10$). Data points at the left of the dashed line (time of outbreak) represent undisturbed sites and are offset for clarity. Superimposed data points are indicated with " $n =$ ". P -values associated with the effects of time since beetle (TSB) class, dataset (1981 vs. 2007 data), and their interaction are shown, but the interaction term is only shown when significant.

Figure 4. (A-D) Fuel load of dead surface fuels in the 1-h to 1000-h size categories, and depth of (E) fuel bed, (F) needle litter layer, and (G) duff layer in the chronosequence sites ($n = 35$). Left panels show means and standard error for the undisturbed, red-stage, and gray-stage stands only. Uppercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 5\%$). Right panels show the relationship between each fuel category and time since beetle for beetle-killed sites only. P -values associated with the effects of time since beetle (TSB), dataset (1981 vs. 2007 data), and

their interaction are shown, but the interaction term is only shown when significant. The “(+)” or “(–)” symbols following TSB effect indicate the sign of the slope when significant ($\alpha = 5\%$). Note that the y-axes in the left and right panels have different ranges.

Figure 5. Vertical profiles of available canopy bulk density in the 2007 chronosequence sites (solid lines; $n = 25$). The vertical dotted line represents the 0.011 kg/m^3 density threshold above which fire can propagate and that determines the effective canopy base height.

Figure 6. (A) Effective canopy base height, (B) density of saplings ($0 \text{ cm} < \text{dbh} < 7.5 \text{ cm}$), (C) canopy foliar moisture content, (D) effective canopy bulk density, (E) available canopy fuel load, (F) live herbaceous fuel load, and (G) live woody fuel load in the 2007 chronosequence sites ($n = 25$). Left panels show means and standard error for the undisturbed, red-stage, and gray-stage stands only. Uppercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 5\%$). Right panels show the relationship between each canopy characteristic and time since beetle for beetle-killed sites only. *P*-values associated with the time since beetle (TSB) effect are shown. The “(+)” or “(–)” symbols following TSB effect indicate the sign of the slope when significant ($\alpha = 5\%$). Note that the y-axes in the left and right panels have different ranges.

Figure 7. (A) Daily mean and (B) mid-afternoon temperature difference between the litter-duff interface and air during the 2008 growing season (common period: June 20 – August 3) in the 2007 chronosequence sites. Bars indicate the average of 3 (undisturbed and gray stage), 4 (red stage), or 6 (25-yr-old attack) sites, and error bars represent 1 standard error. Uppercase letters above each bar indicate ANOVA results testing differences in means among classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 5\%$).

Figure 8. (A) Torching and (B) Crowning Index values in the chronosequence sites ($n = 25$). Left panels show means and 1 standard error for the undisturbed, red-stage, and gray-stage stands only. Uppercase letters above each bar indicate ANOVA results testing differences in means among the three classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 5\%$). Right panels show the relationship between each Index and time since beetle for beetle-killed sites only. P -values associated with the time since beetle (TSB) effect are shown. The “(–)” symbol following TSB effect indicate the sign of the slope when significant ($\alpha = 5\%$). Superimposed data points are indicated with “ $n =$ ”. Note that the y-axes in the left and right panels have different ranges.

Figure 9. Fire behavior simulation results for the five time-since-beetle (TSB) classes in the chronosequence sites. Left panels show change in fire behavior metrics with open wind speed for each TSB class (lines). Each line represents the result of one simulation using the average fuel loads for that class. Right panels show means and standard error of each fire behavior metric for each TSB class at 20, 40, 60, and 80 km/h wind speeds. Each bar represents the average of five simulations (one per site) per TSB class. Lowercase letters above each bar indicate ANOVA results testing differences in means among the TSB classes; means with different letters are significantly different (Duncan's multiple range test; $\alpha = 5\%$). P -values associated with the ANOVA are shown. For Crown fraction burned (A), uppercase letters on each bar indicate predicted fire type from simulation results in the left panel (S = surface fire, P = passive crown fire, A = active crown fire, C = conditional crown fire). Note that the y-axes in the different panels have different ranges.

Figure 10. (A) Hypothesized and (B) modeled net relative change in probability of different fire types relative to pre-outbreak levels (fine dotted line).

FIGURES

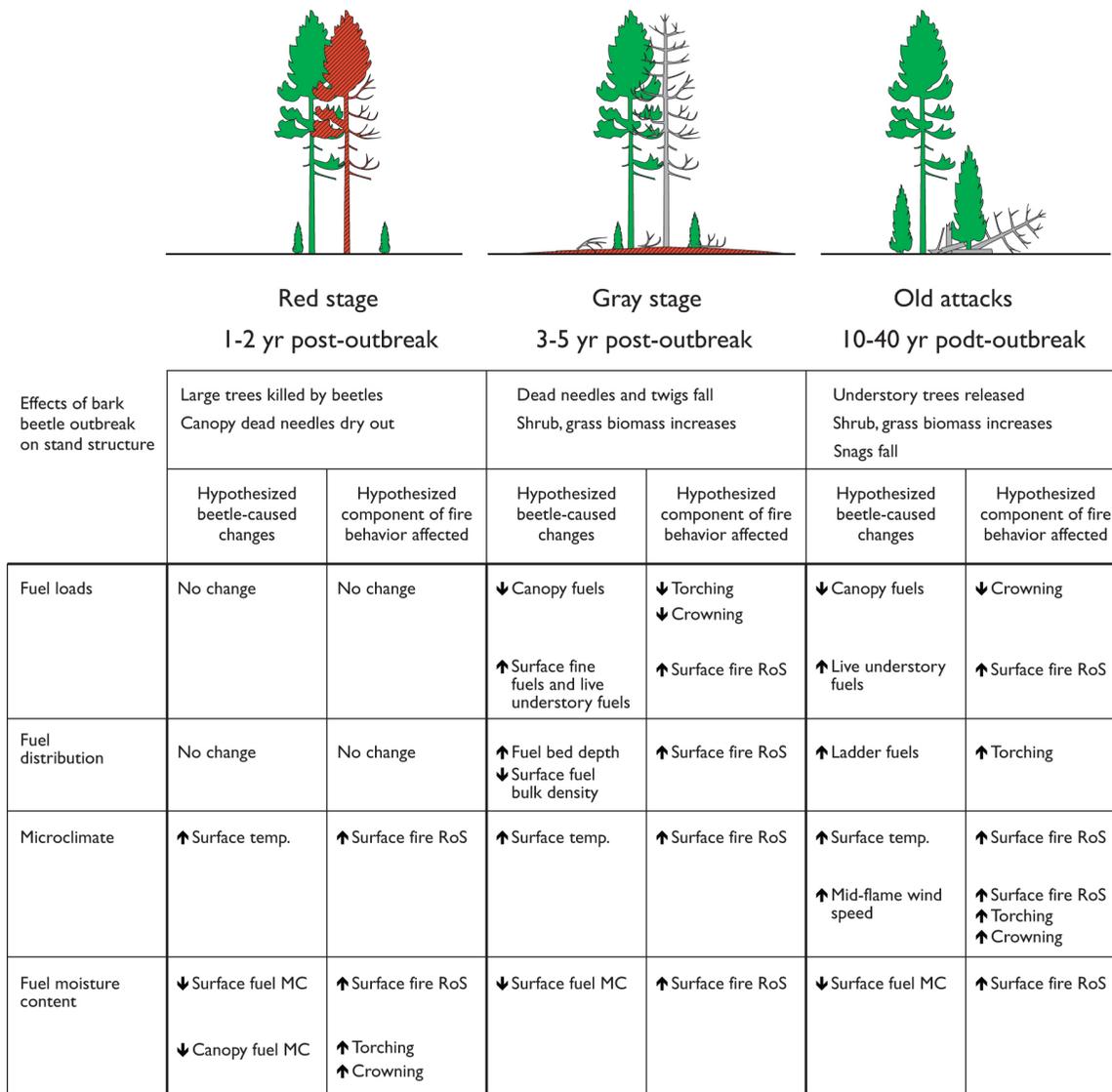


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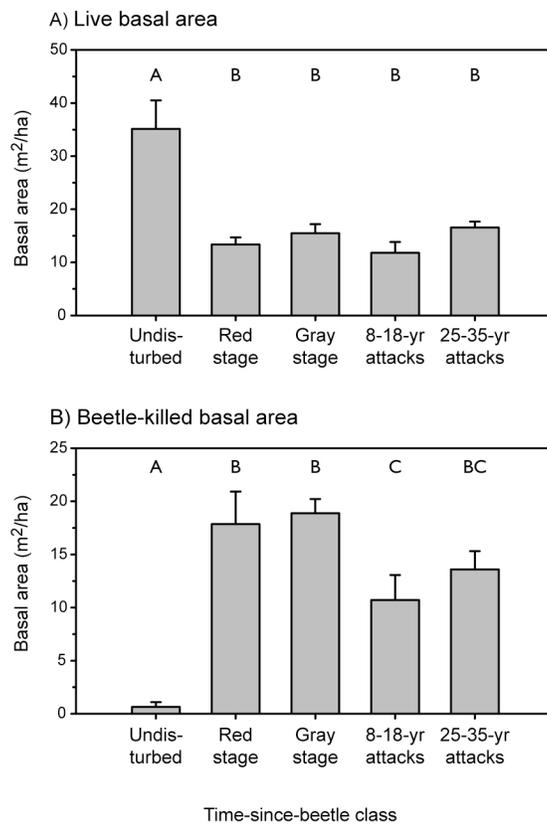


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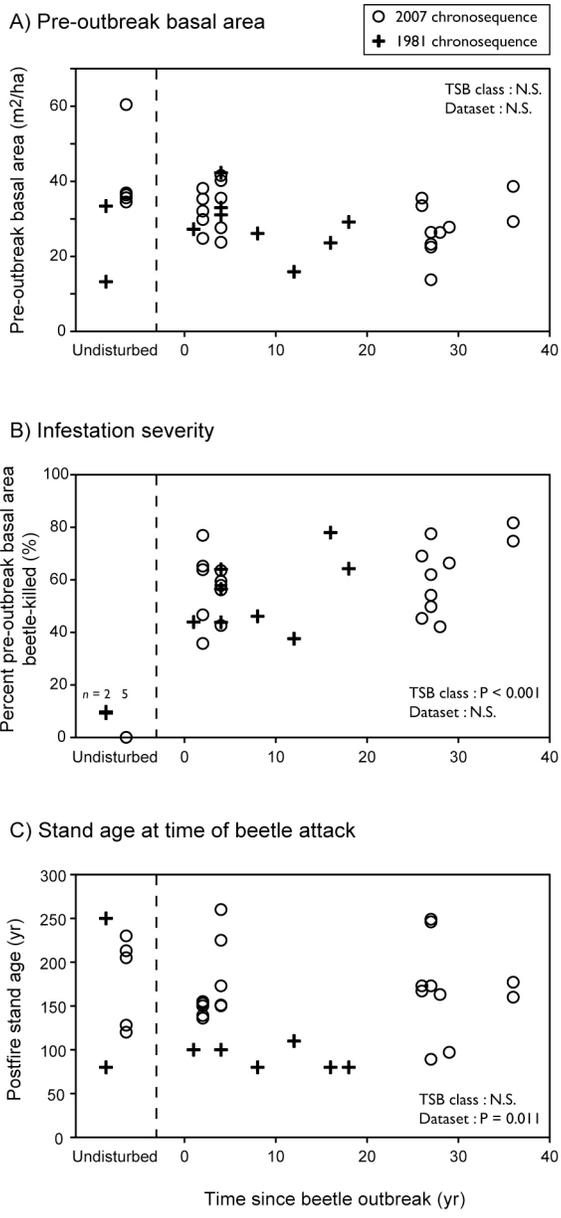


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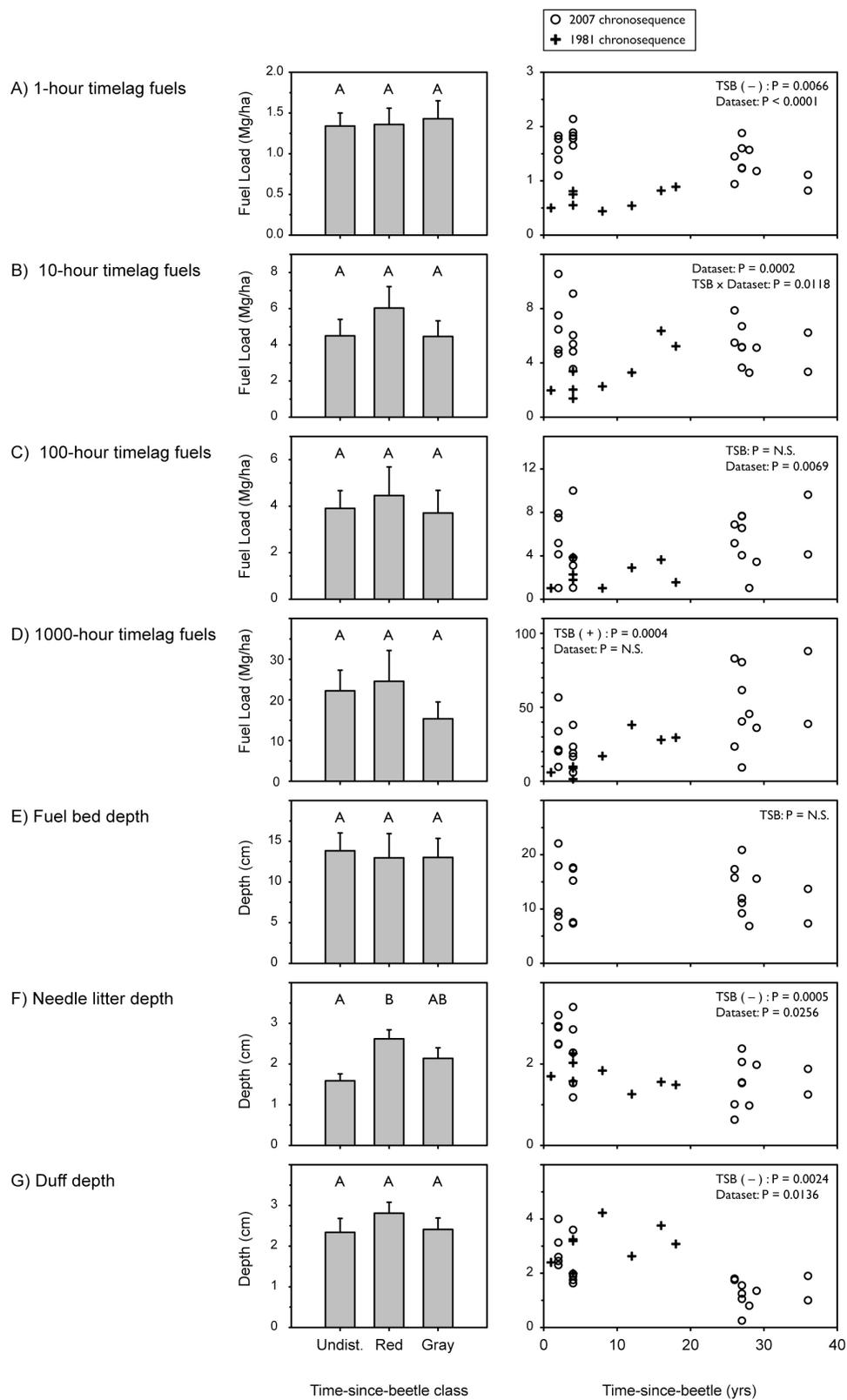


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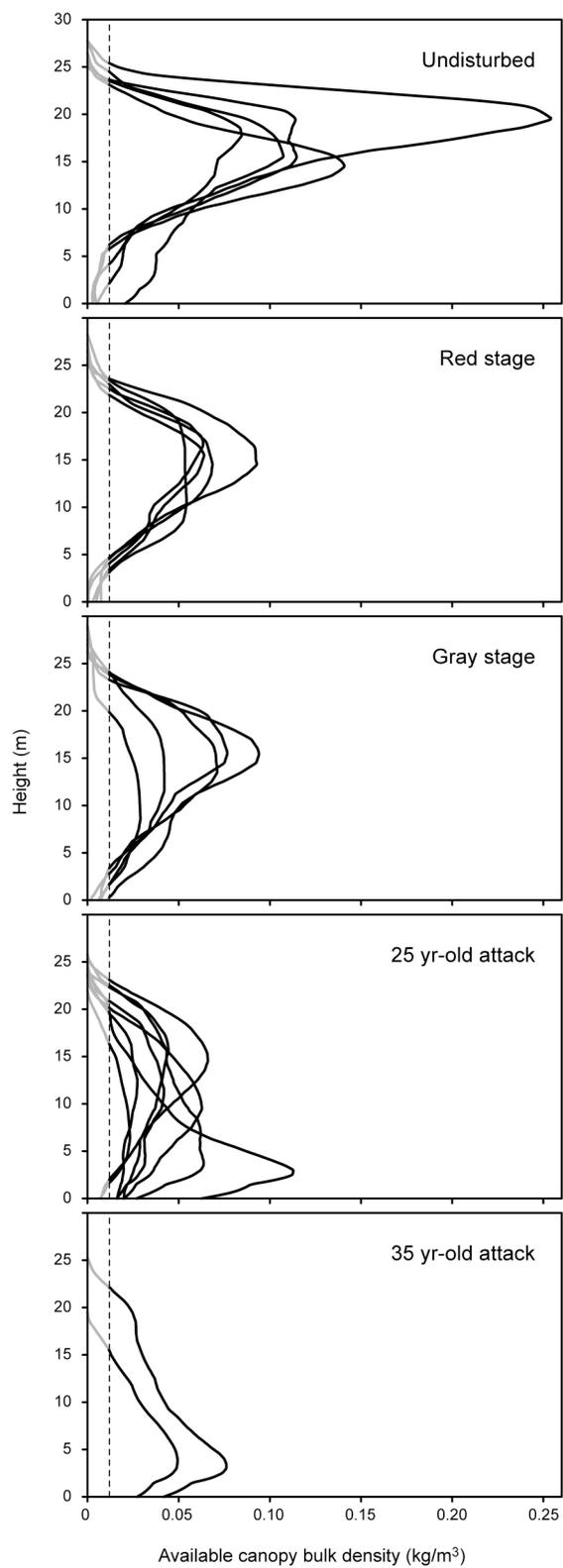


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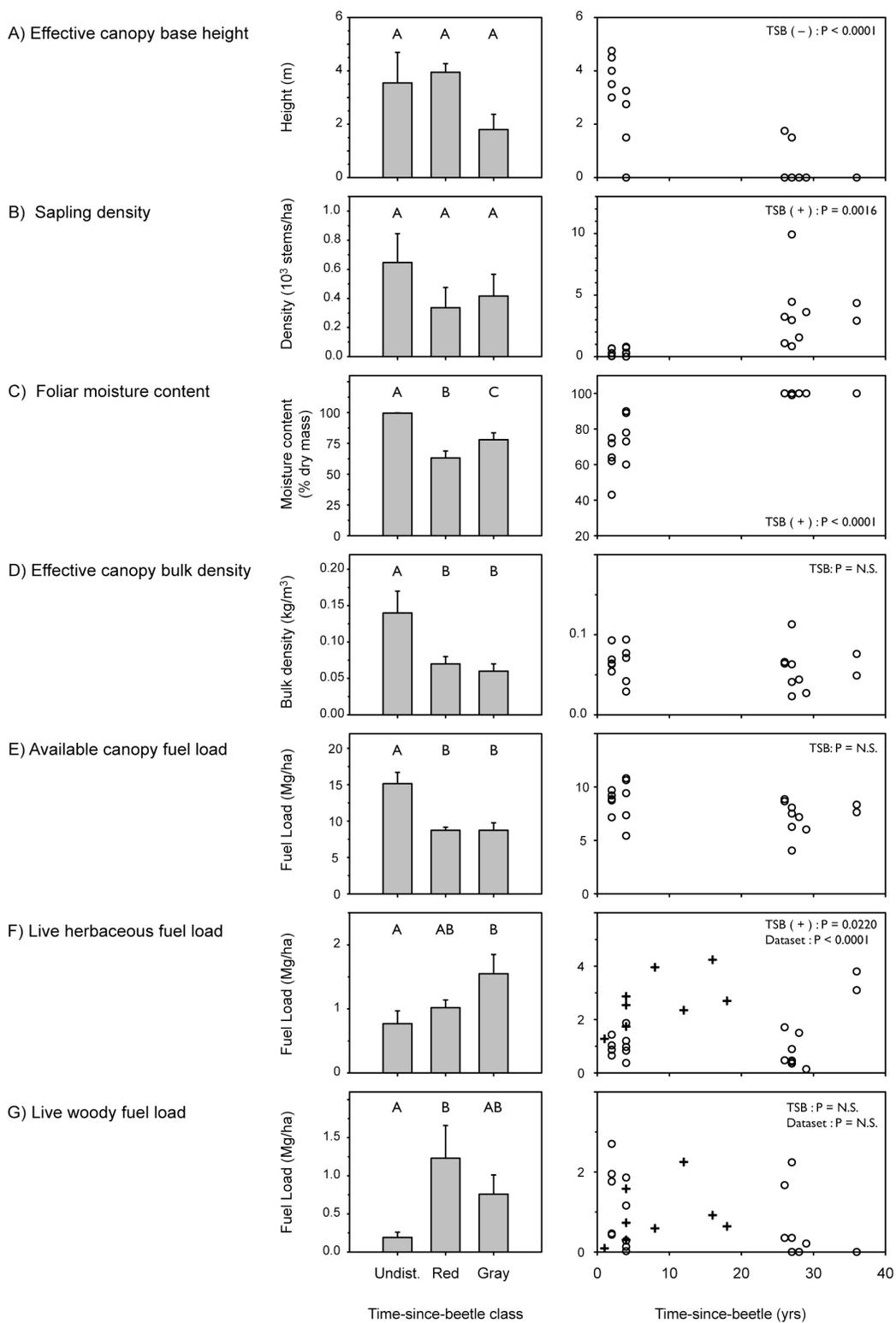


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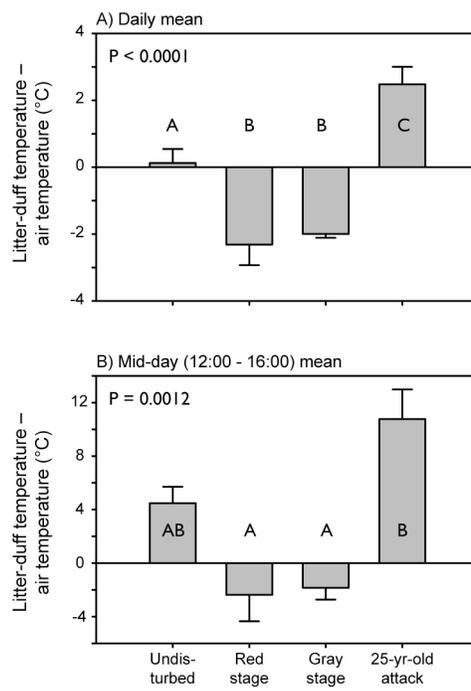


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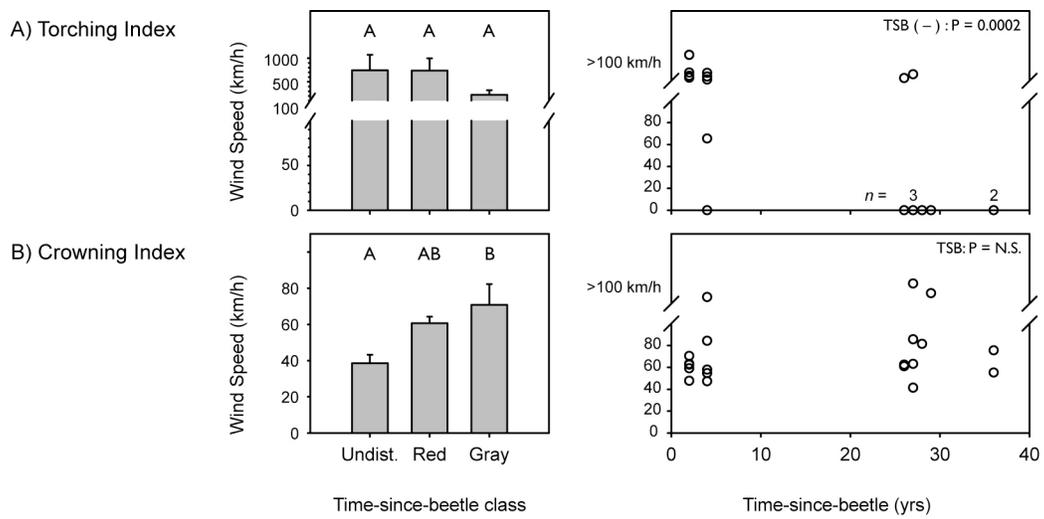


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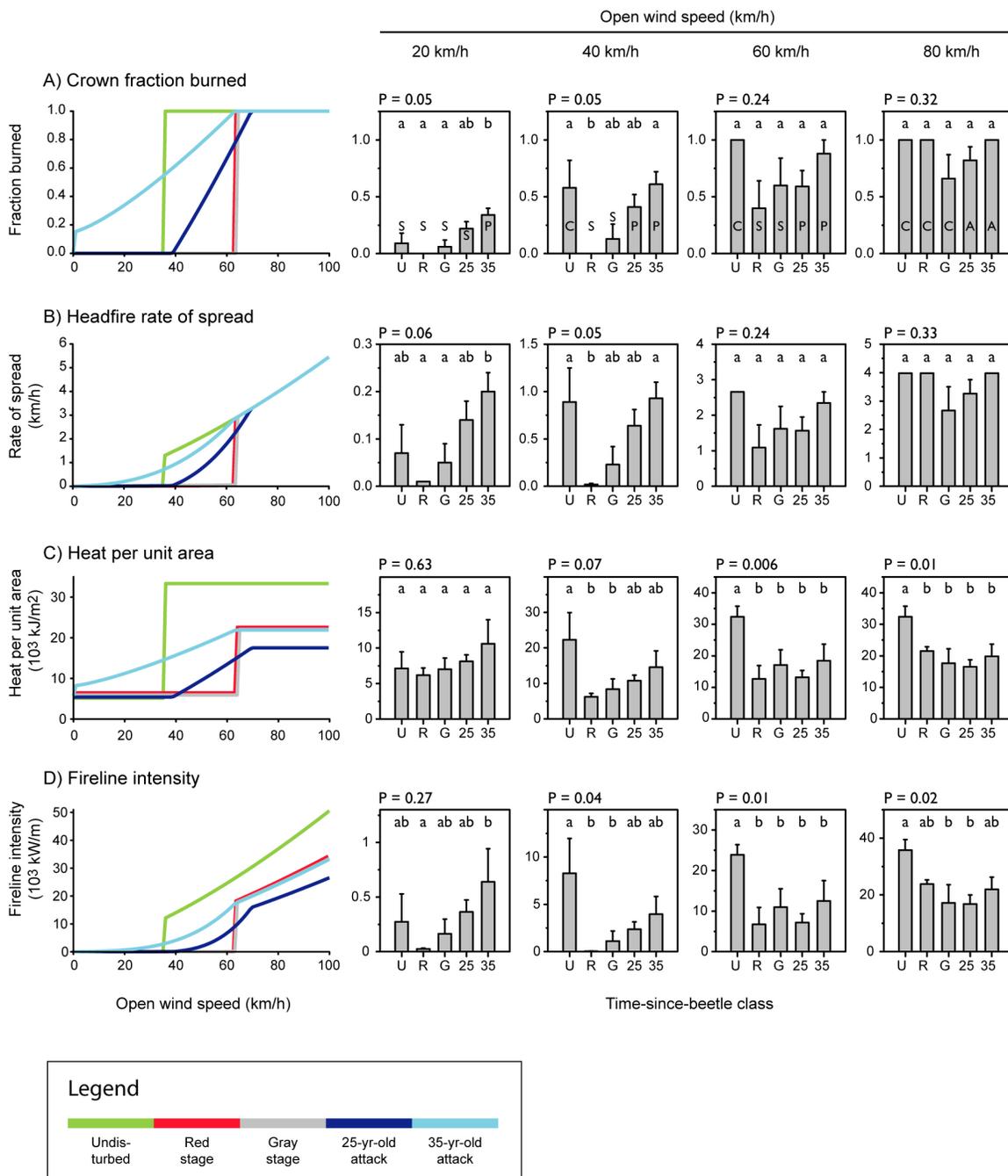
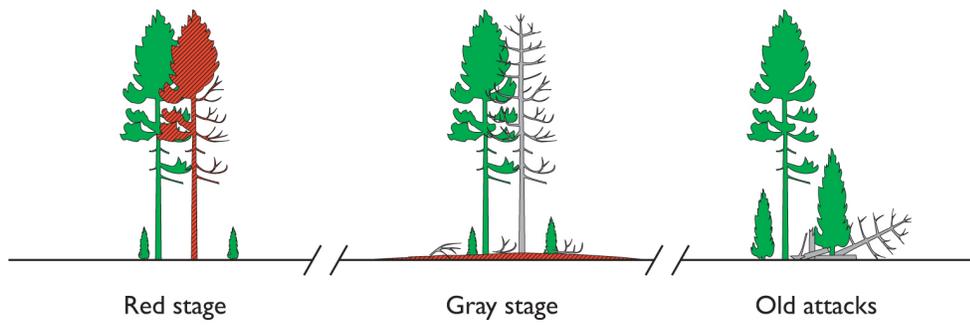
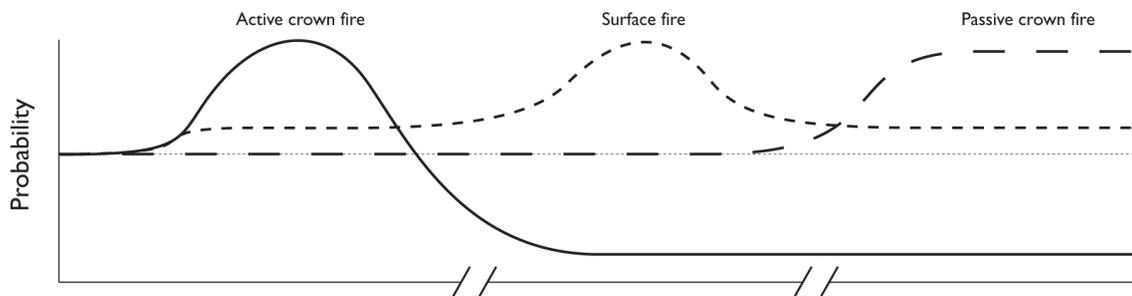


Fig. 9.



A) Hypothesized trends



B) Simulation results

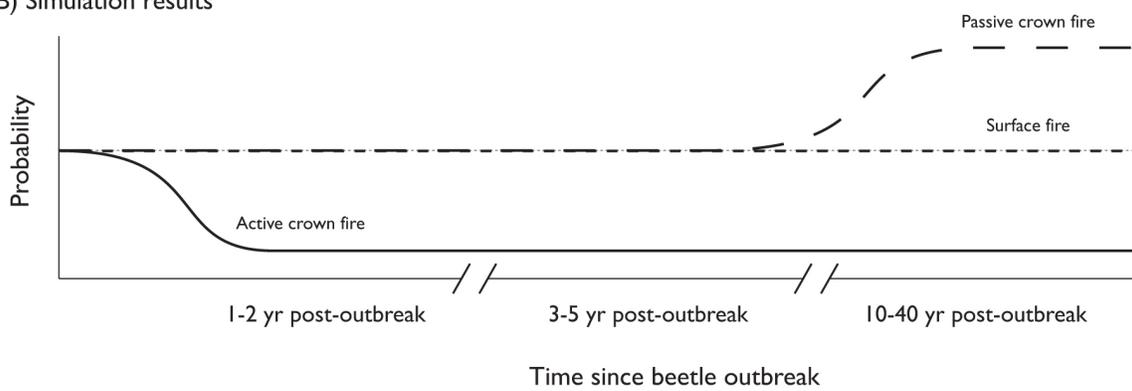


Fig. 10.

APPENDICES

Appendix A. Tree-ring analyses in the 2007 chronosequence

1) Dating of MPB-caused mortality in the 25- to 35-year-old post-outbreak sites

To verify the timing of mountain pine beetle (MPB)-caused mortality in the ten lodgepole pine sites that were infested 25 to 35 years ago, we sampled and dated cross-sections from lodgepole pine trees presumably killed by the MPB. At each site, 20 downed lodgepole pine trees showing clear J-shaped galleries and pupation chambers were randomly selected and a cross-section was sampled in the lower portion of the stem to maximize length of tree-ring series and facilitate cross-dating. Additional sections were occasionally taken higher up in the stem when basal sections were rotten or damaged. Cross-sections were identified and sealed in plastic wrap, then carefully brought back to the laboratory where they were dried, glued if needed, and then sanded at 400 grit until xylem cells were visible. Sections were scanned (3200 dpi) and measured using the measuring system OSM 3 (SCIEM, Brunn am Gebirge, Austria).

To cross-date the dead trees, master chronologies were first constructed at each site from live trees. At each site, 50 trees were randomly selected and cored at 30 cm from the ground. The cores were mounted on wood sticks, sanded (400 grit), and dated under a dissecting microscope (6.7 to 45× magnification). The cores were then scanned and measured using the same methods as for the cross-sections. The chronologies were built and validated using the program COFECHA (Holmes 1983, Grissino-Mayer 2001), starting from a small group of cores showing relatively large rings (to avoid missing rings) and good intercorrelation, then adding other series. Only the longest and/or most correlated series were kept for the master chronologies. After the 10 site chronologies were independently constructed, they were tested against each other with COFECHA to detect any

discrepancies. The resulting master chronologies contained 6 to 20 series, spanned 115 to 268 years, and had an intercorrelation of 0.35 to 0.56 (average Pearson correlation coefficient).

All cross-sections from dead trees were then cross-dated using the corresponding site's master chronology, and occasionally using chronologies from other nearby sites. Cross-dating was facilitated by the presence of diagnostic light rings and by the presence of multiple samples per tree. Samples that could not unquestionably be cross-dated were rejected. Each cross-section was then examined for evidence of blue stain (to confirm MPB as the killing agent) and rated for the likelihood that the last ring measured was indeed the last ring produced by the tree. Sections whose reliability was rated as *very high* had a relatively wide last ring and had intact bark; sections rated as *high* had no remaining bark but had a relatively wide last ring that could be observed around the whole section; sections rated as *moderate* had a relatively wide last ring that could be found on at least 3 radii; sections rated as *low* had normal to narrow outer rings and had the same date on at least 3 radii; sections rated as *very low* had very narrow outer rings, did not have 3 radii with the same date, or showed obvious signs of erosion – these sections were discarded. In total, 196 of the 200 trees sampled were successfully cross-dated.

During tree-ring analyses, MPB scars were serendipitously found on tree cores or cross-section and were used to support mortality data from cross-sections. MPB scars were identified (and distinguished from fire scars) by one of many of the following characteristics: presence of galleries (on cross-sections) and blue stain, small size, presence of multiple lesions during the same year, and location on samples very high up in stems.

Frequency distribution of mortality dates were expressed in terms of basal area killed (computed from the dbh of each tree) to reflect the opening of the canopy, assuming that basal area is a good proxy of crown cover (Fig. A1).

2. Dating of stand age and stand age at time of beetle infestation

In addition to the cross-sections and tree cores collected in the 25- and 35-yr post-outbreak sites, we sampled 10 increment cores at 30 cm from the ground from dominant lodgepole pine trees at each of the other sites (undisturbed, red stage, and gray stage). The cores were processed, cross-dated, and measured as explained above. All sites showed a pulse of tree establishment in a relatively narrow time window (~10 years) during which tree growth was not suppressed, indicating synchronous establishment of a post-fire cohort following a stand-replacing fire. We used the earliest pith data to estimate post-fire stand age at each site. Stand age at the time of the beetle infestation was then calculated by subtracting time-since-beetle outbreak from time-since-fire.

3. Literature cited

- Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205-221.
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Legend

Level of Certainty

Very High High Moderate Low

● MPB scar on live tree
◆ MPB scar on dead tree

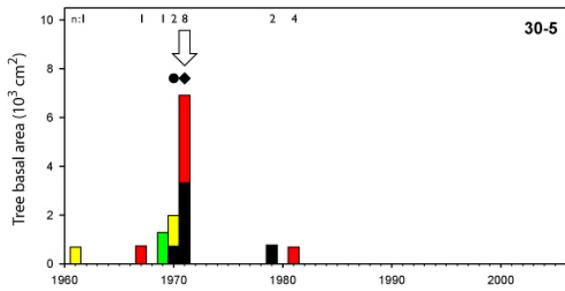
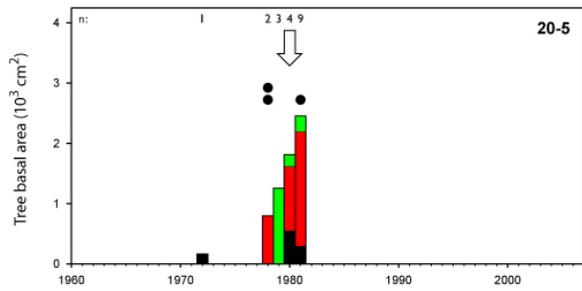
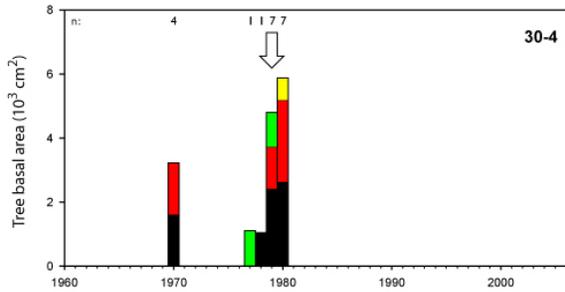
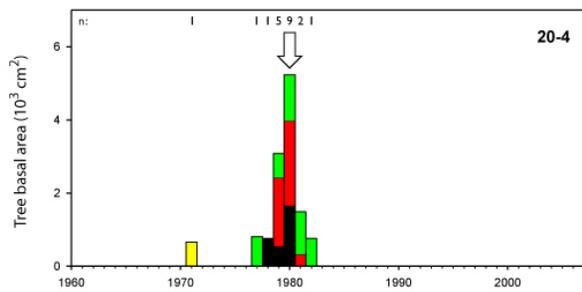
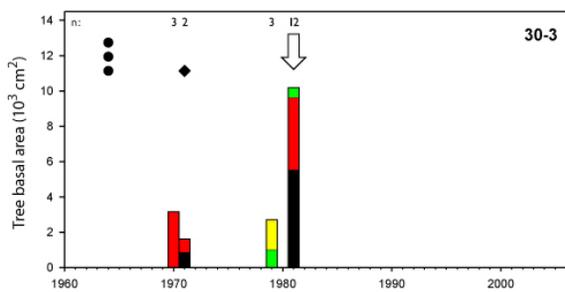
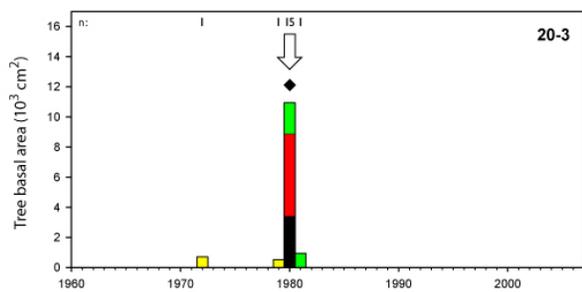
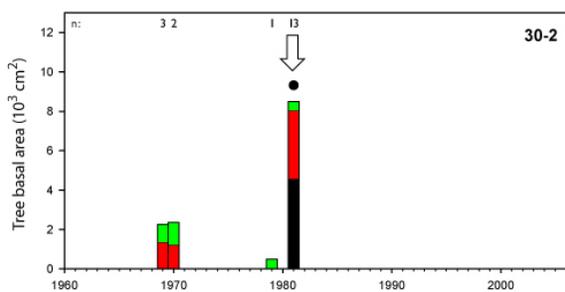
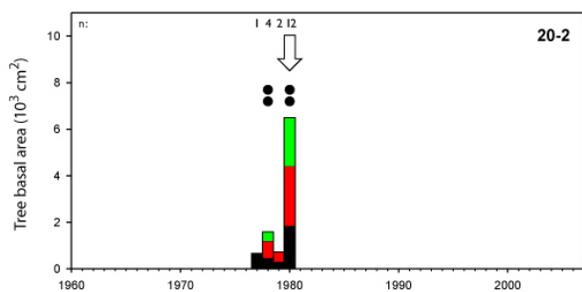
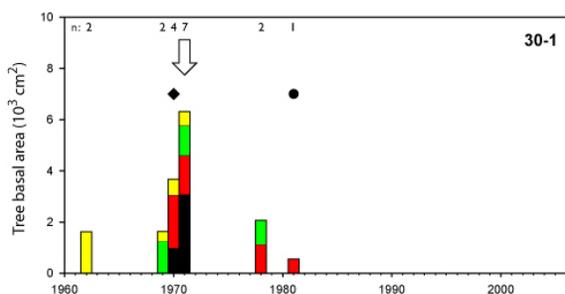
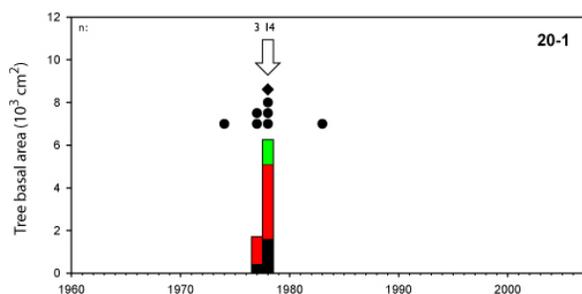


Fig. A1. Frequency of beetle-caused mortality expressed as basal area of sampled trees. The corresponding number of trees sampled is indicated at the top of each panel ($n = \dots$). Time of MPB attack (TSB = 0; open arrows) was defined as the year where cumulative basal area killed exceeded 50%. Although most sites were infested during the time period that was determined from aerial survey maps, three sites (30-2, 30-3, and 30-4) that were originally identified as being attacked during the early 1970s were actually affected during the 1978-81 outbreak. In the text, these sites kept their original identification names but were analyzed using their true TSB date determined from tree-ring analyses.

Appendix B. Description of the stands used for the chronosequence study

Table B1. Characteristics of the chronosequence stands

Year of sampling	Site ID	TSB (yr) ^a	TSB Class ^b	Stand age at time of beetle infestation (yr)	Live basal area (m ² /ha)	Live lodgepole pine basal area (%)	Basal area beetle-killed (m ² /ha)	Reconstructed pre-outbreak live basal area (m ² /ha)	Reconstructed outbreak severity (%)
1981	B4		U	80	30.34	100	3.09	33.43	9.24
1981	B8		U	250	11.96	99	1.29	13.25	9.73
1981	B6	1	R	100	15.29	100	11.98	27.26	43.93
1981	B1	4	G	100	11.18	99	19.91	31.09	64.03
1981	B5	4	G	100	18.4	100	23.9	42.3	56.5
1981	KK	4	G	100	18.52	100	14.43	32.96	43.81
1981	YY	8	8-18	80	15.5	99	9.35	26.11	46.13
1981	II	12	8-18	110	11.2	100	4.65	15.91	37.61
1981	B3	16	8-18	80	6.33	69	14.31	23.62	77.99
1981	B2	18	8-18	80	14.18	100	14.55	29.16	64.24
2007	TSBU-1		U	120	35.58	100	0	35.58	0
2007	TSBU-2		U	128	36.37	100	0	36.37	0
2007	TSBU-3		U	230	36.9	98	0	36.9	0
2007	TSBU-4		U	205	34.48	100	0	34.48	0
2007	TSBU-5		U	213	60.44	100	0	60.44	0
2007	TSBR-1	2	R	136	12.28	98	23.02	35.29	65.22
2007	TSBR-2	2	R	155	8.81	98	29.31	38.12	76.89
2007	TSBR-4	2	R	139	15.92	94	8.86	24.78	35.76
2007	TSBR-3	2	R	153	10.78	100	19.03	29.81	63.84
2007	TSBR-5	2	R	150	17.1	100	14.97	32.06	46.68
2007	TSBG-1	4	G	150	15.58	82	19.93	35.51	56.12
2007	TSBG-2	4	G	151	17.51	81	24.04	41.55	57.87
2007	TSBG-3	4	G	260	23.06	100	17.12	40.18	42.61
2007	TSBG-4	4	G	225	10.08	96	17.53	27.61	63.51
2007	TSBG-5	4	G	173	9.63	97	14.13	23.76	59.46
2007	TSB20-1	29	25	97	14.01	100	14.32	27.78	66.37
2007	TSB20-2	27	25	89	9.28	100	5.79	13.77	54.11
2007	TSB20-3	27	25	249	15.09	97	13.52	22.46	77.51
2007	TSB20-4	27	25	173	18.77	100	10.19	26.39	49.76
2007	TSB20-5	27	25	246	14.35	100	11.18	23.24	61.96
2007	TSB30-1	36	35	160	17.51	94	24.5	38.65	81.65
2007	TSB30-2	26	25	167	20.1	98	19.04	35.52	69.01
2007	TSB30-3	26	25	173	21.51	100	11.79	33.51	45.31
2007	TSB30-4	28	25	163	18.54	100	8.62	26.36	42.1
2007	TSB30-5	36	35	177	16.43	96	16.98	29.28	74.7

^a Time since beetle outbreak; in the red and gray stages, TSB was set at 2 and 4 yr, respectively, whereas in older attacks, it was determined from tree-ring analyses;

^b U: Undisturbed, R: Red, G: Gray, 8-18: 8 to 18-yr-old, 25: 25-yr old, 35: 35-yr-old.

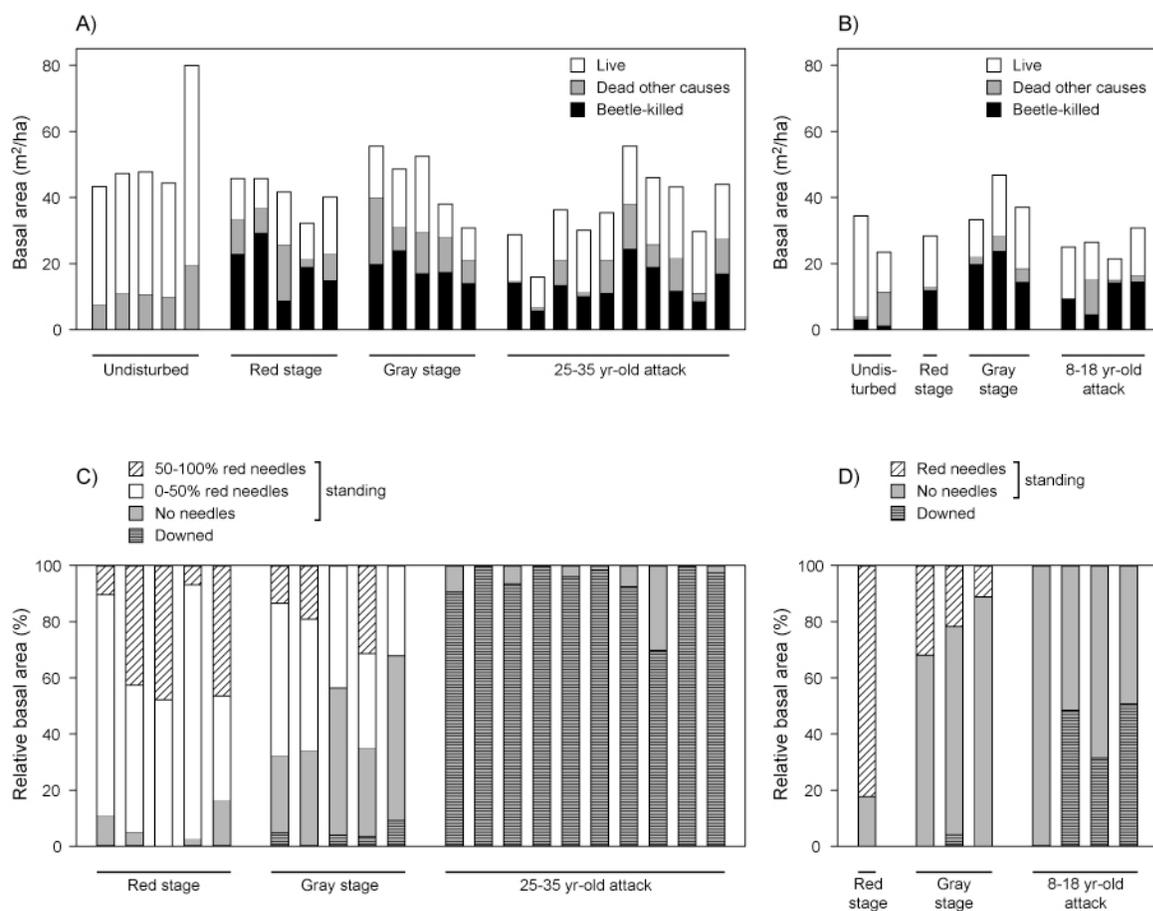


Fig. B1. Standing and downed basal area at time of sampling in the (A) 2007 and (B) 1981 chronosequence sites. Percent basal area beetle-killed of trees that were standing with red needles, standing without needles, or downed at time of sampling in the (C) 2007 and (D) 1981 chronosequence sites. Sites that were recently infested by the mountain pine beetle were classified in the red and gray stages if respectively < 20% or > 30% of their beetle-killed basal area was standing and needle-less.

Appendix C. Pre-outbreak basal area and outbreak severity

To verify the assumption that all chronosequence sites had similar conditions before the outbreak and sustained similar levels of insect damage, we reconstructed pre-outbreak basal area by adding up the basal area of surviving trees minus the basal area grown since the outbreak, and the basal area of beetle-killed trees after adjusting for loss of bark and for shrinking due to loss of water content.

1) Surviving trees

We used tree-ring data from the increment cores sampled in the 25- and 35-yr post-beetle stands ($n = 46$ to 50 cores per site; total $n = 475$ cores) of the 2007 chronosequence (see Appendix A) to calculate basal area grown since beetle outbreak in all stands that were attacked eight or more years ago (ten sites of the 2007 chronosequence and four sites of the 1981 chronosequence); we assumed that regrowth was negligible in younger stands (red and gray stands, 2 and 4 yrs post-beetle, respectively).

For the ten sites sampled in 2007, we first calculated for each increment core the cumulative radial growth between year of outbreak and year of sampling to estimate the radius of each tree at the time of infestation. Because the cores were sampled at 30 cm from the ground, the measurements were converted to breast height values using an allometric equation developed from 831 trees in the chronosequence sites ($R^2 = 0.995$; M. Simard and J.M. Griffin, unpublished data). We then calculated mean total radial growth since beetle outbreak for each site, and subtracted this value from the radius of all sampled live trees before computing live basal area for each site. Because no tree-ring data was available for the sites sampled in 1981, we used the 2007 tree-ring data to estimate regrowth in these four sites following an approach similar to that described above, with the difference that we used the tree-ring data from all ten sites to calculate mean total radial growth between year of infestation and year of sampling.

2) Beetle-killed trees

To compensate for the lack of bark in beetle-killed trees at time of sampling, we adjusted the diameter at breast height of these trees using a simple ratio between inside bark diameter (d) and outside bark diameter (D) developed for lodgepole pines of western Montana (Lange 1971, cited in Koch 1996, p.461):

$$[1] \quad d = 0.9252 * D$$

We also compensated for the shrinkage of beetle-killed trees by using a radial shrinkage value of 4.5% (Koch 1996, p.693).

3) Pre-outbreak basal area and percent basal area beetle-killed

Pre-outbreak basal area varied between 13 and 60 m²/ha (Fig. 3A). We used a linear model (PROC GLM, SAS Institute Inc. 2003) to test the effect of time-since-beetle class (undisturbed, red attack, gray attack, 8 to 18 years, 25 years, and 35 years post-beetle), dataset (1981 vs. 2007 chronosequence) and their interaction on pre-outbreak basal area. None of these variables were significant (alpha = 0.05), suggesting that all stands had a similar basal area before being infested. Outbreak severity (Basal area beetle-killed / pre-outbreak basal area) varied between 0 and 10% for the undisturbed sites, and from 36 to 82% in the other sites, but did not vary between time-since beetle classes, datasets, or their interaction, suggesting again that all disturbed sites sustained a similar level of mortality from bark beetle infestation (Fig. 3B).

4) Literature cited

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APPENDIX D. ANOVA tables for time-since-beetle class analyses.

1. SURFACE FUELS

1-hour fuel load ($R^2 = 0.74$)	d.f.^b	F	P
TSB ^a	–	–	N.S.
Dataset	1	55.33	< 0.0001
TSB*Dataset	–	–	N.S.

^a Time-since-beetle class^b Degrees of freedom

10-hour fuel load ($R^2 = 0.43$)	d.f.	F	P
TSB	–	–	N.S.
Dataset	1	14.32	0.0013
TSB*Dataset	–	–	N.S.

100-hour fuel load	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

1000-hour fuel load ($R^2 = 0.22$)	d.f.	F	P
TSB	–	–	N.S.
Dataset	1	5.35	0.0320
TSB*Dataset	–	–	N.S.

Fuel bed depth	d.f.	F	P
TSB	–	–	N.S.

Needle litter depth ($R^2 = 0.35$)	d.f.	F	P
TSB	2	4.90	0.0200
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Duff depth	d.f.	F	P
TSB	–	–	N.S.

Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

2. CANOPY FUELS

Canopy base height	d.f.	F	P
TSB	–	–	N.S.

Sapling density	d.f.	F	P
TSB	–	–	N.S.

Foliar moisture content ($R^2 = 0.73$)	d.f.	F	P
TSB	2	16.19	0.0004

Canopy bulk density ($R^2 = 0.47$)	d.f.	F	P
TSB	2	5.23	0.0233

Canopy fuel load ($R^2 = 0.65$)	d.f.	F	P
TSB	2	11.11	0.0019

Live herbaceous fuel load ($R^2 = 0.60$)	d.f.	F	P
TSB	2	6.42	0.0097
Dataset	–	–	N.S.
TSB*Dataset	2	4.11	0.0378

Live woody fuel load ($R^2 = 0.29$)	d.f.	F	P
TSB	2	3.67	0.0460
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

3. TEMPERATURE PROBES

Daily mean ($R^2 = 0.84$)	d.f.	<i>F</i>	<i>P</i>
TSB	3	20.27	<0.0001

Mid-day mean ($R^2 = 0.72$)	d.f.	<i>F</i>	<i>P</i>
TSB	3	10.40	0.0012

4. FIRE HAZARD INDICES

Torching Index	d.f.	<i>F</i>	<i>P</i>
TSB	–	–	N.S.

Crowning Index ($R^2 = 0.45$)	d.f.	<i>F</i>	<i>P</i>
TSB	2	4.83	0.0289

5. CROWN FIRE BEHAVIOR METRICS

Crown fraction burned, 20 km/h ($R^2 = 0.36$)	d.f.	<i>F</i>	<i>P</i>
TSB	4	2.85	0.0509

Crown fraction burned, 40 km/h ($R^2 = 0.37$)	d.f.	<i>F</i>	<i>P</i>
TSB	4	2.89	0.0489

Crown fraction burned, 60 km/h	d.f.	<i>F</i>	<i>P</i>
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Crown fraction burned, 60 km/h	d.f.	F	P
TSB	–	–	N.S.

Crown fraction burned, 80 km/h	d.f.	F	P
TSB	–	–	N.S.

Rate of spread, 20 km/h ($R^2 = 0.35$)	d.f.	F	P
TSB	4	2.64	0.0643

Rate of spread, 40 km/h ($R^2 = 0.36$)	d.f.	F	P
TSB	4	2.84	0.0514

Rate of spread, 60 km/h	d.f.	F	P
TSB	–	–	N.S.

Rate of spread, 80 km/h	d.f.	F	P
TSB	–	–	N.S.

Heat per unit area, 20 km/h	d.f.	F	P
TSB	–	–	N.S.

Heat per unit area, 40 km/h ($R^2 = 0.35$)	d.f.	F	P
TSB	4	2.70	0.0602

Heat per unit area, 60 km/h ($R^2 = 0.50$)	d.f.	F	P
TSB	4	4.97	0.0060

Heat per unit area, 80 km/h ($R^2 = 0.48$)	d.f.	F	P
TSB	4	4.63	0.0082

Fireline intensity, 20 km/h	d.f.	F	P
TSB	–	–	N.S.

Fireline intensity, 40 km/h ($R^2 = 0.39$)	d.f.	F	P
TSB	4	3.20	0.0347

Fireline intensity, 60 km/h ($R^2 = 0.45$)	d.f.	F	P
TSB	4	4.14	0.0133

Fireline intensity, 80 km/h ($R^2 = 0.44$)	d.f.	F	P
TSB	4	3.93	0.0164

6. SURFACE FIRE BEHAVIOR METRICS

Rate of spread, 20 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Rate of spread, 40 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Rate of spread, 60 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Rate of spread, 80 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Heat per unit area, 20 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Heat per unit area, 40 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Heat per unit area, 60 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Heat per unit area, 80 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Fireline intensity, 20 km/h	d.f.	F	P
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Fireline intensity, 20 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Fireline intensity, 40 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Fireline intensity, 60 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Fireline intensity, 80 km/h	d.f.	F	P
TSB	–	–	N.S.
Dataset	–	–	N.S.
TSB*Dataset	–	–	N.S.

Appendix E. Scenarios of dead canopy fuel consumption[†]

In many fire modeling systems, it is assumed that during a crown fire, all the foliage and 50% of the fine fuels (1-hour fuels, diameter < 0.64 cm) of the canopy are consumed (Reinhardt and Crookston 2003; Reinhardt et al. 2006). While this approximation might hold for live trees, it may underestimate canopy consumption of dead trees. This discrepancy might not be important in undisturbed stands but could potentially have a great impact on fire behavior predictions in beetle-killed stands, which have a large amount of dead trees. To explore the potential effect on canopy fuel characteristics and fire hazard of the assumptions about consumption of canopy fuels, we compared four scenarios of canopy fuel consumption. First, we used the baseline scenario that is used in most models and in this study, where all the foliage and half of the 1-hour fuels are consumed, both for live and dead trees. For the other three scenarios, live trees were consumed as in the baseline scenario, but dead trees had different consumption levels. In the second scenario, all the foliage (if present, i.e., on red-needle trees) and all the 1-hour fuels of dead trees were available for consumption. In the third scenario, all foliage and 1-hour fuels, and 50% of the 10-hour fuels (diameter between 0.64 cm and 2.54 cm) of dead trees were consumed. In the last scenario, all foliage, 1-hour fuels, and 10-hour fuels of dead trees were available for consumption.

The four scenarios were applied to the 25 chronosequence stands that were sampled in 2007 and for which canopy fuel data were available. We used a two-way ANOVA (PROC GLM, SAS Institute Inc. 2003) to test the effect of time-since-beetle class (TSB; undisturbed, red-needle stage, gray-needle stage, 25-yr post-infestation, and 35-yr post-infestation), scenario (4 scenarios), and their interaction on effective canopy base height, effective canopy bulk density, available canopy fuel load, Torching Index, and Crowning Index. There was no difference among the different scenarios for canopy base height, canopy bulk density, Torching Index, and Crowning Index (Fig. E1). Available canopy fuel load

however was affected by the scenario used, with greater available loads associated with greater fuel consumption levels. For all response variables, TSB class had the greatest explanatory power, and the interactions between TSB class and scenario were not significant at the 0.05 confidence level.

These results suggest that predictions of fire type (surface fire, passive crown fire, active crown fire, and conditional crown fire) may be robust relative to the assumptions on canopy fuel consumption. However, because available canopy fuel load is the main driver of heat per unit area and fireline intensity (all other things being equal), these assumptions could change predictions of these variables. This effect however does not appear to affect the results of this study because the relative difference between TSB classes are significant and similar across scenarios (no TSB class*Scenario effect).

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† We gratefully acknowledge the contribution of Brad Hawkes (Canadian Forest Service, Pacific Forestry Centre) who provided the initial idea behind this analysis.

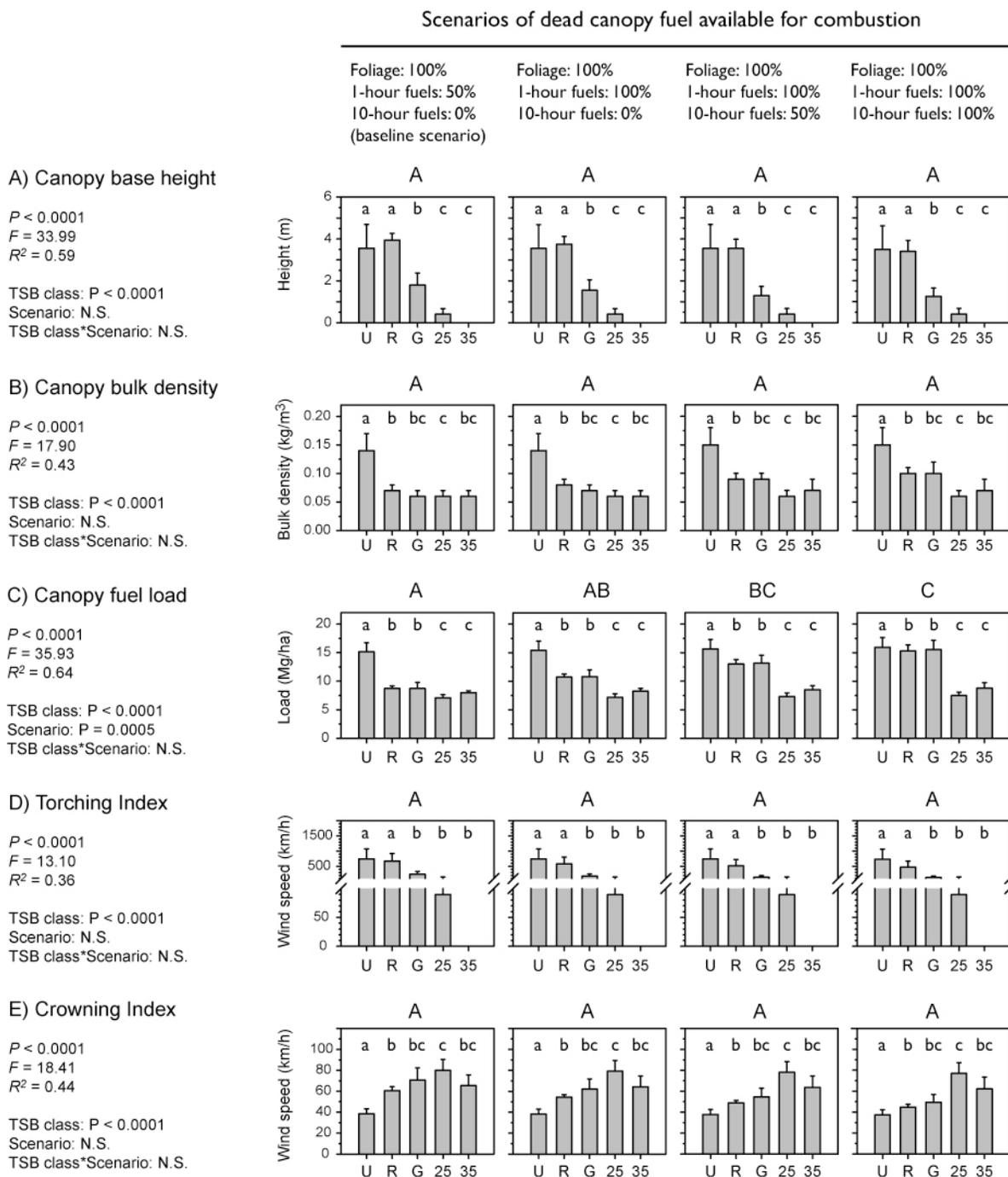


Fig. E1. Effect of four scenarios of dead canopy fuel consumption on canopy fuel characteristics and fire hazard. Lowercase letters above each vertical bar (+/- 1 standard error) indicate differences in means among time-since-beetle classes, and uppercase letter above each panel indicate differences in means among scenarios. Bars or panels with similar letters are not significantly different (Duncan's

multiple range test; alpha = 5%). For each response variable, the P -value, F -value, and R^2 are first presented for the global model, and then P -values are given for individual explanatory variables. Although not significant at the 5% level, the interaction of TSB class and scenario was marginally significant ($P = 0.075$) for canopy fuel load.

THESIS CONCLUSIONS

Disturbance regimes are changing rapidly in several parts of the globe and many ecosystems are subjected to more frequent, intense, or extensive disturbances (Westerling et al. 2006; Raffa et al. 2008). It is therefore critical to understand the possible interactions between different disturbances to avoid ‘*ecological surprises*’ (Paine et al. 1998). Linked disturbances may be particularly important in that regard because positive feedbacks between disturbances could significantly and rapidly affect landscape diversity and stability.

It is increasingly recognized that using complementary approaches in ecological studies is preferable because they yield different types of inference (Carpenter, 1998). In this dissertation, I used multiple approaches to study the interactions between bark beetles and fire. Here are the main conclusions from this research:

1. **Bark beetle outbreaks create and respond to landscape patterns.** Bark beetle outbreak severity is influenced by stand-scale and landscape context factors and thus outbreaks are patchy across the landscape. In turn, beetle outbreaks create heterogeneity in landscapes by transforming closed-crown stands dominated by large trees to more open stands composed of all-sized stems.
2. **Landscape context, particularly beetle pressure, is a strong predictor of bark beetle outbreak severity.** Landscape context variables alone were as good or better at predicting outbreak severity than stand-scale variables. Proximity to initial beetle eruptions or amount of beetle-killed forests in the surrounding landscape were the most consistent predictors of subsequent outbreak severity within susceptible stands.

3. **Lodgepole pine forest biomass is very resilient to bark beetle outbreaks and fire.** During severe outbreaks, not all susceptible forests are attacked by bark beetles. Even within severely impacted stands, bark beetles do not kill all the trees, and surviving tree saplings and seedlings show a vigorous regrowth that rapidly restores canopy closure within 20 to 30 years, a response that was quantified with remote sensing and field surveys.
4. **Wind speed may be a more important driver of fire behavior than fuel abundance and distribution.** Modeling results showed that fuel abundance and distribution, caused by beetle outbreaks or by other causes, may only affect fire behavior under intermediate wind conditions. At low wind speeds, only surface fires were predicted, and at high wind speeds, all stand were predicted to have active crown fires, irrespective of their fuel conditions.
5. **Bark beetle outbreaks do not appear to increase the probability of active crown fire in lodgepole pine forests of Greater Yellowstone.** Instead, probability of active crown fire may decrease in the short term (1-5 years) following beetle outbreak and remain low in subsequent decades because bark beetles are thinning the canopies. Probability or intensity of surface fires did not change throughout the chronosequence but probability of passive crown fire increased in 25- to 35-year-old post-beetle stands because of abundant ladder fuels.
6. **Use of multiple approaches allows a deeper understanding of complex ecological systems.** Bark beetle outbreaks, fire, and forests interact at multiple spatial and temporal scales and are therefore better understood using different methods. This research used field and chronosequence studies, dendrochronology, modeling, remote sensing, and the analysis of time series to study bark beetle–fire–forest interactions across a range of scales.

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