Mountain Pine Beetle-Whitebark Pine Dynamics in a Subalpine Ecosystem of the Pioneer Mountains, Southwest Montana

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This thesis is dedicated to my grandmother, June Margoles, and my grandfather, Dambum.

Abstract

Mountain pine beetle (*Dendroctonus ponderosae*) outbreaks during the past decade have caused widespread mortality across western North American forests. These outbreaks have been notably intense in subalpine whitebark pine (*Pinus albicaulis*) communities – areas historically considered to be climatically marginal for beetle reproduction. Higher temperatures associated with climate change are thought to be important drivers of these outbreaks by lengthening the beetle development period, reducing the frequency cold-induced mortality events, and possibly diminishing host resistance to attack. The scale of recent high elevation outbreaks appears to be historically unprecedented, yet there is only limited understanding regarding the dynamics of past outbreaks in whitebark pine ecosystems. My thesis work focuses on the dynamics of a high elevation mountain pine beetle outbreak in the Pioneer Mountains of southwest Montana that occurred during the late 1920s and early 1930s. This research focuses both the landscape scale and individual tree scale, with the intention of providing context for current high elevation outbreaks. Specifically, I identify (1) the timing of the outbreak and assess the factors that caused the outbreak to end, and (2) differences in growth patterns between whitebark pines that were killed and those that survived the outbreak. The outbreak in the Pioneer Mountains, Montana, began in 1924, peaked in 1930, and abruptly ended in 1933. The termination of the outbreak was synchronous with the coldest recorded temperature for Dillon, MT, and high numbers of suitable hosts for attack persisted following 1933. Had this cold event not occurred, the beetles would have likely caused greater pine mortality and more heavily influenced successional patterns.

During the outbreak, mountain pine beetles killed the most vigorous whitebark pines. Whitebark pines that survived the outbreak had consistently slow growth and their ring-widths responded more strongly to very wet and dry years. Whitebark pines killed earlier in the outbreak had slower growth than those killed later, suggesting a switch in host selection as the outbreak progressed. These results suggest that there may not be a linear relationship between host stress in whitebark pines and susceptibility for mountain pine beetle attack.

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Chapter 1: The role and influence of mountain pine beetles in subalpine communities

Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) have earned a formidable reputation throughout western North America. Their populations have been steadily growing over the past decade, and have affected $3.1x10^7$ ha since 2000 (Figure 1; Canadian Ministry of Forests, 2009; USDA Forest Service, 2010). In Colorado, Montana, and British Columbia, mountain pine beetles have killed up to 90% of large-diameter trees across broad landscapes (Gibson, 2008; Raffa et al., 2008), with significant ecological, social and economic consequences. Outbreaks alter forest processes at almost every spatial scale – from microsite changes in light penetration, landscape scale alterations in fire behavior (Romme et al., 1982; Jenkins et al., 2006; Romme et al., 2006; Simard et al., 2011), and even global scale carbon cycling (Kurz et al., 2008). Economically, outbreaks can dramatically reduce merchantable timber resources as well as residential and commercial property values (Price et al., 2010). Popular media sources have frequently described current outbreaks as ecological catastrophes, helping create a decidedly negative public opinion of the beetles (Flint et al., 2009). Yet mountain pine beetles are native to western forests and a fundamental component to a variety of mountain ecosystems (Romme et al., 1986; Negron et al., 2008). Like wildfire early in the 20th Century, the beetles have often been vilified without regard to the important role they have etched out as a disturbance agent over millennia.

However, the potential for climate change-driven increases in the intensity, duration, and scale of mountain pine beetle outbreaks may have significant long-term impacts on western forests. The beetle's life cycle is intimately linked with air temperature (Logan and Bentz, 1999), and even minor warming may promote population expansion (Raffa et al., 2008). The most pronounced changes in outbreak frequency and intensity will likely occur in the historically colder and more marginal habitats of the beetle – high elevation whitebark pine (*Pinus albicaulis* Engelm.) forests (Logan and Powell, 2001; Hicke et al., 2006) and the northerly boreal forests in Canada (Safranyik et al., 2010). These increases in outbreaks, in tandem with the invasive pathogen white pine blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.) and fire suppression, are increasingly implicated in range-wide declines of whitebark pine (Tomback et al., 2001), a keystone species in subalpine forests (Figure 1, Ellison et al., 2005). The theoretical basis for climate change-driven increases in outbreaks is well established (Logan et al., 2003; Raffa et al., 2008; Bentz et al., 2010), yet, as I will discuss in this chapter, there remain important questions regarding the patterns of whitebark pine mortality during these events.

This introductory chapter frames my thesis research, which broadly investigates whitebark pine-mountain pine beetle interactions during a historic outbreak. Widespread outbreaks occurred during the first half of the 20th Century that spanned nearly the entire range of whitebark pine (Evenden, 1944; Ciesla and Furniss, 1975; Perkins and Swetnam, 1996; Kipfmueller et al., 2002; Gibson et al., 2008; Larson, 2009). I use the mortality

patterns from a watershed in the Pioneer Mountains, MT, during this outbreak as a case study to enhance the understanding of fine-scale interactions between whitebark pines and mountain pine beetles (Figure 2). In this chapter, I contextualize my specific questions by first describing the ecology, disturbance regimes, and successional patterns in my study area – the subalpine forests of the northern Rocky Mountains. Next, I explain the requirements for a mountain pine beetle outbreak, how humans may have modified these conditions, and finally the specific questions I will investigate.

Disturbance in subalpine forests

Disturbance events can profoundly influence the species composition and successional patterns within ecological communities. Disturbances, at a basic level, can be defined as any environmental event that interrupts ecosystem processes, inhabitants, and community structure (Pickett and White, 1985). These events reallocate critical nutrients and can dramatically influence canopy density and diversity (Sousa, 1984). The ultimate influence that disturbances have on landscape patterns depends on their extent, intensity, and frequency (Pickett and White, 1985). Current forest structure can heavily influence the likelihood and severity of future disturbances as well as the species that ultimately predominate. Patterns of reestablishment, in turn, influence the likelihood of future disturbances and are shaped by ecological legacies from the initial forest structure (Pickett and White, 1985; Kulakowski et al., 2003; Kipfmueller and Kupfer, 2005). In the northern Rocky Mountains, here considered western Montana and central/northern Idaho (Kershaw et al., 1998), fire has typically been considered the dominant force shaping
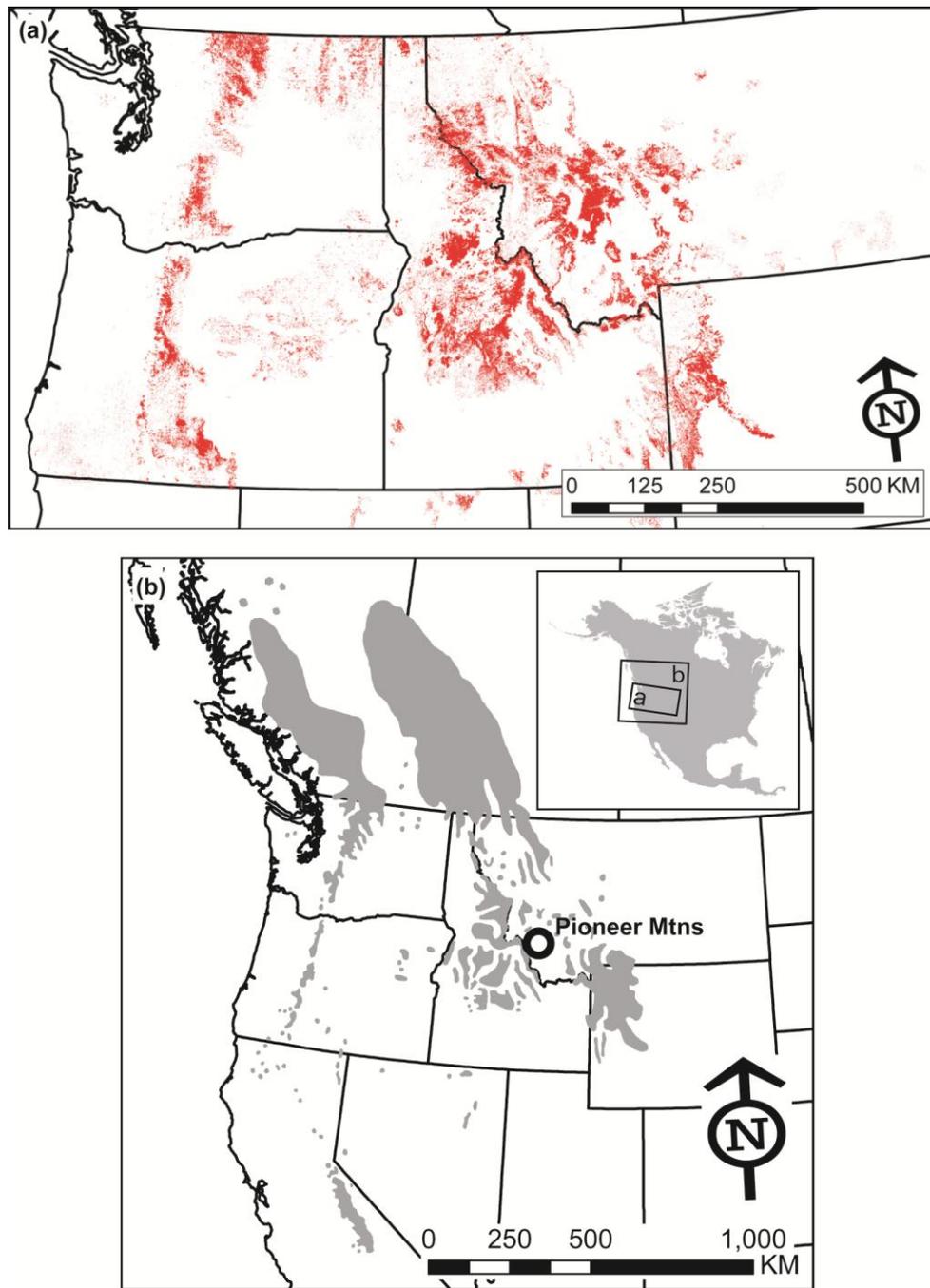
Figure 1. (a) The extent of mountain pine beetle outbreaks in the northwestern U.S. from 2000-2009 (data from USFS Aerial Surveys), and (b) the range of whitebark pine in North America.

subalpine forests (Arno, 1980). More recently, however, the rapid and lasting effects that beetle outbreaks can have on ecological processes are being more acutely considered as significant mechanisms that change forests (Romme et al., 1986; Veblen et al., 1991; Kulakowski et al., 2003; Simard et al., 2011).

Fires in subalpine forests are typically large and infrequent (Arno, 1980; Kipfmueller and Baker, 2000). The life history traits of lodgepole pine make it well-suited to thrive following high-severity fires. Many lodgepole pines in the northern Rocky Mountains develop serotinous cones that are retained in the canopy and only open during fire events (Lotan, 1976), though non-serotinous cones are also often present (Tinker et al., 1994). After germinating, lodgepole pines can produce viable serotinous cones in only 20 years (Lotan and Critchfield, 1990), which means that high severity fires at even relatively short intervals can facilitate lodgepole pine dominance. At landscape scales, the canopies of many subalpine forests, especially at lower elevations, can be almost entirely composed of even-aged lodgepole pines.

Whitebark pines, however, have very different life history characteristics that make that make them respond differently to fire. While they frequently coexist with lodgepole, whitebark pines are better adapted to the colder and moister conditions experienced at the highest elevations of subalpine forests (Arno and Hoff, 1989). Depending upon site conditions and climatic conditions, fire frequency in whitebark pine-dominated stands can be temporally variable (50-300+ years; Arno, 1980) and at more mixed severities than in lower elevation lodgepole pine forests (Murray et al., 1998; Larson et al., 2009). The cones of whitebark pines do not open on their own, but depend

almost entirely upon a single bird species, the Clark's nutcracker, for dispersal (Lanner, 1982; Tomback, 1982). Clark's nutcrackers (*Nucifraga columbiana)* cache the nutritious seeds in the summer and fall to consume during the winter and spring, and preferentially select sites that have been recently disturbed by fire (Tomback et al., 1993; Tomback et al., 2001). The few caches that are forgotten and not discovered by other animals constitute nearly the entire source of germinating whitebark pines (McKinney et al., 2009). Following germination, whitebark pines typically require a minimum of 50 years to reach cone-bearing age – somewhat longer than for lodgepole pine (McCaughey and Tomback, 2001). The longer period to maturation and obligate reliance on animal dispersers makes whitebark pine comparatively sensitive to changes in disturbance regimes (Logan et al., 2010).

Mountain pine beetle outbreaks are increasingly understood to affect subalpine forests on a spatial scale similar fire (Raffa et al., 2008), yet can have very different long-term effects. Most conceptual models of succession in subalpine forests describe stand progression following intense fire from lodgepole pine and whitebark pine to forests increasingly dominated by shade tolerant fir and spruce (while still maintaining a component of long-lived whitebark pine) (Keane et al., 2001, Kipfmueller and Kupfer, 2005). However, mountain pine beetle outbreaks are host-specific disturbances and only affect the generally shade-intolerant pine species. This has been hypothesized to accelerate normal successional processes, causing shade-intolerant species to actually become proportionately more important in stands following the disturbance (Amman, 1977; Veblen et al., 1991; Veblen, 2000). Yet there remain many uncertainties regarding

the effects outbreaks will have on subalpine forests in the northern Rocky Mountains, and the evidence for accelerated succession has been scant. In lodgepole pine-dominated stands in British Columbia, increases in spruce (Shrimpton, 1994) and Douglas-fir (Axelson et al., 2009) have both been observed following mountain pine beetle outbreaks. Conversely, regeneration of both lodgepole pine (Sibold et al., 2007) and whitebark pine (Larson and Kipfmueller, 2010) have been observed beneath beetle-killed trees. The lack of a coherent understanding regarding the stand-level effects mountain pine beetles have on high elevation forests is particularly pressing in light of current and, likely increasing, high elevation outbreaks.

Mountain Pine Beetle Dynamics

The specific triggers for a mountain pine beetle outbreak are complex (Raffa et al., 2008) but fundamentally rely on the joint occurrence of suitable temperatures for beetle reproduction and sufficient numbers of hosts (Safranyik et al., 1975; Safranyik and Carroll, 2006). While mountain pine beetles have a broad temperature tolerance that allows their range to span most of western North America from British Columbia to Mexico (Amman and McGregor, 1990), their outbreaks are typically spatially confined to a smaller portion of their entire range. This is because mountain pine beetles, unlike most other bark beetles, lack diapause, a genetically based winter torpor (Logan and Bentz, 1999), which means that temperatures alone control their life cycle timing. Relatively warm temperatures that occur in lower elevation ponderosa and lodgepole pine forests facilitate a univoltine (single year) life cycle for the beetles, in comparison to high

elevation whitebark pine forests, where semivoltine (multi-year) life cycles often predominate (Bentz et al., 1991; Logan Bentz, 1999). Univoltine life cycles promote synchrony in mountain pine beetle populations, which means adults emerge nearly simultaneously from the trees within which they developed (Bentz et al., 1991). This maximizes the mountain pine beetle's potential for successful "mass attack" in which many beetles simultaneously attack a single tree to overcome its defenses (Raffa and Berryman, 1987). Without the synchronized attack, the likelihood of successful colonization of new hosts can be very low. In contrast, protracted beetle emergence over two or three years in colder climates such as those dominated by whitebark pine results in temporally asynchronous populations and reduced numbers of attacking beetles at a given time (Amman, 1973). As a result, high elevation ecosystems have often been historically associated with only endemic populations (Logan and Powell, 2001).

Extreme low temperatures play another critical role in regulating mountain pine beetle populations and can often be the single greatest cause of mortality in a given year (Cole, 1981). Mountain pine beetles overwinter within their hosts' phloem, which means they must survive the temperature swings that frequently occur in mountainous regions. To do so, mountain pine beetles undergo a cold-hardening process to lower their supercooling point, which is the temperature threshold at which ice forms within body tissues. This process involves the build-up of cryoprotectants (glycerol), which functions like an anti-freeze, and the expulsion of ice-nucleating particles from their guts (Bentz and Mullins, 1999). Glycerol accumulates gradually as a response to seasonal temperature changes, meaning the level of cold-tolerance varies throughout the year and

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in relation to life-cycle stage. Maximum cold tolerance occurs during the winter months and is typically at or slightly above -40° C (Figure 1; Wygant, 1942; Safranyik et al., 1975; Regniere and Bentz, 2007). Substantial levels of beetle mortality can occur if winter temperatures fall below this point, especially for several consecutive days (Safranyik and Linton, 1998), or there are unseasonably cold periods in spring or fall.

Sufficient numbers of susceptible hosts is the second requirement for a mountain pine beetle outbreak to occur. The term "susceptibility" is used here to describe the inherent suitability of a tree, stand, or landscape to support mountain pine beetle populations, and is frequently based on three characteristics: the number of large-diameter hosts, the age of hosts, and the density of hosts in a stand (Shore and Safranyik, 1992). Tree diameter is typically considered the most important factor shaping susceptibility and the potential for an outbreak (Safranyik and Carroll, 2006; Bjorklund et al., 2009). Large lodgepole pines often have thicker phloem (Shrimpton and Thomson, 1985), which means greater amounts of food for attacking beetles and potentially higher brood production (Amman, 1972; Berryman, 1976). Host age has been found to be an important factor affecting susceptibility, since young lodgepole pine (<60 years) appear to have the highest resistance to blue stain fungus, a virulent pathogen associated with mountain pine beetles and highly influential in causing host mortality by inhibiting water-flow (Raffa and Berryman, 1983; Safranyik and Carroll, 2006). Higher rates of competition in dense stands have also has been found to increase susceptibility to attack by reducing individual tree diameter and vigor, and as a result, host defenses to resist attack (Mitchell et al., 1983; Waring and Pitman, 1985). However, the role of vigor in

affecting host defenses and susceptibility is highly complex and is determined by a suite of different variables.

Vigor, host defenses, and the mountain pine beetle

Pines have evolved intricate mechanisms to resist beetle colonization, involving both constitutive and induced defenses (Franchesci et al., 2005). Constitutive defenses exist as preformed resin canals that when severed can "pitch out" or kill attacking beetles (Figure 2; Berryman, 1972). Inducible defenses refer to a tree's rapid response to an attack or other wounding (Franceschi et al., 2005). This response involves cell necrosis in the region of attack to inhibit movement of the blue stain fungus (compartmentalization), the formation of traumatic resin ducts, and most importantly the rapid production of toxic secondary chemicals such as terpenes (Raffa and Berryman, 1982; Raffa and Berryman, 1983; Safranyik and Carroll, 2006). These secondary chemicals can saturate a host's phloem and render it toxic to beetles (Safranyik and Carroll, 2006).

Both constitutive and induced defenses have been positively related to host vigor in lodgepole and ponderosa pine, the most heavily studied hosts of mountain pine beetles (Safranyik and Carroll, 2006). As a result, mountain pine beetle-host interactions have often been associated with the plant-stress hypothesis (Larsson, 1989), which assumes that trees with lower defenses will be more frequently attacked (White, 1969; White, 2009). The processes that alter the effectiveness of these defenses are varied, but are likely controlled by climatic and stand-level factors. Drought conditions have frequently been associated with increases in the potential for mountain pine beetle outbreaks

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Figure 2. (a) An overview of the study area in the Pioneer Mountains, Montana. The bare trees were predominantly killed during the 1920s/1930s mountain pine beetle outbreak. (b) A downed whitebark pine log exhibiting characteristic j-shaped galleries from mountain pine beetles, and (c) a lodgepole pine "pitching-out" attacking mountain pine beetles.

(Craighead, 1925; Thomson and Shrimpton, 1984; Mattson and Haack, 1987; Allen et al., 2010) for two principal reasons. First, moisture availability largely determines a tree's ability to exude resin and "pitch-out" attacking beetles (Craighead 1923; Thomson and Shrimpton, 1984; Mattson and Haack, 1987; Larsonn, 1989). Second, during drought, photosynthesis can be significantly curtailed, which reduces carbon assimilation and potentially the concentration of defensive chemicals used in induced reactions (Waring, 1987; McDowell et al., 2008). Stand-level processes that reduce vigor have been associated with mechanical wounds, high rates of competition (Larsson, 1983; Waring and Pitman, 1985) and the presence of other pathogens (Raffa et al., 2005). Consequently, this suggests that while the most vigorous trees may be nutritionally preferred by mountain pine beetles, they also tend to have the greatest defense reactions and highest thresholds for successful attack (Berryman, 1972; Christiansen et al., 1987).

The applicability of the plant stress hypothesis, however, is limited since it does not take into account beetle population size. At endemic levels, mountain pine beetles may be confined to individually stressed trees. When there are sudden increases in host stress, such as during drought, the number of viable hosts for beetles can increase and facilitate rapid population expansion (Ferrell, 1996; Berg et al., 2006). As beetle populations rise they are increasingly able to attack the most vigorous trees which, through positive feedbacks, can ultimately result in a self-sustaining outbreak (Wallin and Raffa, 2004; Raffa et al., 2008). Once populations surpass a critical threshold, outbreaks are able to continue even when an inciting factor (such as drought) is no longer present (Raffa et al., 2008), so long as other conditions (e.g. host availability) are present.

Yet research from other species of pine suggests that drought and slow growth rates do not always have a negative effect on defenses. Lorio (1986) used the growth-differentiation balance hypothesis to develop a conceptual model for seasonal changes in the interaction between loblolly pine (*Pinus taeda*) and the southern pine beetle (*Dendroctonus frontalis*) (see also Herms and Mattson, 1992). During the spring when there is high moisture availability, loblolly pines appear to invest the bulk of their accumulated photosynthates into growth at the expense of chemical defenses. As a result, southern pine beetles can often overwhelm the defenses of even vigorous trees during these months. During warmer months, however, when water deficits are greater, loblolly pines enhance resistance to attack by reallocating carbon from growth processes to constitutive defenses (Lorio, 1986; Herms and Mattson, 1992). While the interactions described by Lorio (1986) are assumed to operate on all trees across a landscape, other authors have found that individual trees that experience moderate levels of stress may have greater constitutive defenses than their more vigorous counterparts (Lombardero et al., 2000; Salle et al., 2008).

Similarly, slow growing trees often live longer than their "vigorous" counterparts (Schulman, 1954; LaMarche, 1969; Bigler and Veblen, 2009) and may be related to physiological traits that increase resistance to pathogens (Loehle, 1988). High internal investments in growth during juvenile stages can enhance a tree's competitive abilities, yet can also have long-term physiological tradeoffs. Trees with slow growth rates and longer needle turnover rates may allocate higher levels of nitrogen, phosphorous, and carbon for the production of chemical defenses (Coley, 1985; Loehle, 1988). The high

wood densities often characteristic in slow growing trees also appear to make them resistant to pathogens such as fungi (LaMarche, 1969). Slow growing trees may be less palatable to herbivores due not only to high chemical and structural defenses, but also generally thinner phloem.

While a linear relationship between vigor and defense has been developed for lodgepole (Larsson et al., 1983; Mitchell et al., 1983; Waring and Pitman, 1985) and ponderosa pine (Kane and Kolb, 2010) very little is known about the interactions between mountain pine beetles and whitebark pine. Preliminary analyses of whitebark pine resins indicate that they have significantly different chemical compositions than lodgepole pine (Logan et al., 2010). From personal observation, Logan et al. (2010) additionally noted that whitebark pines appear to have lower constitutive and induced defense reactions during mountain pine beetle attacks compared to lodgepole pine. However, very little data has been published that quantitatively describes the interactions between mountain pine beetles and whitebark pine. Further, specific factors shaping individual whitebark pine resistance to attack is largely unknown. A more refined understanding of mountain pine beetle host selection in whitebark pine stands that accounts for life history characteristics and environmental conditions would aid in identifying the response of subalpine forests to future outbreaks. This is critical given that mountain pine beetles are predicted to become a more permanent presence at high elevation under future climate conditions (Hicke et al., 2006).

"These lodgepoles and the mountain pine beetle, they've got an understanding — even if we don't fully understand it ourselves...They've worked out a deal., Those whitebark pines, now…I'm not so sure they've worked out a deal.," (Jesse Logan, High Country News, 2008)

Whitebark pine's apparent paucity of defenses and their consistently harsh environment for mountain pine beetle reproduction has led some researchers to believe that the two species have not co-evolved (Logan, 2007). However, warming temperatures associated with anthropogenic climate change are anticipated to enhance the beetle's presence in these high elevation ecosystems through both direct and indirect effects. Directly, fewer extreme cold events experienced throughout the west (Vavrus et al., 2006; Caprio et al., 2009) are reducing the likelihood of low temperatures capable of terminating outbreaks. Longer growing seasons extend the developmental period for mountain pine beetles and will likely increase mountain pine beetle generation rates (Logan and Bentz, 1999). High elevation whitebark pine habitats are predicted to increasingly be the ideal habitats for univoltine mountain pine beetle populations and the most likely regions to support outbreaks under future climate models (Logan and Powell, 2001; Hicke et al., 2006). In low elevation lodgepole pine forests, modeling suggests that warming temperatures may lead to partial multivoltism (more than one generation per year) and actually diminish the likelihood of synchronous emergence and the potential for an outbreak (Hicke et al., 2006). Indirectly, higher temperatures enhance moisture deficits and reduce vigor in water-limited trees. To minimize water losses, trees reduce

their respiration rates and can thereby diminish sources of carbon to assimilate into chemical defenses (McDowell et al., 2008). While the influence of drought-stress on host defenses is complex (Herms and Mattson, 1992), most researchers have assumed increases in moisture related stress to decreases host defenses and the threshold for successful beetle attack (McDowell et al., 2008; Bentz et al., 2010).

Decades of fire suppression appear to have enhanced the spatial scale of current outbreaks in low elevation forests. In lodgepole pine forests of central British Columbia, the annual area burned dropped from 100,000 ha prior to suppression to a mere 1,000 ha in recent years (Taylor et al., 2006). Historically, severe but isolated fires would maintain the landscape in a patchwork of tree ages and size classes, meaning different susceptibilities for supporting an outbreak. Currently, fewer patches of young and unsuitable lodgepole pine hosts may be increasing connectivity for outbreak populations and enhancing the spatial extent of outbreaks (Taylor et al., 2006). The influence that fire suppression has had on subalpine forests, however, is less clear. In whitebark pine-dominated forests, fire suppression is suggested to have initiated widespread forest conversion to shade-tolerant species (Keane and Arno, 1993; Keane, 2001), which in theory would actually decrease stand susceptibility to attacks. However, many researchers have found fire regimes in subalpine forests to be largely operating within the historic range of variability, since fire return intervals at high elevations can be substantially longer than the period of effective fire suppression (Johnson et al., 1990; Larson et al., 2009; but see Kipfmueller and Baker, 2000; Murray et al., 2000).

The current outbreaks that are occurring at both low and high elevations are frequently considered to be unprecedented in scale, yet are anticipated to have fundamentally different long-term effects on either ecosystem. The effects of mountain pine beetles on low elevation forests have been extensively investigated, and even though current outbreaks are widespread, they are not anticipated to significantly diminish the distribution or abundance of lodgepole pine in the future (Romme et al., 2006; Kaufmann et al., 2008). Alternatively, current outbreaks in high elevations are thought to be outside the range of historic variability in terms of duration and intensity (Logan et al., 2010). This, coupled with potentially low defense reactions, an obligate reliance on Clark's nutcrackers, and the effects of blister rust have raised serious questions about the viability of whitebark pine as an ecologically significant component of subalpine communities in the future (Logan et al., 2010).

The potential for substantial or even permanent losses of whitebark pine from high elevation communities is tempered by a general uncertainty regarding the nature of mountain pine beetle disturbances in subalpine forests. Mountain pine beetles appear to have had a presence in these ecosystems for millennia (Brunelle et al., 2008), and the early 20th Century outbreak that occurred in whitebark pine communities had perhaps a similar spatial extent as the current event (Gibson et al., 2008). Forest Service documents during the 1920s and 1930s outbreak attest to the widespread nature of the event, yet only briefly mention the conditions in high elevation whitebark pine communities (Evenden, 1928; Gibson, 1931; Evenden, 1934; Evenden, 1936; Evenden, 1944). The effects of this outbreak, however, are still visible throughout much of the central and northern Rocky

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Mountains in the form of desiccated graying whitebark pine snags (figure 2; Ciesla and Furniss, 1975; Perkins and Swetnam, 1996; Kipfmueller et al., 2002; Larson, 2009). While there are some indications that whitebark pines are able to regenerate in mountain pine beetle-affected stands (Larson, 2009; Larson and Kipfmueller, 2010) the actual patterns of mortality during and after the event are relatively unclear. A better understanding of these mortality patterns at the individual tree and stand scale would enhance predictions for the long-term effects that climate change-driven outbreaks will have on whitebark pine communities.

Research methods and questions

I employed dendroecological methods in a variety of ways to conduct my thesis research. Broadly, dendroecology is the use of tree rings to understand ecological phenomena (Swetnam and Fritts, 1985; Kipfmueller and Swetnam, 2001). To accurately identify patterns of establishment, mortality, and growth, I crossdated every tree. Cross-dating is a fundamental principle of dendrochronology and involves matching patterns in ring widths across many different trees to construct a "master chronology" that reflects generalized patterns of narrow and wide rings for a particular region (Fritts, 1976; Stokes and Smiley, 1996). By cross-dating the trees I was able to accurately assign precise calendar dates to each individual ring and was a critical step for identifying patterns of establishment and mortality surrounding an ecological event that occurred decades ago.

This thesis focuses on the internal dynamics of the early 20th Century high elevation mountain pine beetle outbreak within a watershed of the Pioneer Mountains,

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Montana (Figure 2). The research is divided into two chapters that focus on the outbreak at different scales. In Chapter 2 I first identify the timing of the historic outbreak in the study area, and then identify the potential factor that caused the outbreak to end. One of two conditions typically limit an outbreak: the progressive reduction of susceptible hosts or the occurrence of extreme cold temperatures that kill substantial levels of overwintering beetles. These two different limits, however, have manifestly different effects on landscape structure in terms of available seed sources. After I reconstruct the outbreaks limits, I then consider the influence that climate change will have on future beetle disturbances in the study area with respect to changes in the frequency of extreme cold events and stand-level characteristics that influenced host mortality patterns.

Chapter three focuses on the individual tree scale, and identifies distinguishing characteristics in growth patterns between whitebark pines that were killed and those that survived the outbreak. Specifically, I examine whether the size, age, or growth rate of a tree alters its selection by beetles or ultimate survival., To the best of my knowledge, no research has been published on mountain pine beetle discrimination between whitebark pine hosts. Yet the identification of influential factors shaping mortality are important in light of a questioned evolutionary history between the two species and warming temperatures that may alter host defenses and facilitate higher mountain pine beetle populations.

Between 2008 and 2009, twenty 1/10th ha plots were sampled in a watershed of the Pioneer Mountains, Montana, encompassing Lake of the Woods, Odell Lake, and Schwinegar Lake (Figure 1). Increment cores were extracted from all trees >5 cm

diameter at breast height (DBH) in the ten plots sampled in 2008, while only trees in a smaller 1/20th ha subplot were cored in the 10 plots sampled in 2009. Between the twenty plots, 1688 individual trees were successfully crossdated. For Chapter 3, 33,987 rings from 123 whitebark pine series were measured. Although this study takes place in a single watershed, it is an exceptionally rich and detailed data set.

There are a number of other aspects to this study that are not directly discussed in my thesis. The dendroecological data describing establishment and mortality patterns will be used to identify potential influences that the mountain pine beetle outbreak had on successional processes (see Figures 3 and 4). The identification of such patterns may suggest the future ecological conditions in high elevations forests now experiencing mountain pine beetle outbreaks.

Lake of the Woods Age Structure

Engelmann Spruce
(n=99)

Subalpine Fir
(n=498)

Lodgepole Pine
(n=381)

Whitebark Pine
(n=708)

Year
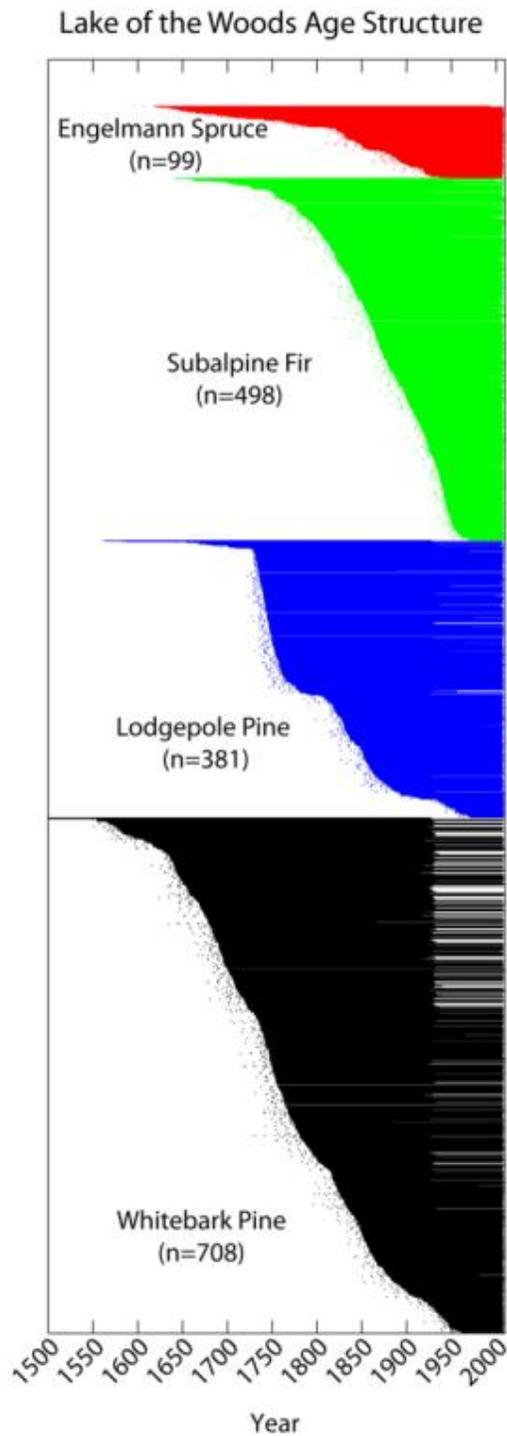
Figure 3. All crossdated trees from the twenty 1/10th ha plots in the Pioneer Mountains study area. Each line represents the lifespan of an individual tree, and the dotted lines represent the estimate rings to center. Trees are arranged by species and inner ring date, and facilitates identifying establishment patterns.
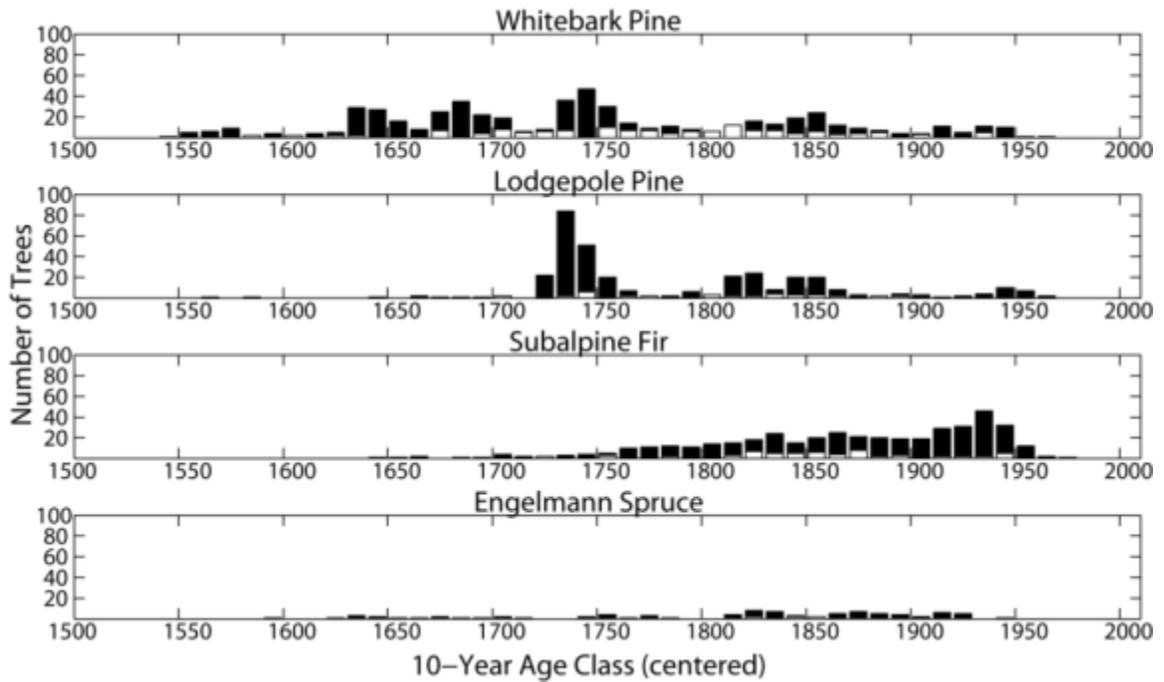
Figure 4. Decadal establishment patterns in the Pioneer Mountains study area. Black bars represent the inner ring dates for trees that have good estimates to pith, and white bars represent the inner ring dates of trees that could not be estimated to pith.

Chapter 2: Historic and future limitations to high elevation mountain pine beetle populations in the Pioneer Mountains, MT

Introduction

Rising temperatures associated with anthropogenic climate change are increasingly altering species interactions (Parmesan, 2006). Insects, as poikilothermic organisms, have few internal mechanisms to regulate their body temperatures and will react disproportionately to climate change (Robinet and Roques, 2010). Rapid reproductive rates enable insect populations to respond quickly to only moderate changes in temperature, and have facilitated pole-ward expansions in species distributions across a wide range of taxa (Hickling et al., 2006). Recent mountain pine beetle outbreaks in north-central Canada and in high elevation whitebark pine (*Pinus albicaulis* Engelm.) forests have received considerable attention because these regions are considered, respectively, novel and historically marginal habitats for the beetles. Given sufficient warming, jack pine (*Pinus banksiana* Lamb.) forests of central Canada may become susceptible to mountain pine beetle populations; however, there are serious uncertainties regarding this potential (Bentz et al., 2010; Safranyik et al., 2010). Increases in outbreak frequencies at high elevations may have negative long-term effects on whitebark pine (Logan et al., 2010), an ecologically sensitive keystone species (Ellison et al., 2005). Unlike in the boreal forests of Canada, outbreaks in whitebark pine ecosystems do not

appear to have been historically limited by host availability, but primarily by consistently cold temperatures (Safranyik et al., 2010).

Temperatures directly regulate mountain pine beetle populations by influencing developmental rates and overwintering survival., Mountain pine beetles lack diapause (Logan and Bentz, 1999), a genetically-based torpor initiated by adverse environmental conditions (Bale and Hayward, 2010), which means developmental cues for the beetle are initiated by seasonal temperatures alone (Bentz et al., 1991). Throughout most of the beetle's range, there is sufficient accumulated heat throughout the growing season to allow a single-year (univoltine) life cycle (Safranyik and Carrol, 2006). Univoltinism facilitates synchronous beetle emergence from hosts in the summer and aids their mass-attack strategy to overcome host defenses (Bentz, 1991). Consistently cold temperatures at high elevations typically lengthened beetle development to two years (semivoltinism), and drastically reduced the potential for outbreaks (Amman, 1973). Extreme cold temperatures also heavily influence mountain pine beetle populations and are often the single greatest cause of beetle mortality in a given year (Cole, 1981). To survive low temperatures, mountain pine beetles go through a cold hardening process that involves the buildup of glycerol (Bentz and Mullins, 1999). Glycerol accumulates gradually as a response to seasonal temperature changes, leading to fluctuations in the cold-tolerance threshold over the course of a year. Maximum cold tolerance occurs during the winter months and is typically at or slightly above -40° C (Figure 1; Regniere and Bentz, 2007; Safranyik et al., 1975; Wygant, 1942). Substantial levels of beetle mortality can occur if

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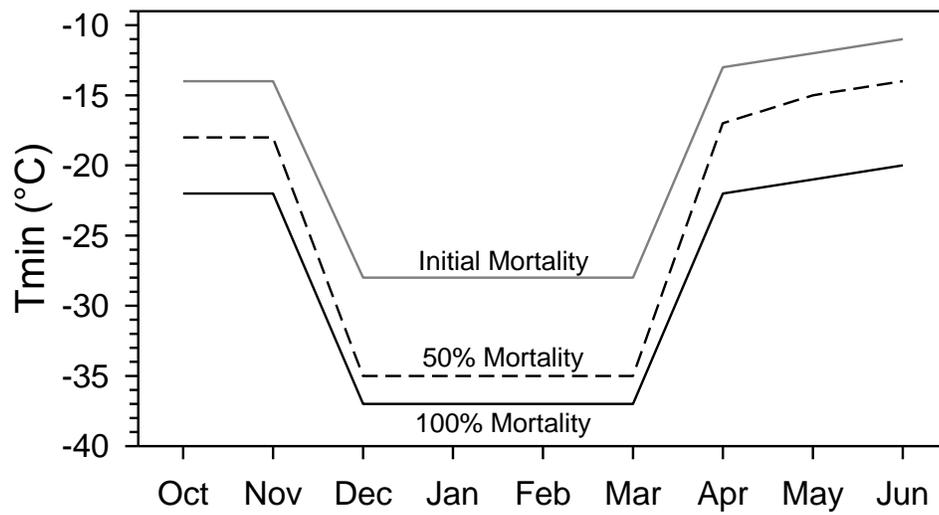
Figure 1. Linear interpolations of cold induced mortality thresholds for mountain pine beetles during different months (adapted from Wygant, 1942).

winter temperatures fall below this point, especially for several days (Safranyik and

Linton, 1998), or if there are unseasonably cold periods in spring or fall.

The potential for an outbreak to occur and persist also directly depends upon the

availability of susceptible hosts. Here, the term susceptibility refers to the inherent

suitability of a tree, stand, or landscape to support mountain pine beetle populations

(Shore and Safranyik, 1992). Typically, the number of large-diameter hosts is considered

the most important factor for supporting an outbreak (Anhold and Jenkins, 1987;

Bjorklund et al., 2009; Shore and Safranyik, 1992). Large trees frequently have thicker

phloem (Amman, 1969; Shrimpton and Thomson, 1985), which can enhance beetle brood

size and population expansion (Berryman, 1976). However, in lodgepole and ponderosa

pine, the healthiest trees with the thickest phloem are often the best defended (Berryman,

1972; Waring and Pitman, 1985). As a result, the ability for an outbreak to occur depends

not only on the presence of susceptible hosts, but also on the ability of beetles to

overcome their defenses (Shore and Safranyik, 1992). In a given stand, the ability for

beetles to successfully attack vigorous trees may be aided by environmental stress such as

drought (Berg et al., 2006; Ferrell, 1996; Raffa et al., 2008), or beetle immigration from

nearby outbreak populations (Shore and Safranyik, 1992). During latter stages of an

outbreak that has not been affected by lethal temperatures, beetle populations are

increasingly relegated to nutritionally poor and/or heavily defended trees, and will

ultimately dwindle in size (Safranyik and Carroll, 2006). While these dynamics have

been carefully studied with respect to lodgepole pine, the beetle's dynamics in subalpine

forests, especially those dominated by whitebark pine, is considerably less clear (but see Perkins and Roberts, 2003).

While climate change is predicted to ameliorate previous limits on beetle development and survival at high elevations (Hicke et al., 2006), there have been widespread outbreaks in those ecosystems in the past. Palynological data suggests that mountain pine beetles have been present in whitebark pine ecosystems for millennia (Brunelle et al., 2008). More recently, an outbreak spread throughout subalpine forests in the northern Rocky Mountains from 1909-1940 (Ciesla and Furniss, 1975; Evenden, 1944; Furniss and Renkin, 2003; Kipfmueller et al., 2002; Perkins and Swetnam, 1996). In terms of spatial scale and tree mortality, it was the most comparable historic event to current high elevation outbreaks (Gibson et al., 2008) yet it appears to have been shortened in duration in some locations due to extreme low temperatures (Evenden, 1944). While Forest Service surveys at the time described the dynamics of the outbreak in lodgepole pine stands (e.g. Evenden, 1928; Evenden, 1934; Gibson, 1931), few reports noted the intensity of the outbreak within high elevation stands. Since the reason an outbreak ends – either extreme low temperatures or host reductions – has significant impacts on stand structure and available seed sources, the identification of stand-level limits on historic outbreaks would better contextualize current whitebark pine mortality

This research examines why the historic 1920s/1930s outbreak ended within a watershed of the Pioneer Mountains, Montana. Dendrochronological techniques are used to identify the timing of the outbreak and to reconstruct stand structure prior to and following the event. Daily minimum temperature data and the stand susceptibility index

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(SSI; Shore and Safranyik, 1992) are then used to identify factors that contributed to the cessation of the outbreak. This study also considers the potential influence that climate change will have on whitebark pine-mountain pine beetle interactions in the study area with respect to changes in the frequency of extreme cold events and stand-level characteristics that influenced host mortality patterns.

Study area

The study site (PMT) is located within the Pioneer Mountains of southwest Montana (Figure 2). The Pioneer Mountains are in effect a forested island rising out of a grass- and sage-dominated community that is characteristic of the high intermountain valleys in the northern Rocky Mountains. The changes in species composition from the montane to subalpine ecosystems reflect the progressively cooler and moister conditions as elevation increases. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) are dominant at lower elevations of the range. Subalpine communities at higher elevations are mixed and support substantial components of whitebark pine, lodgepole pine, Engelmann spruce (*Picea engelmanii* Parry), and subalpine fir (*Abies bifolia* A. Murray). Within PMT, nearly homogenous lodgepole pines stands, likely initiated by wildfire, occupy large areas. Large whitebark pines are abundant both as living trees and dead snags. Subalpine fir grow in very high densities in some stands, and, along with Engelmann spruce, tend to inhabit sites with higher moisture availability (Alexander et al., 1990). The distributions and densities of these species are highly influenced by both

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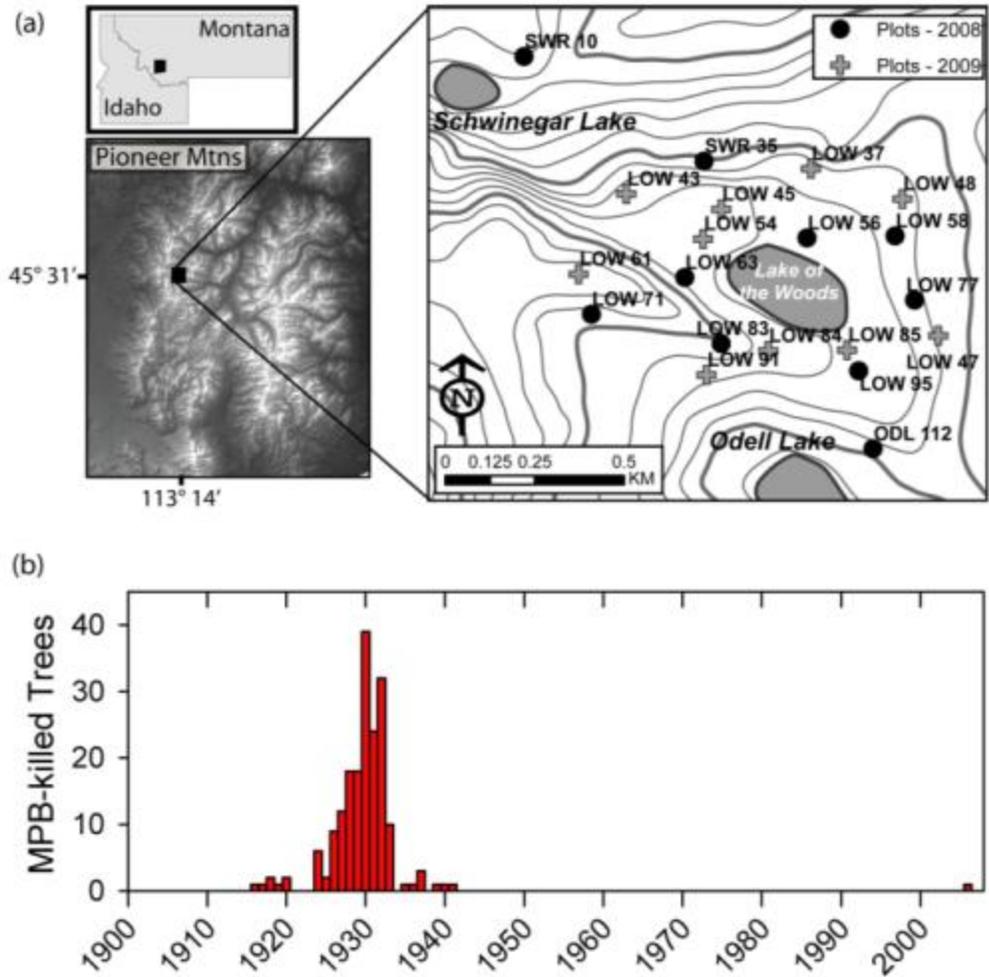
Figure 2. (a) Location of study area and 1/10th ha plots surrounding Lake of the Woods in the Pioneer Mountains, southwest Montana. Plots sampled in 2008 (black circles) were used in this analysis. (b) Crossdated death dates of mountain pine beetle- (MPB) killed trees within all sampled plots.

biophysical site characteristics and disturbance histories (Kipfmueller and Kupfer, 2005; Larson, 2009; Larson and Kipfmueller, 2010). The Pioneer Mountains at 2500 m are generally cool, averaging -9.2 C in January and 12.8 C in July, and are comparatively drier than nearby ranges, averaging only 77 cm of precipitation annually.

Along with the Beaverhead Mountains to the east, and the Anaconda Mountains to the north, the subalpine region of the Pioneer Mountains suffered heavy pine mortality during the early 20th Century mountain pine beetle outbreak. This outbreak is evident both visually, in the form of dead standing snags, as well as historically from Forest Service reports (e.g. Evenden, 1928; Gibson, 1931; Evenden, 1934; Evenden, 1936; Evenden, 1944). Beginning around 1910, a major outbreak was first recorded in the Flathead National Forest in north-central Montana (Evenden, 1944). In 1911 and 1912, mortality in lodgepole pine stands surrounding the Bighole Basin were first noticed, yet subsided for unknown reasons until 1924 (Evenden, 1944). After 1924, Evenden (1944) indicated widespread outbreaks throughout Montana, and portions of Idaho and Wyoming lasting into the early and mid 1930s.

Methods

Dendrochronological field and laboratory methods

Twenty 1/10th ha plots were sampled at PMT in 2008 and 2009 in the forests surrounding Lake of the Woods, Odell Lake, and Schwinegar Lake (Figure 2) as part of a study examining species composition and age structure. In 2008, ten plots were sampled, with two increment cores collected from every tree >5cm diameter at breast-height

(DBH) in the plot. The remaining ten plots were sampled in 2009 in the same manner, except that only trees within a more limited 1/20th ha subplot were cored for age structure information.

All of the whitebark pines categorized as mountain pine beetle-killed in this study exhibited characteristic j-shaped galleries and had blue-staining fungus visible within the core. In this subalpine ecosystem, most whitebark pine snags are remarkably intact and standing, despite having died primarily in the 1920s and 1930s (Figure 2). However, physical weathering has the potential to erode the outer rings from these trees. In order to identify whether extreme cold temperatures led to the termination of the outbreak, the exact year of mortality for each tree must be known. To enhance the likelihood that the tree's actual death date was captured, multiple cores from different places on the tree's bole were collected from each tree. At least one core was always collected from the angle that visually appeared to have the least weathering. Increment cores were mounted, surfaced until individual xylem cells were clearly visible under magnification, and cross-dated using standard dendrochronological techniques (Stokes and Smiley, 1968). If the death dates from different cores of a single mountain pine beetle-killed trees were different, the core with the most recent date was used.

Extreme cold temperatures

I first compared the occurrence of extreme cold temperatures with the timing of the mountain pine beetle outbreak. Records of daily minimum temperature were collected from the US Historical Climatology Network for Dillon, MT, the nearest location with

long-term climate data (Menne et al., 2009). Dillon lies at 1555 m in a valley directly to the southeast of the Pioneer Mountains. Since Dillon is roughly 1000 m lower in elevation than PMT, winter temperatures would be generally warmer and precipitation lower.

Using daily minimum temperatures from September through April, I identified extreme cold periods that may initiate significant levels of beetle mortality. I identified each year and incident that (1) temperatures were below the 50% mortality threshold (LT_{50}) and (2) temperatures met or exceeded the 100% mortality threshold (LT_{100}) defined by Wygant (1942), and (4) there was a cold snap in which minimum temperatures over a three day period averaged below the LT_{50}. Since mortality thresholds change throughout the year as a result of the cold-hardening process (Regniere and Bentz, 2007), I present the most extreme daily temperatures for each month as a departure from mountain pine beetle-killing temperatures for that given month. I further compared the occurrence of these extreme temperatures with the termination of the outbreak. Potential changes in the frequency of extreme cold events between the first and second half of the 20th Century are also evaluated using a two sample Student's t-test.

Stand susceptibility

Various indices have been developed to calculate the suitability of a given stand to support a mountain pine beetle outbreak. One of the most commonly used metrics has been the stand susceptibility index (SSI) of Shore and Safranyik (1992). The SSI uses the percentage of susceptible pine basal area, mean age of pine hosts, stand density, and

geographic location to calculate the probable severity of an outbreak in a given stand.

Shore et al. (2000) field-tested the SSI in British Columbia and found there to be good

agreement between SSI values and lodgepole pine mortality following the end of a

localized outbreak. Shore et al. (2006) updated the original SSI model to use continuous

functions instead of categorical variables. While the SSI model was developed for use in

lodgepole pine-dominated stands, Perkins and Roberts (2003) found characteristics

affecting susceptibility in whitebark pine to be similar to those of lodgepole pine.

I use the SSI model (Shore et al., 2006) to calculate stand susceptibility in the

PMT as of 1933, the year that there were major reductions in mountain pine beetle-

caused pine mortality. This procedure is used to assess whether there were sufficient

numbers of pine hosts for the beetles to continue an outbreak, or whether host depletion

led to population declines and the cessation of the outbreak. Ten of the twenty plots from

which data were collected are used in the stand susceptibility analysis. The ten plots

contain a variety of age and stand structures and are representative of the heterogeneity in

PMT. In order to reconstruct stand conditions in 1933 with increment cores collected in

2008, I used the following:

$$\text{DBH}_{1933} = \text{DBH}_{2008} - 2\text{RI}_{1933\text{-}2008}$$

where DBH_{2008} is the diameter at breast height (cm) recorded in the field during 2008,

$\text{RI}_{1933\text{-}2008}$ is radial increment from 1933-2008 measured by hand from the increment core

to the nearest 0.1 cm, and DBH_{1933} is the calculated diameter at breast height for a given

tree in 1933 (Perkins and Roberts, 2003). DBH_{1933} is not necessarily the precise DBH for a given tree in 1933, yet it functions as a useful and likely close approximation. Here, I did not incorporate the location variable into the SSI calculation because all of the trees used in this study came from the same general geographic region. Shore and Safranyik (1992) also developed a beetle pressure index that, along with SSI, was used to determine the stand risk index, which estimates total mortality for a given stand. Since accurate accounts of beetle populations are unavailable for the Pioneer Mountains in the 1920s and 1930s, I did not calculate the beetle pressure index. This is not an issue, however, since I only aimed to identify whether sufficient numbers of suitable hosts were present to support beetle populations. I used following equations from Shore et al. (2006) to compute SSI:

$$SSI = P \ x \ A \ x \ D$$

where P is the percentage of susceptible pine (both lodgepole and whitebark) basal area relative to other species, A is the age factor (determined from the average age of susceptible hosts), and D is the density factor (determined from stems per hectare (sph) of all hosts). The percentage of susceptible pine is calculated as:

$$P = \frac{\text{basal area of pine} \geq 15\text{cm DBH}}{\text{basal area of all species} \geq 7.5\text{cm DBH}} \ x \ 100$$

The age factor is calculated as:

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If the average age of susceptible pine is:	Then the age factor (A) is:
<40 years	0.1
40-80 years	$0.1 + 0.1 \left[\dfrac{(\text{age} - 40)}{10} \right]^{1.585}$
81-120 year	1.0
121-510 years	$1.0 - 0.5 \left[\dfrac{(\text{age} - 120)}{20} \right]$
Greater than 510 years	0.1

The density factor is calculated as:

If the density of the stand in stems per ha (sph) (for all species ≥ 7.5 cm DBH) is:	Then the age factor (A) is:
<650	$0.0824 \left(\dfrac{\text{sph}}{250} \right)^{2}$
650-750	$1.0 - 0.7 \left(\dfrac{3 - \text{sph}}{250} \right)^{0.5}$
751-1500	1.0
Greater than 1500	$\dfrac{1.0}{\left[0.9 + \left[0.1 \exp \left(0.4796 \left(\frac{\text{sph}}{250} - 6 \right) \right) \right] \right]}$

The basal area and sph of mountain pine beetle killed trees were also included to identify

stand conditions prior to the outbreak and outbreak intensity for each individual plot. To

help test the efficacy of the SSI to predict mortality in mixed whitebark pine-lodgepole

pine forests, I identified relationships using Spearman rank-order correlations between

percent of susceptible pines killed by mountain pine beetles, ratio of whitebark pine to

lodgepole pine, and SSI values before and after the outbreak. Spearman rank-order

correlation is non-parametric, and is better suited to compare relationships between low

numbers of variables than Pearson product-moment correlations. While these correlations

are based on only ten plots, they may still reveal important patterns of mortality in

subalpine ecosystems.

In addition to updating the original model, Shore et al. (2006) developed a pine

susceptibility index (PSI). While SSI measures the susceptibility of the entire stand,

which includes non-pine species, PSI identifies how susceptible the pine-only component

of the stand is to beetle-caused mortality. PSI values do not reflect the amount of

susceptible pine, but only the susceptibility of the pine to attack.

$$PSI = \frac{100}{(1 + \exp(-(P - 22.7)/5.3))}$$

Results

Timing of the outbreak

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Within all twenty plots, 185 mountain pine beetle-killed trees could be precisely dated. These death dates reveal that the outbreak began slowly around 1924 and consistently rose until its peak in ~1930 (Figure 2). Mortality was high through 1932, after which there was an abrupt decline. Outbreak conditions appeared to end in 1933. Mountain pine beetles killed trees after 1933 at very low levels.

Extreme cold temperatures

Since 1900, twelve years had low temperatures that met or exceeded the LT_{100} threshold (Figure 3). Temperatures exceeded the LT_{50} threshold 84 times (without exceeding the LT_{100}; Figure 6), and minimum temperatures averaged below the LT_{50} over three consecutive days only six times (Figure 3).

The -40°C extreme low temperature in 1933, as well as a three day period during the same year that averaged below the LT_{50}, temporally corresponds to greatly reduced numbers of mountain pine beetle-killed trees (Figure 3). There was, however, another cold event in 1927 that met the LT_{100} and five years from 1924-1932 that temperatures met or exceeded the LT_{50}. There were no other years during the outbreak that experienced a 3+ day cold snap.

Overall, years after 1950 had a lower frequency of lethal mountain pine beetle temperatures compared to those from 1900-1950 (Figure 4). Daily temperatures met or exceeded the LT_{50} and LT_{100} significantly more frequently prior to 1950 (64 times) compared to the years since 1950 (39 times, n=106, t=2.06, p<0.05). This statistic, however, may be misleading since the 31 of these cold events occurred in the 1930s

Figure 3. The incidence that the lowest daily temperature per month from Oct.-Apr. exceeded the LT_{100} ($\triangledown$) for mountain pine beetles (see Figure 1). Negative departures indicate temperatures below the LT_{100}. Years when minimum temperatures averaged below the LT_{50} over a 3-day period are also identified ($\blacklozenge$). Bottom graph represents the cross-dated death dates for all mountain pine beetle-killed trees in the study area.
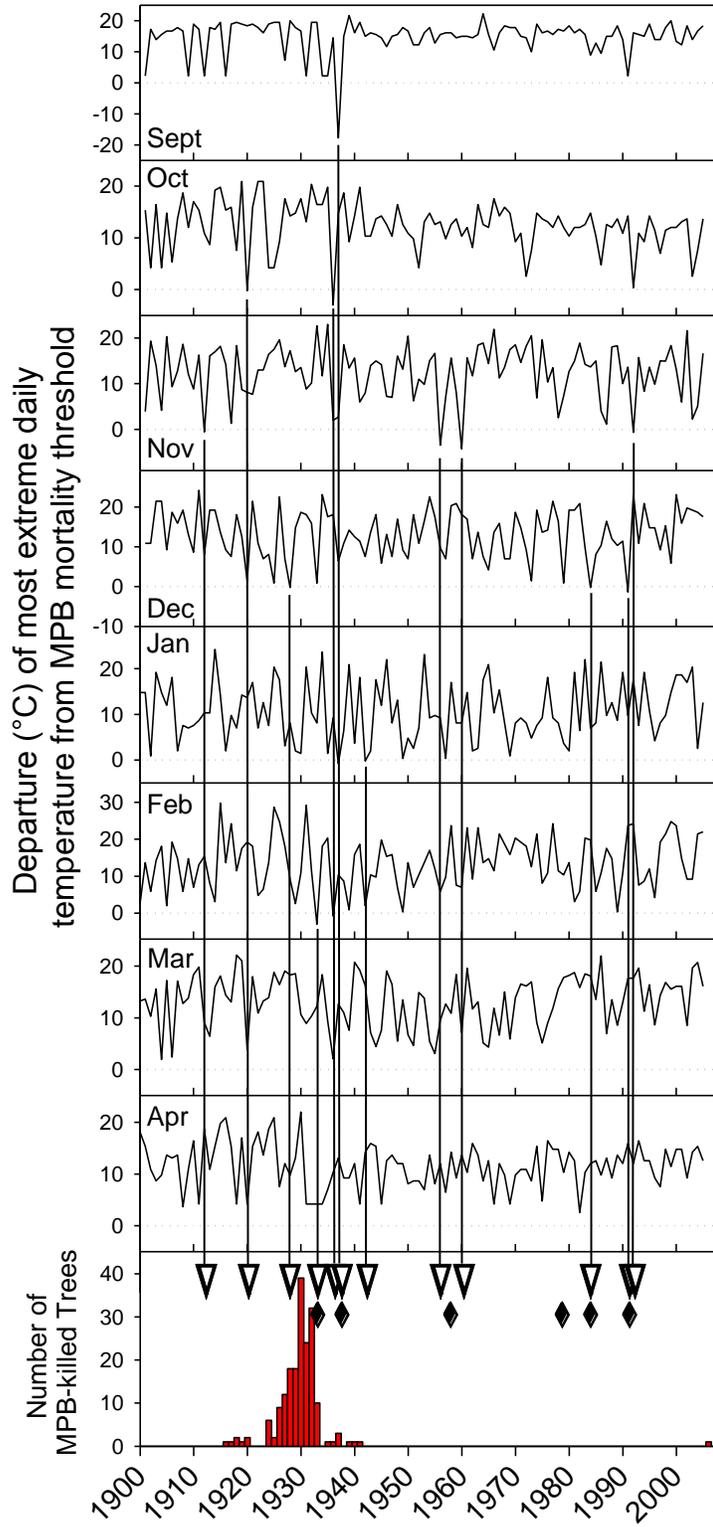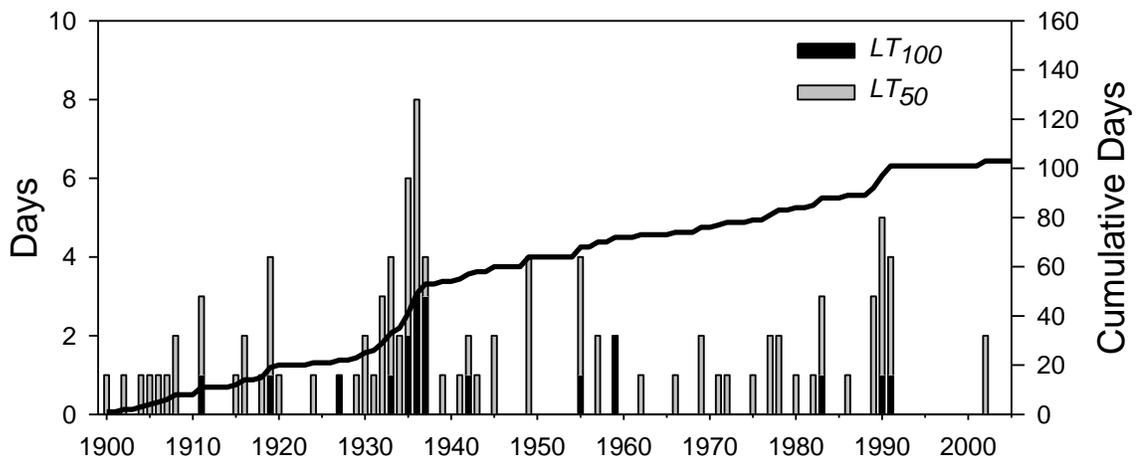
Figure 4. The number of days per year that daily minimum temperatures in Dillon, MT, exceeded the LT_{50} and LT_{100} for mountain pine beetles, and cumulative distribution of extreme low temperatures.

alone. Yet the frequency of extreme cold events similarly occurred in 60% of years prior to 1950, and only in 34% of years since 1950 (n=106, t=2.76, p<0.01).

Stand susceptibility

Potential SSI values for a given stand range from 0-100, with higher values suggesting more conducive conditions for mountain pine beetle attacks. Stands with SSI values >30 are most frequently associated with mountain pine beetle outbreaks (Safranyik et al., 2010). Prior to the outbreak, SSI values ranged from 34.0 to 96.0, and had a mean of 67.5 (Figure 5; Table 1). SSI values generally declined after the outbreak ($\bar{x}$=49.0) but were still relatively high (Figure 5, Table 1, ranging up to 83.6) and indicates that many susceptible pines persisted in PMT following the outbreak. The observed declines in SSI values were clearly caused by host mortality from mountain pine beetle attacks. These levels of mortality varied considerably between plots (from 0-72.9% of susceptible pines killed; Table 1) and, interestingly, had no clear relationship with pre-outbreak SSI values (Figure 6). The ratio of whitebark pine to lodgepole pine appears to more closely correspond with mortality levels and post-outbreak SSI values (Figure 6); however, the low n used here makes these correlations tentative.

Discussion

Climate suitability regulates both the potential for an outbreak to begin by influencing beetle phenology and host physiology (Bentz et al., 2010), and the ability for outbreak populations to persist across a landscape through the presence or absence of

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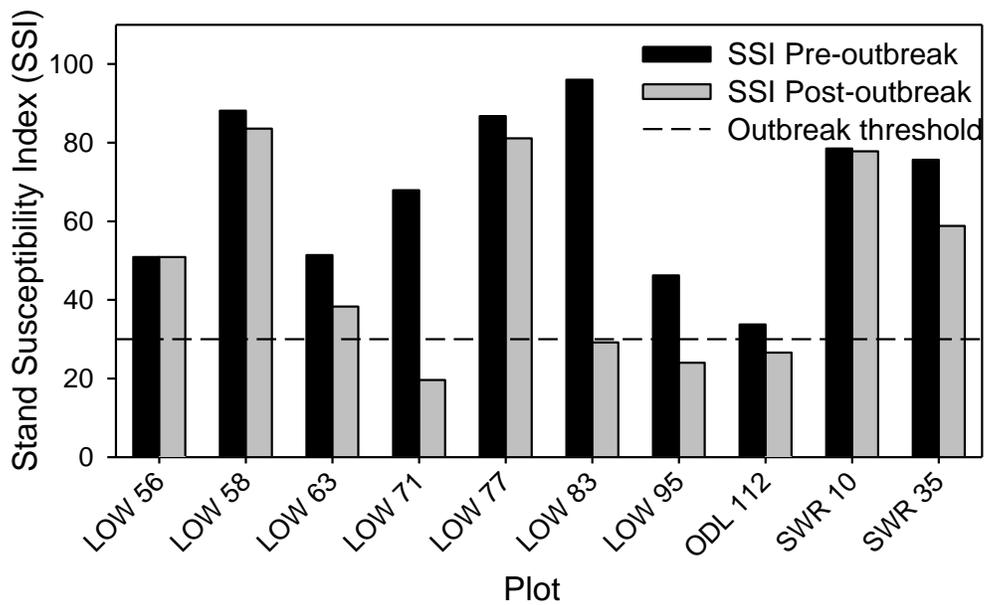
Figure 5. Change in SSI values for each plot before and after the outbreak. Dotted line indicates the threshold at which an outbreak is likely to occur within a plot (Safranyik et al., 2010).
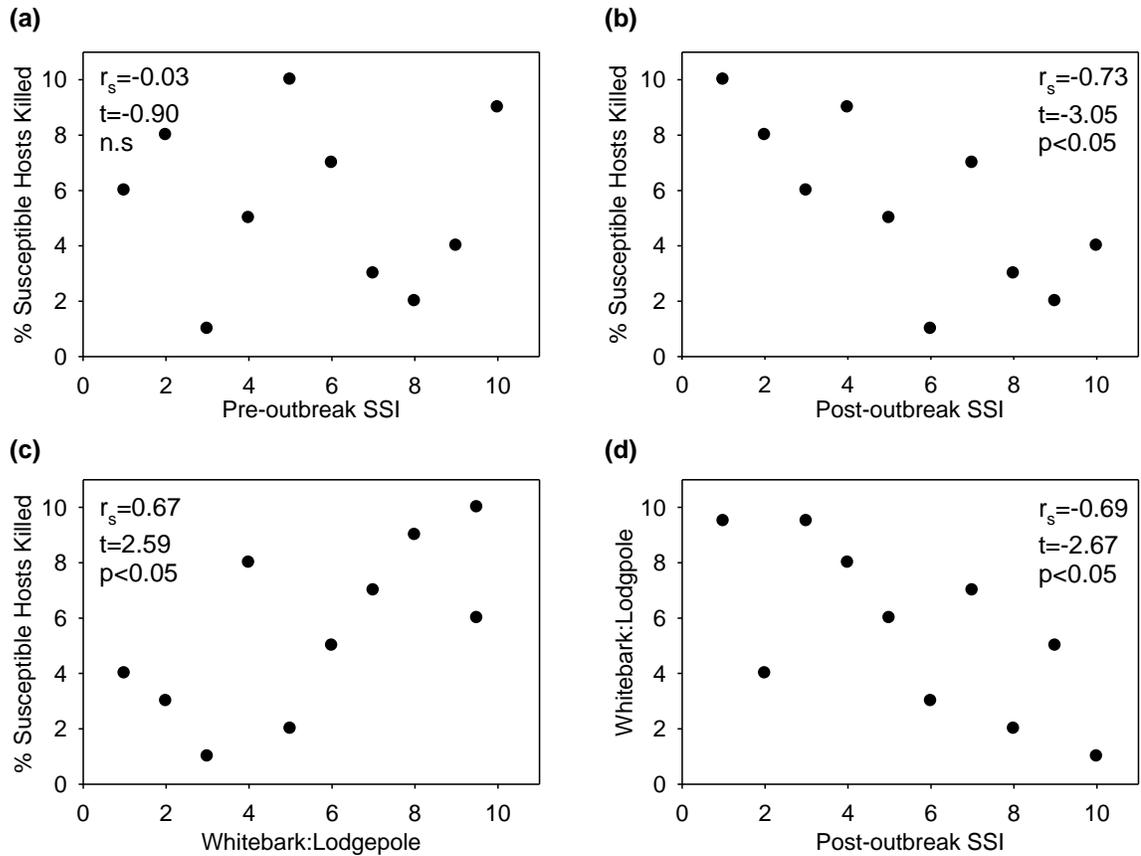
Figure 5. Spearman rank-order correlations between plots (n=10). In the study area, (a) there was no significant relationship between pre-outbreak stand susceptibility index (SSI) values and outbreak intensity in terms of total host mortality, however, (b) there was a close relationship between the outbreak intensity and post-outbreak SSI. (c) The ratio of whitebark pine to lodgepole pine appears to more closely explain mortality levels and (d) post outbreak SSI values.

Plot	Pre-outbreak SSI	Post-outbreak SSI	PSI	% Susc. Killed	Susc. PIAL:PICO	Importance Values			
						PIAL	PICO	ABBI	PIEN
LOW 56	50.9	50.9	99.9	0.0	0.45	77.8	64.4	57.8	0.0
LOW 58	88.1	83.6	99.9	4.9	0.07	19.5	171.2	6.1	3.3
LOW 63	51.4	38.3	95.9	20.0	0.67	60.0	29.8	53.6	56.6
LOW 71	67.9	19.6	91.9	72.7	1.00	54.9	5.6	46.1	93.4
LOW 77	86.8	81.1	99.9	2.3	0.65	110.5	68.4	21.1	0.0
LOW 83	96.0	29.2	99.9	55.4	0.99	195.7	2.0	2.3	0.0
LOW 95	46.2	24.0	99.5	53.8	0.60	65.7	41.6	88.9	3.8
ODL 112	33.7	26.6	99.9	25.0	1.00	158.7	4.5	33.7	3.1
SWR 10	78.5	77.8	99.9	2.8	0.18	39.2	156.7	4.2	0.0
SWR 35	75.6	58.8	99.9	38.0	0.96	112.4	18.6	33.0	36.0
All sites	67.5	49.0	98.7	27.5	0.70				

Table 1. Plot characteristics for each plot used in this analysis. Importance values (relative basal area + relative stem density) were also calculated for each species within all plots as of 1933. Species include whitebark pine (PIAL), lodgepole pine (PICO), subalpine fir (ABBI), and Engelmann spruce (PIEN).

cold events. During an intense outbreak, mountain pine beetles can kill nearly 90% of susceptible hosts at regional scales prior to the deleterious effects of host depletion on populations (Romme, 1986; Raffa et al., 2008). Alternatively, extreme cold events can quickly terminate an outbreak before all susceptible trees are killed. Whitebark pine death dates from the Pioneer Mountains, Montana indicate a major decline in beetle-caused mortality in 1933 and was temporally synchronous with the most extreme cold event recorded in instrumental climate data from Dillon, Montana. The high numbers of susceptible hosts that persisted across the landscape suggest that, had cold temperatures not occurred, the outbreak would likely have persisted and further reduced pine densities. During the latter part of the 20th Century, there were also apparent reductions in the frequency of extreme cold events. This, coupled with higher rates of beetle attack on whitebark pine compared to lodgepole pine, has potentially negative implications for whitebark pine in a warming climate in which host-depleting outbreaks may become more prominent, particularly if unchecked by periodic cold events.

Limits on early 20th Century outbreak

Prior to the outbreak, PMT was structurally very susceptible to beetle attack. SSI values before the outbreak were >30 in each plot, which is considered the threshold for epidemic mountain pine beetle populations in lodgepole pine stands (Safranyik et al., 2010). Mountain pine beetle-caused mortality appears to have steadily increased from 1924-1930, stayed high until 1932, and then declined dramatically in 1933. This decline is coincident with temperatures dropping below the LT_{100} and the LT_{50} over a 3-day

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period. These extended cold periods may be the most important for overwintering

mortality since air pockets within beetle galleries can insulate the overwintering insects

for limited periods from outside air temperatures (Safranyik and Linton, 1998). Evenden

(1944) similarly noted that extreme low temperatures during 1933 may have diminished

beetle populations throughout the region. There were, however, sufficient numbers of

mountain pine beetles in 1933 to successfully colonize hosts (Figure 2). This low-level

survival is not uncommon, since differences in microsite conditions can buffer beetles

from outside air temperatures (Safranyik and Carroll, 2006). In British Columbia,

Safranyik and Linton (1991) found that even though -30°C temperatures in the fall of

both 1984 and 1985 killed the majority of overwintering mountain pine beetles, beetles

overwintering below the snow level largely survived the events.

　　　Following the extreme temperatures in 1933, the PMT still had sizeable numbers

of susceptible pines. SSI values were >30 in six of the ten plots in 1933, suggesting that

much of the area had sufficient hosts to support epidemic populations. All of the plots

were within close proximity to one another (<2 km between the furthest plots), meaning

that distance likely did not inhibit beetle movement into different stands (Shore and

Safranyik, 1992). PSI values were also consistently high for all plots and indicate that the

pines which survived the outbreak were almost exclusively large and susceptible to

attack. The inverse relationship between outbreak intensity and post-outbreak SSI (Figure

6) is to be expected, and indicates that heavily attacked plots had reduced host

availability. Yet despite these differences, overall mortality only exceeded 55% of the

susceptible pines in one plot (Table 1). These mortality levels are considerably lower than

those observed during current high elevation outbreaks in the Greater Yellowstone

Ecosystem, where mountain pine beetles have killed >95% of susceptible whitebark pines

in some stands (Gibson et al., 2008). It should be noted, however, that even though

decomposition rates are extremely slow in these ecosystems, there were downed beetle-

killed snags in certain plots during the time of data collection. This means that actual

mortality levels were probably slightly higher than reconstructed here.

Extreme low temperatures occurred six other times during the course of the

outbreak (Figures 3 and 4), yet had little or no effect on beetle populations and points to

the difficulty of predicting specific mortality events. Two key factors limit the ability to

identify specific cold events capable of producing substantial mortality: the dynamic

cold-hardening process of the beetles and the geographic distance between the climate

station and PMT. Since the beetle's supercooling point (SCP), the temperature threshold

at which ice forms within body tissues, is principally driven by daily temperatures, they

are not necessarily the same between different locations and between different years in

the same location (Regniere and Bentz, 2007). The models used in this study (Wygant,

1942; Safranyik et al., 1975), however, assume a constant mortality threshold, and as a

result, only reflect a generalized potential for beetle mortality (see Regniere and Bentz

(2007) for a mechanistic model). Second, while the climate station in Dillon is only 60

KM from PMT, it is on a valley floor, 1500 m lower in elevation. Temperature inversions

are common in the region and result from cold air settling off mountains and pooling in

nearby valleys. As a result, actual temperatures in PMT may have been warmer than

those observed in the Dillon record.

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Whitebark pines attacked more frequently

The lack of any clear relationship between pre-outbreak SSI values and host mortality levels suggests that factors other than those used in the SSI model influenced beetle attack patterns. The SSI model was developed for lodgepole pine stands in British Columbia, and has unknown applicability to mixed pine stands in the northern Rocky Mountains. Here, plots with higher levels of whitebark pine tended to have greater levels of beetle-caused mortality (Figure 6). This suggests that when the two species are mixed, the typical susceptibility characteristics used in the SSI model may be less important than host species composition. In Yellowstone National Park, an outbreak during the same time period appears to have similarly initiated in high elevation whitebark pine stands (Furniss and Renkin, 2003). However, as the outbreak in Yellowstone National Park progressed, beetles eventually expanded into the lower elevation lodgepole pine forests (Furniss and Renkin, 2003). Had extreme temperatures in the Pioneer Mountains not reduced beetle populations, they may have also expanded into the lodgepole pine-dominated stands. Recent work has supported these early observations, indicating mountain pine beetle preferentially attack whitebark pines when lodgepole pines are also present (Bockino, 2008).

The physiological characteristics driving the apparent mountain pine beetle preference for whitebark pines remain elusive. While Amman (1982) observed greater mountain pine beetle fecundity in whitebark pine compared with lodgepole pine, Gross (2008) found the opposite. Other research has indicated whitebark pine to have different

defense characteristics compared to lodgepole pine. From personal observation, Logan et al. (2010) found whitebark pines to have noticeably diminished defense reactions compared to lodgepole pine. Regardless of the mechanisms, since the SSI model does not weight host preference, it may have diminished capacity to accurately predict susceptibility between stands in mixed lodgepole-whitebark pine forests.

Climate change and high elevation outbreaks

During the 21st Century, extreme cold events are predicted to decrease by 50-100% in most areas of the northern hemisphere (Vavrus et al., 2006). In western Montana, average minimum winter temperatures have risen nearly 2.5°C during the 20th Century (Pederson et al., 2010), and the frequency of extreme low minimum temperatures have declined by approximately 10% per decade since 1938 (Caprio et al., 2009). In Dillon, MT, the frequency of mountain pine beetle-killing low temperatures similarly dropped from 60% of years during the first half of the 20th Century to 34% of years after 1950. Recent reductions are most striking, in which there has been only one extreme cold event since 1991 (Figure 4). In light of these reductions, extreme cold events may have a minimal role in regulating mountain pine beetle populations in the future.

Rising minimum temperatures and fewer extreme cold events are increasing the likelihood that the current outbreak will only end when hosts are depleted. Coupled with the widespread nature of the event (Gibson et al., 2008), current outbreaks may dramatically reduce mature cone-bearing whitebark pines throughout tree's range. If

whitebark pine mortality occurs beyond a critical threshold, it has been speculated that

Clark's nutcrackers (*Nucifraga columbiana* Wilson), the primary dispersing agent of

whitebark pine seeds (Lanner, 1982; Tomback, 1982), may leave heavily affected areas

in search of more food and prevent the remaining whitebark pines from effectively

reproducing (McKinney et al., 2009; Logan et al., 2010). The invasive pathogen white

pine blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.) may lead to further

reductions in seed sources by infesting and killing cone-producing branches (McKinney

et al., 2009; Tomback and Achuff, 2010). It should be noted, however, that substantial

whitebark pine regeneration has been observed in stands following mountain pine beetle

outbreaks (Larson and Kipfmueller, 2010), which suggests that if sufficient seed sources

persist, whitebark pines may be able to effectively repopulate attacked stands particularly

since competition will be reduced. Still, the potential for ecosystem-wide changes along

with the apparent range-expansion of the beetles (Carroll et al., 2004) has led researchers

to consider mountain pine beetles a "native-invasive" species in high elevations (Logan,

2007).

Despite these threats to whitebark pine populations, a clear perspective of whether

current high elevation outbreaks are unprecedented is complicated by coarse and spatially

limited written historic accounts, a common limitation to framing historic ecological

processes (Swetnam et al., 1999). Dendroecological analyses suggest that the

1920s/1930s outbreak was widespread in whitebark pine regions (Perkins and Swetnam,

1996; Kipfmueller et al., 2002), and palynological data indicates mountains pine beetles

have been present in whitebark pine ecosystems for millennia (Brunelle et al., 2008).

However, those accounts have not effectively described the stand-level intensity and mortality patterns of historic outbreaks. The data presented here does so for a single lake basin in the Pioneer Mountain. However, using this method to reconstruct mortality patterns throughout the range of the historic outbreak, when the beetles were not functioning as native-invasive species, would help contextualize the potential long-term effects current outbreaks could have on subalpine ecosystems. There are indications that beetle populations in other regions, such as the Targhee National Forest in southeast Idaho, were not affected by the lethal temperatures in 1933, and would provide a potentially valuable comparison to current mortality patterns (Evenden, 1934).

Conclusions

This research characterizes high elevation pine mortality during the widespread 1920s/1930s mountain pine beetle outbreak. Correspondence between cross-dated death dates, historic Forest Service surveys, and analyses of daily climate data suggest that extreme cold temperatures in 1933 led to the abrupt termination of the outbreak within the Pioneer Mountains. The similarity between the three lines of evidence supports the ability of using dendrochronological approaches to identify interannual patterns of mortality in high elevation ecosystems up to 90 years after an event. Reconstruction of stand-level mortality patterns indicates that while many whitebark pines were killed throughout PMT, sufficient numbers of susceptible hosts persisted to maintain beetle populations. These survivors are now the seed sources for future whitebark pine populations in the area.

During the recent period, however, the frequency of extreme cold events has substantially decreased in the Pioneer Mountains and throughout western Montana (Caprio et al., 2009); a trend likely linked with anthropogenic climate change (Vavrus et al., 2006). These reductions, coupled with univoltinism now observed at high elevations (Bentz et al., 2010), increases the likelihood that current outbreaks will continue until hosts are depleted and may contribute to the observed declines of whitebark pine in the northern Rocky Mountains (Logan et al., 2010). Despite a still unclear understanding of region-wide mortality levels during the historic event, potentially higher rates of host-depletion will likely cause the current outbreak to have a higher intensity than those within the historic record.

At a finer scale, an interesting yet preliminary finding was the lack of relationship between pre-outbreak SSI values and ultimate mortality levels. Instead, plots with high levels of beetle-caused mortality typically had relatively higher numbers of whitebark pine compared to lodgepole pine. This finding is supported by recent observations of mountain pine beetle host selection patterns (Bockino, 2008) and indicates that whitebark pine are more preferred and/or more susceptible to mountain pine beetle attack than lodgepole pine. Common metrics used to identify stand susceptibility in lodgepole-only stands may not adequately describe susceptibility when species composition is mixed at high elevations. The seemingly higher susceptibility of whitebark pine to beetle attack and reductions in extreme cold events will ensure heavy beetle presence in these stand as climate continues to warm.

Chapter 3: Growth patterns of whitebark pines influence mortality during a mountain pine beetle outbreak.

Introduction

Mountain pine beetle outbreaks have been a pervasive disturbance throughout the western U.S. and Canada during the past decade. Since 2000, 25×10^7 ha have been affected by the beetles, and the area attacked within the U.S. is continuing to grow (Canadian Ministry of Forests, 2009; USDA Forest Service, 2010). From 2002-2007 alone, mountain pine beetles have killed over 6.7×10^5 ha of high elevation whitebark pine (*Pinus albicaulis* Engelm.) forest (Gibson et al., 2008); a habitat located at the beetle's upper tolerance zone due to climatic limitations (Amman, 1972). These outbreaks are significant because whitebark pine function as a keystone species (Ellison et al., 2005) and may be facing substantial declines throughout its range (Kendall and Keane, 2001). These declines are attributed in part to mountain pine beetle outbreaks in combination with the invasive pathogen white pine blister rust (*Cronartium ribicola* Fisch.), and fire suppression (but see Larson et al., 2010).

Higher temperatures associated with anthropogenic climate change are identified as a driving factor behind these high elevation outbreaks. Mountain pine beetle population growth is facilitated by warmer temperatures in two ways: (1) fewer extreme cold events that can kill overwintering beetles and thereby check populations (Bentz et al., 2010) and (2) higher summer temperatures that promote univoltine (single-year) life cycles in beetle populations (Logan and Powell, 2001; Bentz and Shen-Langeheim,

2007). High temperatures also increase severely affect water-limited trees by increasing respiration rates and stomatal closure. This drought stress is predicted to reduce carbon stores that are critical for defensive compounds and thereby increase susceptibility to attack (Waring, 1987; McDowell et al., 2008). Recent climate-driven increases in drought frequency, length, and/or severity have been linked to drought-induced stress and widespread bark beetle outbreaks within the western U.S. (Allen and Breashears, 1998; Breshears et al., 2005; Berg et al., 2006; Negron et al., 2009) and worldwide (Rouault et al., 2003; Faccoli, 2009; see Allen et al., 2010). In the northern Rocky Mountains, where whitebark pine ecosystems are being heavily affected by mountain pine beetles (Gibson et al., 2008; Logan et al., 2010), it is evident that temperatures during each season throughout the past century have increased (Pederson et al., 2010) and, especially recently, are enhancing the effects of summer drought by lengthening the growing season (Westerling et al., 2006).

Many investigators have studied the effects that environmental conditions can have in determining the susceptibility/suitability of a tree insect attack (see Stamp, 2003). Of the many models, host selection by mountain pine beetles has been typically linked to the plant-stress hypothesis (White, 1969; Larsson, 1989). This hypothesis assumes that less vigorous trees are more susceptible to attack because they have fewer carbon reserves that can be metabolized into secondary defenses such as terpenes (Waring, 1987). Many processes that lower tree vigor have been associated with increased mountain pine beetle success, ranging from mechanical wounding from lightning or windthrow, drought (Craighead, 1925; Thomson and Shrimpton, 1984), competition

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(Larsson et al., 1983; Waring and Pitman, 1985; Mitchell and Preisler, 1991), and the presence of other pathogens (Raffa et al., 2005). Studies have also indicated that mountain pine beetles preferentially attack whitebark pines suffering from the invasive pathogen white pine blister rust (*Cronartium ribicola* Fisch) (Six and Adams, 2005; Bockino, 2008). Additionally, during periods of stress, nutrients tend to accumulate within the phloem, the beetle's food source, which would further aid beetle reproductive success and the potential for an outbreak to grow and persist (Clancy et al., 1994; White, 2009).

There are, however, other alternative plant defense theories that may be helpful for understanding mountain pine beetle-host dynamics. For example, the plant vigor hypothesis predicts that herbivores attack the healthiest plants because they represent the highest quality nutrition (Price, 1991). The growth-differentiation balance hypothesis assumes tree defenses operate in a non-linear fashion with growth (Herms and Mattson, 1992). In effect, trees invest more energy into growth during periods of high resource availability, while periods of moderate stress cause trees to increase investment in chemical defenses (differentiation) (Lorio, 1986; Herms and Mattson, 1992; Lombardero et al., 2000; Salle et al., 2008).

Specific physiological attributes of long-lived trees can also enhance their resistance to beetle predation. Individual long-lived trees are most frequently characterized by their slow growth rates (Schulman, 1954; Lamarche, 1969; Loehle, 1988; Bigler and Veblen, 2009). While slow growing trees can be less competitive and may never reach the canopy (Landis and Peart, 2005), they can often have greater

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investments in chemical defenses (Coley, 1985; Loehle, 1988) and structural characteristics such as lignins which make them less palatable (Bigler and Veblen, 2009).

While whitebark pine's habitat is typically considered the upper tolerance limit for mountain pine beetles due to a short growing seasons (Amman, 1972), intense high elevation outbreaks have been recorded in the past (Gibson, 1931; Evenden, 1944; Ciesla and Furniss, 1975; Perkins and Swetnam, 1996; Kipfmueller et al., 2002; Brunelle et al., 2008). Throughout the Pioneer Mountains of Montana, I observed large numbers of standing whitebark pine trees killed during a mountain pine beetle outbreak in the late 1920s and 1930s. There were, however, substantial numbers of seemingly suitable whitebark pine trees that survived this event. I use this differential mortality to investigate whether specific growth characteristics influenced whitebark pine survival during an outbreak. Using dendrochronological techniques, I compare beetle-killed whitebark pines with surviving whitebark pines based on (1) the diameter at the time of the outbreak, (2) growth rate, and (3) climate sensitivity. I further compare whitebark pines killed early in the outbreak with those killed later, during the apex of mountain pine beetle-induce mortality when beetle populations were likely higher, to understand whether density-dependant feedbacks influenced host selection. Identifying specific host characteristics that influenced historic mountain pine beetle selection and success is critical towards understanding the long-term outcome of their increased presence at high elevations.

Study area

The Pioneer Mountains encompass approximately 520,000 ha of southwest Montana (Figure 1). There are two principle regions within the Pioneer Mountains: the western portion with taller and more precipitous mountains, and the eastern portion with lower and gentler slopes. Despite the difference, elevations in the eastern portion still reach 2866 m at Odell Mountain and support a substantial subalpine community (Pfister, 1977). Lower elevations are dominated by Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). High elevation communities in the range are mixed and support substantial components of whitebark pine, lodgepole pine, Engelmann spruce (*Picea engelmanii* Parry), and subalpine fir (*Abies bifolia* A. Murray). Large whitebark pines are abundant both as living trees and dead snags. The specific composition of the numerous species that coexist at these elevations are highly influenced by site characteristics and disturbance histories (Kipfmueller and Kupfer, 2005). Cool temperatures prevail in the Pioneer Mountains at 2500 m, averaging -9.2 C in January and 12.8 C in July. The Pioneer Mountains are comparatively drier than other nearby ranges such as the Bitterroot and Beaverhead Mountains, and average 77 cm of precipitation annually. Precipitation is highest in the cooler months, while July and August are the driest months and the periods that trees are most likely to experience water deficits.

I located the study site in the subalpine region of the eastern portion of the Pioneer Mountains because of the visible and recorded historic mountain pine beetle outbreak that occurred in the region (Gibson, 1931). Beginning around 1910, a major
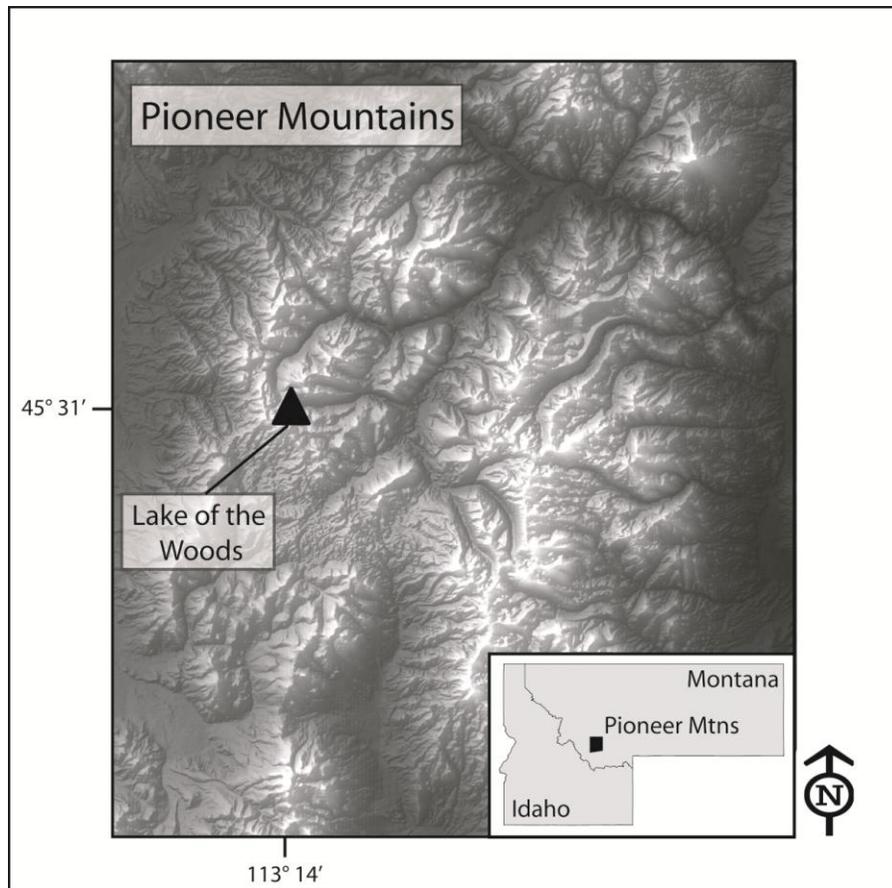
Figure 1. Study area within the Pioneer Mountains, Montana.

outbreak was first recorded in the Flathead National Forest in north-central Montana

(Evenden, 1944). By 1920 the outbreak expanded west and south, eventually reaching the

Bighole Basin and the Pioneer Mountains with notable impacts by 1925 (Gibson, 1931).

Whitebark pine and lodgepole pine snags from this outbreak remain throughout the

region (see also Ciesla and Furniss, 1975; Perkins and Swetnam, 1996; Kipfmueller et al.,

2002).

Methods

1. Dendrochronological field and laboratory methods

Twenty 1/10th ha plots were sampled between 2008 and 2009 in the areas

surrounding Lake of the Woods, Odell Lake, and Schwinegar Lake as part of a study

examining species composition and age structure. In 2008, we sampled ten plots and

collected two increment cores from every tree >5cm DBH in the plot. We sampled the

remaining ten plots in 2009, and collected cores from every tree within a more limited

1/20th ha subplot to reduce sampling density and associated impacts. All of the whitebark

pines categorized as mountain pine beetle-killed in this study exhibited characteristic j-

shaped galleries and had blue-staining fungus visible within the sampled core.

A subset of sixty-six mountain pine beetle-killed and sixty-two surviving

whitebark pine trees were selected from the larger data set for this analysis. I chose only

trees that germinated prior to 1750 for this analysis to help remove the influence that

young age can have on susceptibility to attack (see Shore and Safranyik, 1992). I

randomly selected the trees used in this analysis from those that satisfied the age criteria.

To maximize the number of trees used in this analysis, the paired cores from each tree were high-graded by choosing the core with (1) the longest series length and (2) an absence of anomalous growth patterns based on visual inspection. Increment cores were mounted, surfaced until individual xylem cells were clearly visible under magnification, and cross-dated using standard dendrochronological techniques (Stokes and Smiley, 1996). Ring-widths were measured to the nearest 0.001 mm on a Velmex measuring bench using MeasureJ2X software (VoorTech Consulting, Holderness, NH, USA).

Death dates of mountain pine beetle-killed trees from the age structure study indicate that the peak of the outbreak occurred in 1930 (for details see chapter 2). Since the host selection behavior of bark beetles can be influenced by beetle population size (Wallin and Raffa, 2004), I separately compared trees killed prior to 1930 with those killed in 1930 or after. Accordingly, for the following analyses, I first compared trees on the basis of whether they survived (n=62) or were killed (n=66), and then split the killed trees into two subgroups based on whether they were killed early (≤1929, n=22) or later (>1929, n=44) in the outbreak.

2. Analysis of growth characteristics

Mountain pine beetles preferentially attack larger (Cole and Amman, 1969) and generally older trees (Safranyik et al., 1974). Larger trees can have thicker phloem, meaning greater amounts of food for attacking beetles and their broods (Amman, 1972; Shrimpton and Thomson, 1985). These large trees can also have thicker bark which may act as an insulator against both low temperatures (Cole, 1981) and phloem desiccation

(Safranyik and Carroll, 2006). Perkins and Roberts (2003) found the diameter threshold for probable attack in whitebark pine (18 cm) during the early 20th Century outbreak to be slightly lower than that frequently assigned to lodgepole pine (20 cm; Cole and Amman, 1969) and ponderosa pine (25 cm; Negron et al., 2008). Lodgepole pine resistance to blue stain fungus appears to decrease with age, with the result that older stands are typically considered more conducive for an outbreak (Safranyik and Carroll, 2006).

I compared the diameter and age of the mountain pine beetle-killed trees with the surviving trees during the outbreak using a two-sample Student's t-test. Diameters of all trees were recorded in the field. Death dates of mountain pine beetle killed trees from the age structure study reveal the last major year of the outbreak was 1932 (see Chapter 2). To compare the diameters of surviving trees with those that were killed, I subtracted the growth between 1933-2008/2009 from the diameters recorded in the field for the surviving trees (Perkins and Roberts, 2003). This closely approximates the inner bark diameter of surviving trees at the end of the outbreak in 1932. Mountain pine beetle-killed trees, however, generally did not have bark when their diameters were recorded in the field, resulting in a systematic underestimation of the diameters of killed trees. This underestimation should not substantially alter the analysis since whitebark pines have relatively thin bark (<1cm) (Fryer, 2002).

Previous studies have compared lodgepole pine susceptibility to mountain pine attack using measures of tree vigor (Larsson et al., 1983; Mitchell et al., 1983; Waring and Pitman, 1985). Waring et al. (1980) measured vigor as annual increment (grams of stemwood produced) per square meter of crown leaf surface, and assumed a linear

relationship between sapwood basal area and crown leaf area. By combing measures of

crown leaf area and annual increment data, sapwood volume, which represents carbon

reserves, could be accurately predicted. Here, I converted ring-width measurements into

basal area increment (BAI) to use as a proxy for host vigor. BAI has advantages over raw

ring widths because it represents the total area of annual growth, and removes the

influence that tree diameter can have on radial growth (West, 1980). I averaged the BAI

values of individual trees to make four separate chronologies: (1) surviving trees, (2) all

killed trees, (3) trees killed ≤1929 (killed early), and (4) trees killed >1929 (killed late). I

used two-sample Student's t-tests to identify whether there were significant differences in

growth rates between the four different groups. Since the number of years observed is

very high and would influence the t-statistic, BAI values for each chronology were also

bootstrapped 1000 times. Further, I compared mean growth with two-sample Student's t-

tests during different time periods (1700-1799, 1800-1899, 1900-1928/1932) to identify if

relative growth between the groups changed over time. I compared similarities of inter-

annual growth variations between the four groups using Pearson correlations over the

entire time-span.

3. Growth sensitivity

Since climate patterns have direct influence on tree physiology and growth (Fritts,

1976), and in turn influence bark beetle susceptibility (Allen et al., 2010), I compared the

climate-related growth patterns of mountain pine beetle-killed trees with surviving trees.

Growth related characteristics of the four different groups of trees (surviving, killed early,

killed late, and all killed) are compared in two principal ways (details on each method explained below). First, I compare the mean sensitivity of ring-widths between the four groups to identify whether there are differences in interannual growth patterns. Second, I identify whether moderate to extreme wet and dry conditions may differentially influence growth in killed and surviving trees.

Mean sensitivity (MS) for the four groups (surviving, all killed, killed early, and killed late) as well as each individual trees was determined in order to assess the relative influence external factors (such as climate) exert on growth. This statistic determines the relative difference in width between temporally adjacent annual growth rings and represents the high frequency variation within a series or chronology (Fritts, 1976). Larger MS values indicate greater interannual variation, while low values suggest little interannual variation in growth. Differences in MS values between groups were ascertained with t-tests from individual series.

In order to compare climate-related growth, each tree series was standardized to remove the trends related to changes in bole-geometry and tree aging (Fritts, 1976). In my analysis, deterministic standardization techniques, including a negative exponential curve, straight line through the series mean, and linear regression, were employed when suitable. However, the trees in this study were growing in moderately-closed- or closed-canopy forests where competitive interactions and disturbance processes can strongly influence growth. When a deterministic approach did not fit a series, likely as a response to competitive interactions, I used a stiff cubic smoothing spline, set to 67% of the

segment length (Cook and Peters, 1981). Individual series were averaged to construct a composite chronology for each of the four groups.

I identify potential climate-related growth differences between killed and surviving trees by comparing the standardized chronologies with reconstructed Palmer Drought Severity Index (PDSI) values for southwest Montana (Grid Cell 84; Cook et al., 2004) during moderate to extreme wet and dry years. Reconstructed PDSI was chosen because (1) instrumental climate data only covers the most recent period, which would exclude the majority of the years of interest; (2) preliminary analyses using instrumental climate data indicate growth in both killed and surviving trees is most highly correlated with previous summer drought conditions (see Appendix); and (3) drought conditions are frequently associated with reducing host defenses and initiating bark beetle outbreaks (Safranyik et al., 1975; Thomson and Shrimpton, 1984; Ferrell, 1996; Allen et al., 2010). "wet" years were considered those with moderate to extremely wet conditions (PDSI values ≥ 2), and "dry" years were considered those with moderate to extreme drought conditions (values ≤ 2; Palmer, 1965). I first identified the standardized ring-width values for each of the groups of trees in the years following wet and dry years (since these whitebark pines respond most strongly to previous year conditions). I used Student's t-tests to identify differences in standardized growth in each group of trees from their mean (which always equals 1 in a standardized chronology) for both wet and dry conditions. This test is meant to indicate potential differences in the magnitude that wet and dry conditions can have on growth between the four groups of trees.

Results

Growth characteristics

Mean diameters of mountain pine beetle-killed whitebark pines (35.3±15.0 cm,

n=62) were significantly greater than surviving trees (23.0±10.9 cm, n=61) at the end of

the outbreak in 1932 (Figure 2, t=-5.30, p<0.001, n=123). Alternatively, there were no

significant differences in diameters between whitebark pines killed early in the outbreak

(32.7±10.8, n=21) with those killed later (Figure 2, 36.5±16.6 cm, n=41; t=0.92, p>0.05,

n=62). In this study, there was no significant difference in age between killed and

surviving whitebark pines (Table 1, Figure 3, t=1.16, p>0.05, n=123). Trees killed early

in the outbreak were generally older than surviving trees (t= 2.22, p<0.05, n=82),

however, appear to be influenced by three very old killed whitebark pines (>550 years)

that were 150+ years older than all other trees in this analysis. There were no appreciable

differences in age between surviving trees and trees killed late in the outbreak, nor

between trees killed late in the outbreak and trees killed early. These results only reflect a

subset of data, that, when taken as a whole may yield different results.

Basal area increment was greater in beetle-killed trees than in surviving trees over

the period 1700-1932 (t=37.2, p<0.001, n=232) (Figure 4), and within shorter time

periods (Table 2). Bootstrapped confidence intervals were all significantly different and

support the results of the t-tests (Figure 5). There was no year that the composite

chronology of surviving trees met or exceeded the incremental growth of mountain pine

beetle-killed trees. Mean BAI of mountain pine beetle-killed trees (3.50±0.46 cm²) far

exceeded that of the surviving trees (2.02±0.34 cm²). There were, however, significant

(a)

(b)
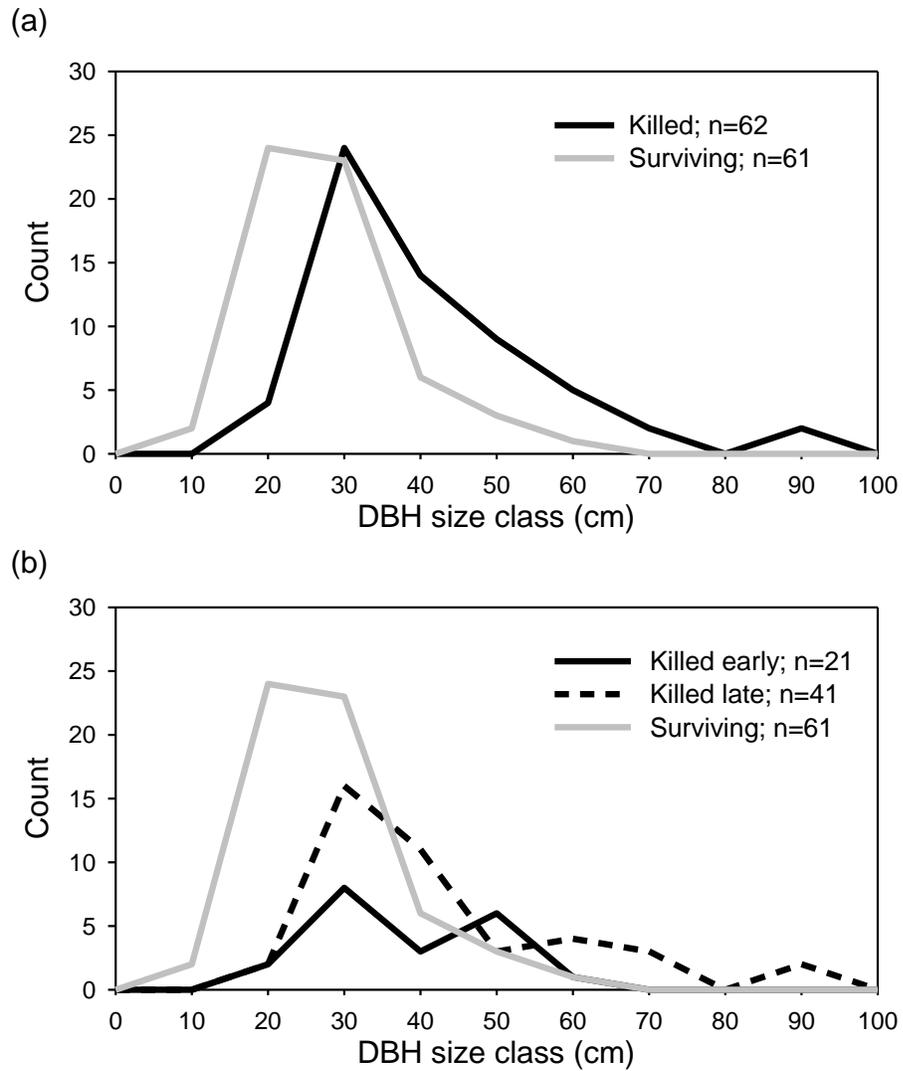
Figure 2. Diameter distributions of (a) mountain pine beetle-killed trees at death compared with diameters of surviving trees in 1932, and (b) trees killed early and late in the outbreak. Distributions are represented in 10 cm size classes.

Class	n	MS	ISC	Mean age at 1932
Surviving	61	0.212	0.505	271
Killed, all	62	0.190	0.496	290
Killed early	21	0.196	0.462	316
Killed late	41	0.186	0.485	277
Combined	123	0.200	0.490	276

Table 1. Basic chronology characteristics (MS, mean sensitivity; ISC, inter-series correlation; and mean age at 1932) for surviving and mountain pine beetle killed trees.
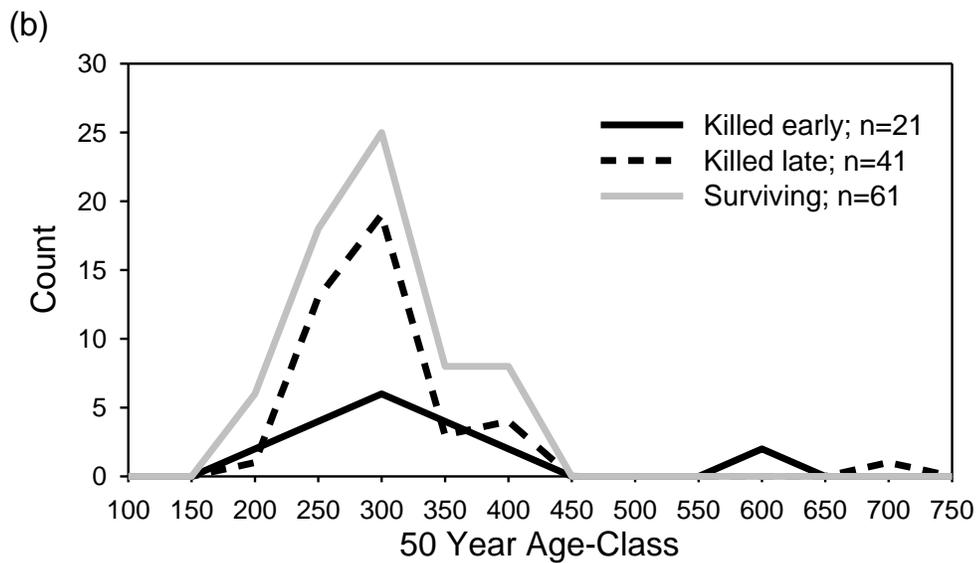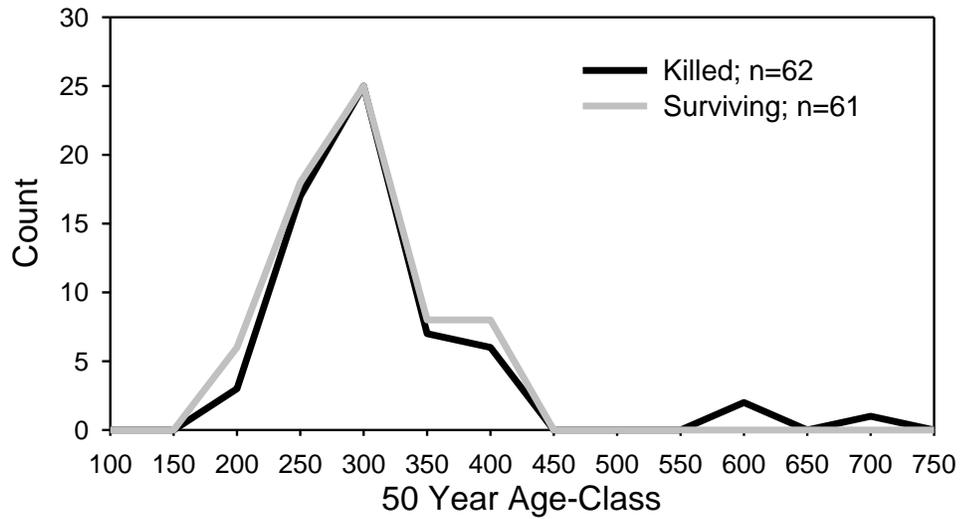
Figure 3. (a) Killed and surviving whitebark pines had very similar age-class distributions. (b) This pattern was also similar for trees killed early and late in the outbreak.

differences between the BAI chronologies of trees killed early compared with those killed later (Figure 4, Table 2). From 1700-1799, the two groups of mountain pine beetle-killed trees had similar and relatively rapid growth rates compared with surviving trees. Yet after 1800, trees killed early have progressively declining growth rates, while growth consistently increases for those killed late in the outbreak. While the BAI chronologies of the four groups show substantial differences in growth patterns, the standardized chronologies are all significantly correlated (Table 3), indicating that on an annual scale, each group is likely responding to similar broad-scale environmental influences.

Growth sensitivity

Surviving whitebark pines had higher mean sensitivity (MS) compared with mountain pine beetle-killed trees (t=3.94, p<0.001, n=123; Figure 6). Similarly, surviving trees had higher mean sensitivities compared to both trees killed early (t= 2.04, p<0.05, n=82), and trees killed late (t=3.97, p<0.001, n=102) (Figure 6). However, there was no significant difference in MS between whitebark pines killed early and killed later in the outbreak (Table 1).

All of the whitebark pines used in this study had a similar response to climate (see Appendix), yet there were significant differences in the magnitude of this response during wet and dry years (Table 4). Surviving trees had significantly lower growth than their mean during dry years and had significantly greater growth during wet years. While killed trees also had reduced growth dry years and higher growth during wet years, the departures from their means were considerably lower and not significant.

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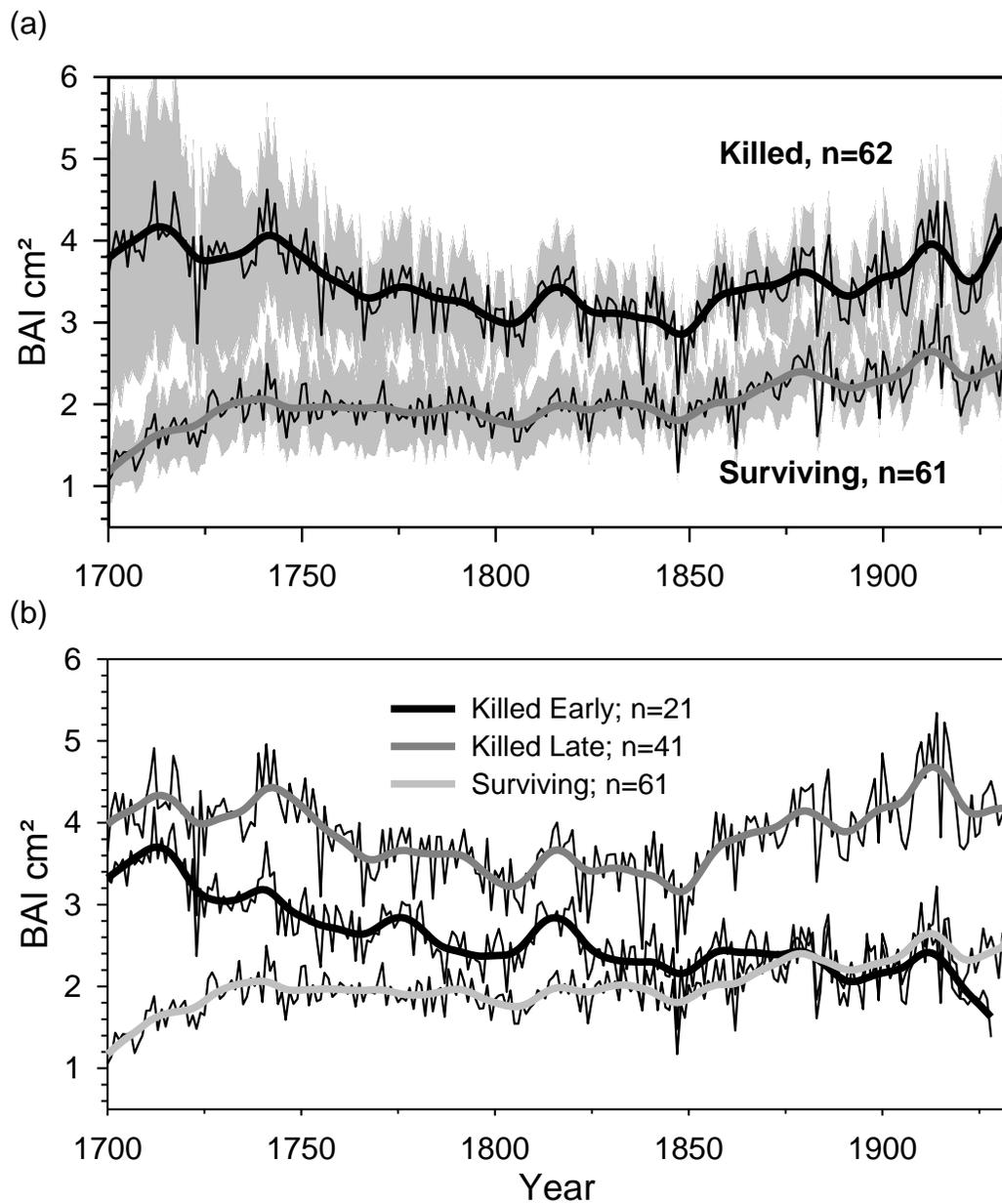
Figure 4. (a) Mean annual basal area increment for mountain pine beetle killed and surviving trees with 95% confidence intervals (gray). (b) Mean annual basal area increment for surviving trees, trees killed early in the outbreak, and trees killed late in the outbreak. Each series was smoothed with a 20 year cubic spline.
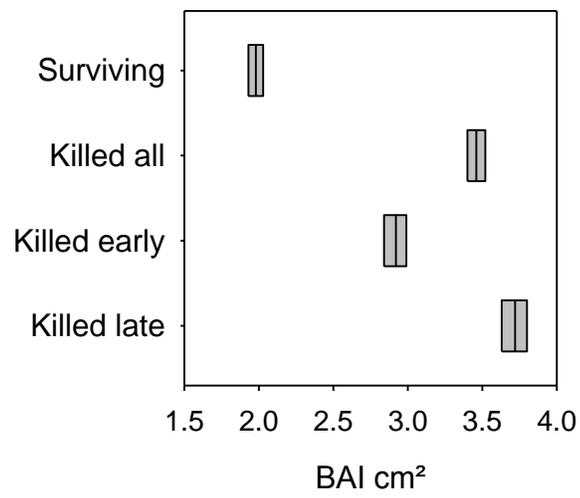
Figure 5. Bootstrapped confidence intervals of BAI for the four composite chronologies. Note that growth rates are distinctly different for each group.

Years	K v S	KE v KL	KE v S	KL v S
1700-1799	**35.81*****	**-15.34*****	**20.85*****	**40.49*****
1800-1899	**26.01*****	**-22.78*****	**7.63*****	**29.95*****
1900-1928/1932	**12.05*****	**-19.37*****	**-3.54*****	**15.44*****
All years	**39.05*****	**-26.46*****	**14.57*****	**45.23*****

Table 2. Student's t-tests comparing BAI values of whitebark pines killed early in the outbreak (KE), killed late in the outbreak (KL), all killed trees (K), and ones that survived (S). Values shown are t-values with corresponding levels of significance. Positive values indicate the first variable is greater.

	Killed all	Killed early	Killed late	Surviving
Killed all	1			
Killed early	**0.94**	1		
Killed late	**0.98**	**0.86**	1	
Surviving	**0.78**	**0.69**	**0.79**	1

Table 3. Pearson correlations of standardized ring-width chronologies between each of the groups of trees. For correlations between trees killed, killed late, and surviving trees, n=233. For correlations between trees killed early and the other groups, n=229.

	Dry (n=56)	Wet (n=72)
Killed all	-1.51	1.90
Killed early	-1.43	1.73
Killed late	-1.50	1.90
Surviving	**-2.49***	**2.76****

Table 4. Student's t-tests comparing the standardized ring width values for each group from their long term mean during dry (PDSI values $\leq$-2) and wet (PDSI values $\geq$2) years. Values shown are t-scores with corresponding levels of significance. Negative values indicate below average growth.
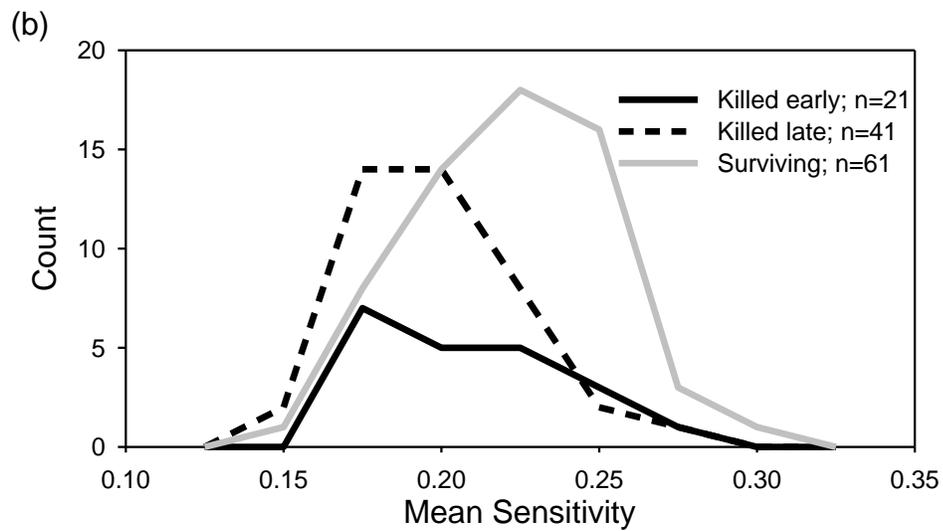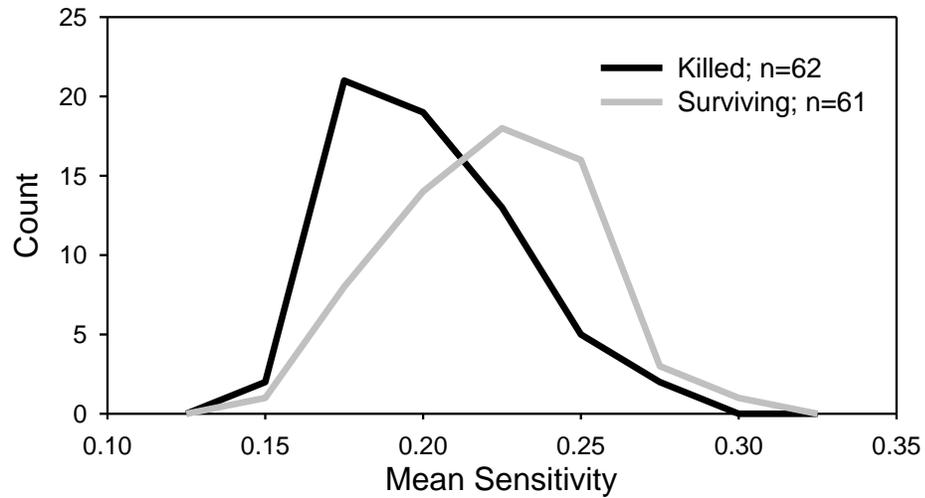
Figure 6. (a) Surviving whitebark pines had greater mean sensitivity than killed trees, and similarly, (b) surviving trees had greater mean sensitivity compared to both whitebark pines killed early and late in the outbreak.

Discussion

Warmer temperatures associated with climate change are predicted to both directly and indirectly benefit mountain pine beetle populations. Directly, higher temperatures may lead to more rapid life cycles (Logan and Powell, 2001; Hicke et al., 2006; Bentz and Shen-Langeheim, 2007) and reduce overwintering mortality. Indirectly, increases in water deficits may lead to enhanced water stress, reduced tree vigor, and, in accordance with the plant-stress hypothesis, diminished host defenses to beetle attack (McDowell et al., 2008; Bentz et al., 2010). However, during the early 20th Century outbreak in the Pioneer Mountains, Montana, mountain pine beetles preferentially attacked and colonized the least climatically sensitive and most vigorous whitebark pines. While those trees appeared to be the most preferred, during the earliest years of the outbreak beetles more frequently colonized trees that had low climatic sensitivity and with rapid initial growth rates that progressively declined. Trees that survived the event had consistently slow growth and may respond more strongly to water deficits. These results suggest there is a more complex relationship between host susceptibility and drought stress/growth rate than is described in the plant stress hypothesis. At least for whitebark pines in the Pioneer Mountains, there is not likely to be a linear relationship between warming temperatures and increased susceptibility/suitability to mountain pine beetle attack.

Mountain pine beetle preference

Mountain pine beetle preference for larger-diameter trees has been well documented in lodgepole pine (Cole and Amman, 1969; Shrimpton and Thomson, 1985) as well as whitebark pine (Perkins and Swetnam, 1996; Perkins and Roberts, 2003). The thicker bark typically found on larger trees acts as an effective insulator against extreme winter temperatures, inhibits phloem desiccation, and is protective against potential predators (Safranyik et al., 1974; Cole, 1981). Further, and more importantly, larger trees generally have thicker phloem, meaning greater amounts of food for successful brood production (Berryman, 1976; Shrimpton and Thomson, 1985). While killed trees were significantly larger, the surviving trees selected for this study were still generally large, averaging 23.3 cm in 1932. Overall, killed and surviving trees were relatively similar in age, but the oldest trees appear to have been killed earlier in the outbreak (Table 1). Age may play an important role in beetle host selection more generally, but I attempted to remove it as an influential factor by only including trees of roughly the same age. As a result, the differences in size suggest that the smaller diameters of surviving trees and those killed early in the outbreak truly reflect slower growth rates.

Overall, killed whitebark pines had much higher growth rates than surviving trees (Figure 4); a pattern that likely reflects discrepancies in both the nutritional quality and defensive capabilities between the groups. Slow and senescing growth patterns that, respectively, were characteristic of surviving trees and ones killed early in the outbreak have both been correlated with thinner phloem (Berryman, 1982; Shrimpton and Thompson, 1985) and reduced mountain pine beetle brood sizes (Amman, 1972; Berryman, 1976). While the relationship between host physiology and phloem thickness

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is complex, Reid and Robb (1999) found that recent growth rates, not phloem thickness, more accurately predicted pine engraver (*Ips pini*) offspring survival in already dead jack pine (*Pinus banksiana* Lamb). While phloem thickness and nutrient levels are unknown for the trees used in this study, the considerably higher growth rates of trees killed late in the outbreak suggest they may have been more nutritionally preferred by attacking beetles.

Climate-related growth differences between the groups suggest that whitebark pine vigor and susceptibility to attack is related to microsite growing conditions. Trees that grow in harsher conditions often have higher MS, and are typically favored for climate reconstructions since they are more responsive to interannual variations in precipitation and/or temperature (Fritts, 1976). Soil thickness, slope, and aspect can vary dramatically in subalpine ecosystems and all have important influences on tree growth. The strong correlations between the standardized chronologies suggest that the whitebark pines in the study area have similar top-down controls on growth determined by climate (Table 3), and this is also reflected in their climate responses (see Appendix). However, the higher MS of surviving trees suggests a different magnitude of response and sensitivity to climate. Surviving trees had significantly reduced growth during dry conditions and amplified growth during wet conditions, while departures in growth rates for killed trees were substantially lower. These data suggest that surviving trees may be more sensitive to changes in moisture availability, and are potentially more prone to drought-related stress compared to killed trees. These climate-related growth differences suggest that surviving trees may inhabit edaphically less-favorable sites that are more

prone to moisture deficits. Notably, there were not substantial differences in either MS or climate-related growth departures between trees killed early and late in the outbreak. This would suggest that ecological factors other than moisture availability, such as canopy position and light availability, would account for their differences in BAI.

Whitebark pine defenses

The finding that, overall, mountain pine beetles killed the most vigorous whitebark pines tends to contradict previous comparisons between tree growth and beetle-caused mortality, and may indicate low defense capacity of whitebark pines to mountain pine beetles. Previous dendrochronological-based studies of host interactions with mountain pine beetles (Larsson et al., 1983; Mitchell et al., 1983; Waring and Pitman, 1985), spruce beetles (Hard, 1985; Doak, 2004), and the western balsam bark beetle (Bleiker et al., 2003; Bleiker et al., 2005) consistently found reduced host vigor to be positively associated with attack likelihood. It is often assumed that lower vigor trees have reduced thresholds of attack and are preferentially selected by the bark beetles. Unlike the above interactions, however, mountain pine beetles are often considered a "native-invasive" in whitebark pine ecosystems and potentially lack coevolved mechanisms of defense (Logan, 2007). Constitutive resin ducts act as a tree's first line of defense that, once severed, can quickly exude resin and ultimately "pitch-out" attacking beetles (Berryman, 1972; Franceschi et al., 2005). Induced resinosis, or secondary defenses (Reid et al., 1967; Berryman, 1972; Raffa and Berryman, 1983), is a tree's rapid response to beetle entry and involves the breakdown of parenchyma cells, formation of

traumatic resin ducts, and increases in the levels of defensive chemicals (Raffa and

Berryman, 1982; Safranyik and Carroll, 2006). While these processes are well understood

for lodgepole pine, Logan et al. (2010) noted that whitebark pines had both noticeably

diminished constitutive defenses, in the form of relatively few pitch tubes, as well as

visibly lower induced defense rates.

Shifts in mortality patterns between early and late stages of the outbreak suggest

that mountain pine beetle host selection of whitebark pine may change with population

size. Similar density-dependent shifts in host selection behavior has been observed

between mountain pine beetles and lodgepole pine (Raffa and Berryman, 1983) as well as

for the spruce beetle (*Dendroctonus rufipennis*) (Wallin and Raffa, 2004). As bark beetle

populations become higher, they tend to increasingly attack trees with higher levels of

chemical defenses (Wallin and Raffa, 2004). If growth rates in whitebark pines are

positively associated with defense reaction, then the shifts in host selection patterns

observed here may indicate that the fastest growing whitebark pines have some level of

resistance to beetle attack. To accurately assess this, however, more refined investigations

of the chemicals defenses in whitebark pines are clearly needed. At a broader scale,

however, mountain pine beetles primarily attacked whitebark pine despite high numbers

of susceptible lodgepole pines growing throughout the study area (see chapter 2) and may

reflect different defense reactions between the species.

While whitebark pines may have been favored as hosts, individuals that shared

the specific characteristics of slow growth and relatively high MS appeared to more

frequently survive the outbreak. These growth patterns contrast with those of trees killed

early in the outbreak that, despite also having slow growth during the outbreak, had initially rapid growth rates and generally low mean sensitivities. Fast juvenile growth can have significant physiological tradeoffs. It can be competitively advantageous, especially in a species like whitebark pine whose seeds typically germinate within groups from underground caches (Tomback, 1983; Tomback and Kendall, 2001). However, investment in rapid growth can come at the expense of other internal biological processes. In four high elevation conifers, Bigler and Veblen (2009) found individuals with rapid early growth rates to have shorter life-spans compared with slower growing individuals of the same species. They attributed the longer lives of slow growing trees to, among other factors, greater investments in defensive compounds and structural characteristics leading to higher wood densities and increased levels of lignin – all of which would hinder the success of mountain pine beetles and their associate blue stain fungus. Even though trees killed early in the outbreak were generally older than surviving trees (Table 1), differences in juvenile growth characteristics could still have important long-term effects. Consistently slow growing trees can also have reduced needle turnover rates which diminish losses of nitrogen, phosphorous, and carbon, and may ultimately increase available nutrients and carbon for chemical defenses (Coley et al., 1985). Additionally, mild and consistent water-stress in other pine species has been associated with increased levels of constitutive defenses and reduced bark beetle success (Herms and Mattson, 1992; Lombardero et al., 2000; Salle et al., 2008). In effect, the consistent stress experienced throughout the lives of surviving trees likely made them less palatable and/or nutritious, and potentially more structurally resistant to beetles. This suggests that

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not all slow-growing trees are similarly susceptible to attack, and depends on specific life history traits of individual trees. As a result, determining host susceptibility based strictly on recent growth rates may be misleading.

While I primarily associate differences in vigor with microsite growing conditions, the influence of genetic variability cannot be discounted. Ruel and Witham (2002) found piñon pines (*Pinus edulis*) with rapid early growth rates to be more susceptible to herbivory by the stem-boring moth (*Dioryctria albovittella*) when mature than those with initially slower growth. They postulated the difference to be genetically based and driven by different selective pressures: one to maximize juvenile survival, and the other to maximize cone production. A genetics-based approach to mountain pine beetle-whitebark pine interactions could open an intriguing line of inquiry, but is beyond the scope of this research.

Implications for future interactions

The effects of climate change are reshaping the biophysical environment in complex, poorly understood, but also in predictable ways. Summer temperatures in the northern Rocky Mountains are steadily increasing (Pederson et al., 2010), and will likely lead to reductions in available moisture (Littell et al., 2010) with potentially adverse impacts on whitebark pines. Warmer conditions are predicted to reduce the suitable habitat for whitebark pines the spatial extent of whitebark pine (Bartlein et al., 1997; Schrag et al., 2008) by shifting their suitable habitat towards higher elevations. In some cases, there may not be any more room for whitebark pine to migrate up-slope. Longer

growing seasons and reduced snowpack are anticipated to increase fire frequency in subalpine forests (Westerling et al., 2006) and may hasten the expansion of the more drought-tolerant lodgepole pine. In the Sierra Nevada Mountains, the annual water deficits for whitebark pines are projected to increase >30% by 2020 (Lutz et al., 2010). Increases in water deficit in the Pioneer Mountains will likely lead to general reductions in BAI and increases in MS for whitebark pines that respond most strongly to precipitation. This should cause growth patterns in most trees to increasingly resemble that of surviving trees, thereby reducing the number of suitable hosts for mountain pine beetles. Yet the surviving trees in this study experienced low, and even progressively increasing, BAI throughout the entire observed time period; not the consistent reductions in growth that are expected for many water-limited trees under future warming (Millar et al., 2007; Littell, 2010). Large vigorous trees with greater leaf areas would be especially affected by changes in moisture availability, and often have less ability to regulate respiration and transpiration during periods of water stress (Arendt, 1997; McDowell, 2008). As a result, lower net carbon accumulation could reduce the defenses of previously vigorous whitebark pines with some level of resistance to mountain pine beetle attack, and result in similar levels of susceptibility to those killed early in the outbreak. Alternatively, growth in whitebark pines at their highest elevations is sometimes more limited by temperature than precipitation (Kipfmueller, 2008; Kipfmueller and Salzer, 2010). Assuming tree defenses are related to growth rates, trees in those ecosystems might become increasingly vigorous and thus resistant to attack.

My findings that there are growth-mediated differences in host mortality raise a number of important directions for future research and management priorities. First, it is important to note that my results come from whitebark pine growth characteristics during a historic outbreak. While there is evidence that mountain pine beetles and whitebark pines have interacted for millennia (Brunelle et al., 2008), and that the early 20th Century outbreaks were very widespread (Evenden, 1944), a good deal of current research has focused on the novelty of current outbreaks in terms of spatial scale, duration, and ultimately intensity (Raffa et al., 2008; Logan et al., 2010). As a litmus test for my results, the growth patterns of killed and surviving whitebark pines during the current outbreak should be compared. Second, my findings suggest that the most vigorous and surviving trees may both have characteristics that render them resistant to beetle attack. These results highlight the need for specific analyses that address the effectiveness of whitebark pine terpenes in resisting mountain pine beetles. Third, since the most "stressed" whitebark pines survived the intense 1920s and 1930s outbreak, management practices aimed at reducing whitebark pine losses during the current outbreak should focus efforts on protecting vigorous trees, growing in the most favorable conditions. While this runs counter to common notions of host susceptibility, vigorous trees were most preferred and/or less resistant than more stressed trees, and were ultimately killed by the beetles.

Conclusions

In this chapter, I described differences in growth characteristics between whitebark pines killed during a historic mountain pine beetle outbreak with whitebark pine that survived the event. This outbreak occurred during the 1920s and 1930s, and was part of a widespread mortality event covering much of the northern Rocky Mountains during the early part of the 20th Century (Evenden, 1944; Ciesla and Furniss, 1975). I found that growth characteristics highly influenced the incidence and timing of whitebark pine mortality during the outbreak. Unlike previous studies of whitebark pine susceptibility (e.g. Six and Adams, 2007), the most vigorous trees, with the lowest susceptibility to drought conditions were preferentially attacked. Trees killed early in the outbreak had similarly slow growth rates to surviving trees, but still had lower mean sensitivities. In general, mountain pine beetle-killed trees appear to have occupied sites with the most favorable growing conditions, while those whitebark pines growing in under harsher conditions survived the attack due to lower suitability as food for attacking beetles and/or greater resistance to attack.

The effects of climate change, fire suppression, and recent beetle outbreaks are substantially altering current biophysical site conditions and competitive interactions in these subalpine forests. Yet it remains unclear precisely how higher temperatures and potentially greater moisture deficits will impact whitebark pine defenses to mountain pine beetles. General reductions in vigor of previously healthy trees could create a pulse of susceptible hosts that beetles could easily colonize. However, low vigor whitebark pines were not the preferred hosts of mountain pine beetles, and increases in their frequency may have significantly negative impacts on beetle population dynamics. This would be

most explicitly the case for whitebark pines germinating now, which, even at favorable

sites, may increasingly have growth most similar to that of surviving trees. However,

changes in host susceptibility operate on a slower temporal scale than beetle populations

themselves. Many areas throughout the west are reporting rapid reductions in mature

cone-bearing whitebark pines during the current outbreak, and possibly jeopardizing the

long-term viability of the species (Gibson et al., 2008; Logan et al., 2010). Further

research on current mortality patterns would benefit predictions for the long-term

survival of whitebark pine.

Standardized Chronologies
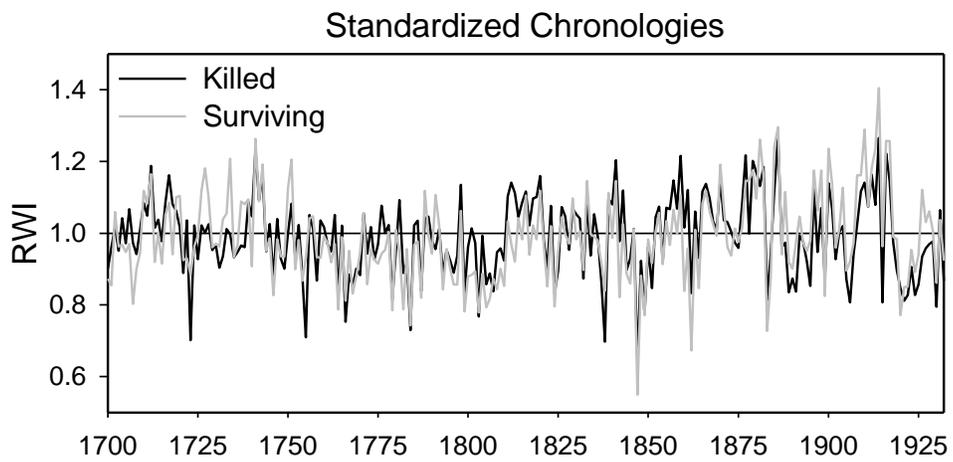
1. Composite chronologies of mountain pine beetle-killed and surviving whitebark pine trees.
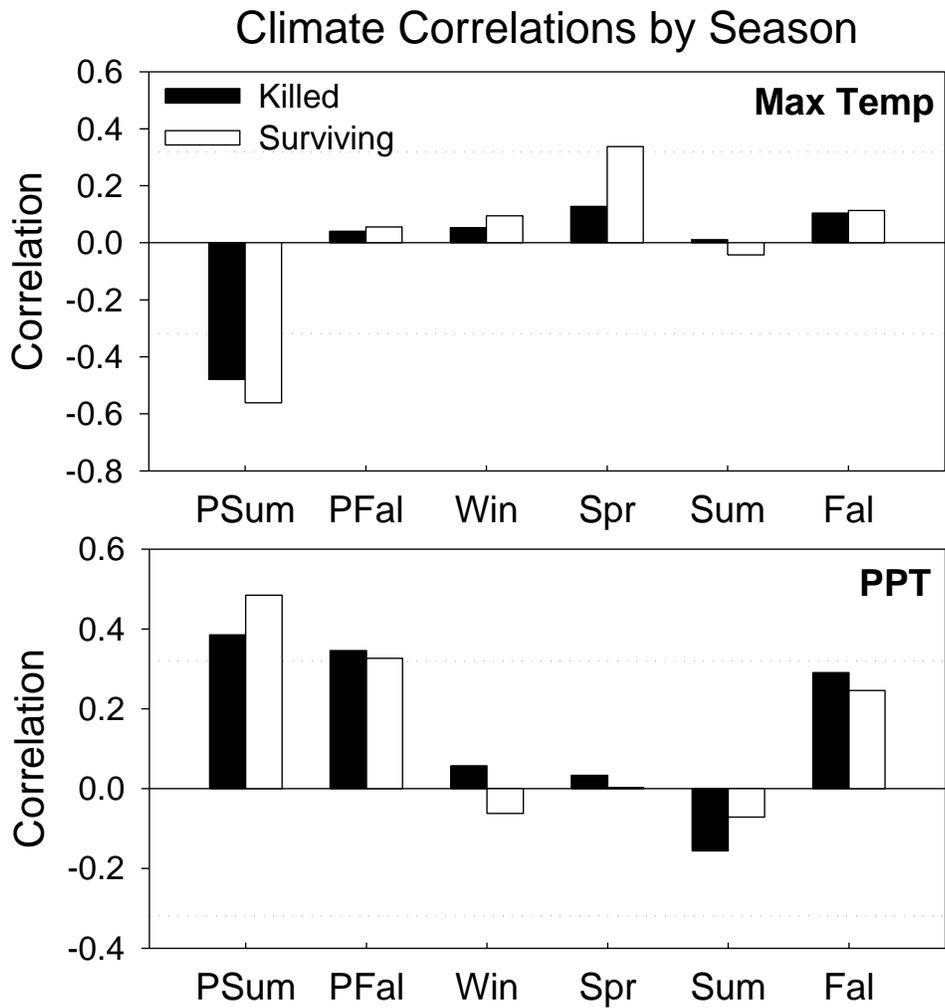
2. Pearson correlations between standardized composite chronologies of mountain pine beetle-killed and surviving trees and seasonalized maximum temperature and precipitation. Climate data used in these correlations were obtained from the PRISM data set (Precipitation-elevation Regressions on Independent Slopes Model, Oregon State University, http://www.prismclimate.org) (Daly et al., 2008). Climate correlations were conducted over the period 1895-1932 between seasonalized maximum temperature and precipitation and composite chronologies of mountain pine beetle-killed and surviving trees.

Chapter 4: Conclusions and synthesis

The early 20th Century mountain pine beetle outbreak in the Pioneer Mountains, Montana, lasted roughly eight years and ended in 1933. Prior to the outbreak, all of the plots analyzed in Chapter 1 were capable of supporting epidemic-level mountain pine beetle populations. The outbreak lead to high but variable mountain pine beetle-caused mortality in certain areas of the watershed. From preliminary analyses, there actually appears to have been no clear relationship between the number of killed hosts and common metrics of stand susceptibility. Instead, mountain pine beetle-caused mortality tended to be highest in plots dominated by whitebark pine and almost nonexistent in stands dominated by lodgepole pine. Mortality was also highest in whitebark pines that exhibited specific growth characteristics. Beetle-killed trees were larger and, somewhat surprisingly, were faster growing and had relatively low climatic sensitivity. The outbreak ended in 1933, after the most extreme cold event ever observed in Dillon, Montana. These findings suggest that (1) climatic conditions played an important role in regulating beetle populations and mortality levels in this historic outbreak; (2) whitebark pines may be more preferred and/or susceptible to attack than lodgepole pine; and (3) whitebark pine vigor has an important yet seemingly complex role in influencing whitebark pine risk for attack.

The extreme cold event in 1933 had significant and likely lasting impacts on the stand structure in the study area. Had that event not occurred, substantially greater numbers of pine would likely have been killed by the beetles. As a result, the present composition of the study area, and possibly throughout much of the region, may be more

heavily populated by whitebark pine (and potentially lodgepole) than it otherwise may have been. This is particularly noteworthy since the frequency of extreme cold temperatures in the study area declined significantly after 1950. If this warming pattern is occurring elsewhere throughout the West, as it appears to be, it is likely that current and future outbreaks will continue until nearly all available hosts are depleted. This has the potential to have long-term consequences to whitebark pine populations and the communities associated with them. However, the long-term successional response of subalpine forests to mountain pine beetle outbreaks is still largely unclear.

High rates of whitebark pine mortality were observed in much of the study area despite low mortality in very susceptible lodgepole-dominated stands. While the most common between-tree metric for susceptibility, diameter, appears to have influenced the likelihood of individual whitebark pine mortality, the stand-level SSI model appears to have been ill-suited for predicting total mortality. In mixed whitebark-lodgepole pine regions, stand susceptibility may instead be largely driven by individual species' susceptibility to attack. Whitebark and lodgepole pine frequently grow together in subalpine ecosystems of the northern Rocky Mountains which, due to climate change, may be the most suitable location for future mountain pine beetle outbreaks (Hicke et al., 2006). As a result, the development of new susceptibility models incorporating host ratios would be helpful to understand future mortality patterns in subalpine forests.

Between individual whitebark pines, specific growth-related patterns also appear to have influenced the likelihood of attack. Surviving whitebark pines had consistently slow growth rates for 200+ years prior to the outbreak and appeared to be more prone to

growth reductions during drought conditions. Trees killed early in the outbreak had low mean sensitivity and had rapid initial growth rates that progressively declined, while those killed later had consistently fast growth throughout their lives. Microsite growing conditions likely had important influence over these growth patterns and ultimately the likelihood for attack. These findings, however, would benefit from further investigations. Particularly, it is unclear whether surviving trees were able to successfully resist mountain pine beetle attacks, or whether surviving trees were preferentially selected against because they represented nutritionally poor food sources (or a combination of the two). If the former, then warming temperatures and potentially greater water deficits may ultimately reduce the ability of beetles to overwhelm whitebark pine defenses. If the latter, then increases in water deficits may lower thresholds to attack in vigorous trees, while also making them less nutritionally preferred.

As is evident in the Pioneer Mountains, Montana, mountain pine beetle outbreaks can have long-lasting impacts on subalpine communities. Outbreaks on similar scales are now occurring throughout the west and, unless an extreme cold event occurs, will likely continue to spread until hosts run out. However, the potentially different effects that host-depleting outbreaks will have on species composition is still relatively unknown. This research suggests that whitebark pines may have an important influence on stand susceptibility to outbreak conditions at high elevations. Further, whitebark pine susceptibility/suitability for attack may have a non-linear relationship with climate or other stress agents, unlike other mountain pine beetle hosts. Comparisons between the

findings presented here and current mortality patterns will help contextualize the long-term implications of current mountain pine beetle-whitebark pine interactions.

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