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The current mountain pine beetle (*Dendroctonus ponderosae* Hopk.) activity in whitebark pine (*Pinus albicaulis* Englem.) ecosystems in the Greater Yellowstone Ecosystem (GYE) is historically unprecedented in extent and severity. In addition, a non-native pathogen, white pine blister rust (*Cronartium ribicola* Fisch.) is widespread and infection rates continue to intensify. Interactions between the beetle and blister rust are placing this species in a precarious state. I recorded stand- and tree-level data on four biogeographically variable sites in the GYE to quantify how four variables; severity of white pine blister rust; the presence of the alternate host lodgepole pine (*Pinus contorta* var. *latifolia* Englem.); whitebark pine density; and diffusion by non-alternate host species influence probability of selection by the mountain pine beetle for individual whitebark pine. Summary data show that 52% of the whitebark pine sampled in this study were dead, 70% attacked by mountain pine beetle, 85% infected with blister rust, and 61% were afflicted with both. Chi-square tests indicated that beetle activity was lower than expected in whitebark pine with light blister rust and increased significantly in whitebark pine with heavy blister rust. Habitat use-availability selection ratios (HSRs) indicated that, on sites with two potential host species, mountain pine beetle preferentially select whitebark pine over lodgepole pine. In addition, HSR analyses indicated that mountain pine beetle preferentially select whitebark pine with heavy blister rust over those with light rust. Whitebark pine diameter, rust severity, and overstory tree

species composition were significant, not mutually exclusive predictors in logistic regression models. This work reveals that blister rust increases whitebark pine probability of selection by, and that lodgepole pine are not the preferred host of, the mountain pine beetle. Concurrently, climate change has resulted in the expansion of habitats thermally favorable to bark beetle reproductive success in whitebark pine ecosystems. This research suggests that interactions among these disturbance agents will enhance whitebark pine mortality, widespread population decline, and alter ecological functions and processes to which these trees are critical. However, mountain pine beetle selection preference for whitebark pine with severe blister rust infection accelerates the rate of change in the proportion of whitebark pine with severe rust in the remaining population.

INTERACTIONS OF WHITE PINE BLISTER RUST, HOST SPECIES, AND MOUNTAIN PINE BEETLE IN WHITEBARK PINE ECOSYSTEMS IN THE GREATER YELLOWSTONE.

By

Nancy Karin Bockino

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and the Graduate School of the University of Wyoming
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DEDICATION

I dedicate this project to the whitebark pine, whose tenacity reminds us to be rooted in place, patient, and nurturing. This ecosystem reveals that life is full of interwoven complexities, that the choices we make influence one another, and we must stand tall and endure. As we face imminent challenges to care for the natural world, upon which we depend entirely, the lessons embodied by the whitebark pine will emerge.

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CHAPTER ONE: ECOLOGICAL BACKGROUND

INTRODUCTION

The magnitude of current mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Coleoptera: Scolytidae) activity combined with high incidence of white pine blister rust (*Cronartium ribicola* Fisch.) in whitebark pine (*Pinus albicaulis* Engelm.) ecosystems in the Greater Yellowstone Ecosystem (GYE) has provided a timely opportunity for a deeper understanding of disturbance interactions (McDonald & Hoff 2001; Kendall & Keane 2001; Smith et al. 2006; Tomback 2007). The dynamic interactions of blister rust and mountain pine beetle in whitebark pine ecosystems remain largely uncharacterized.

In recent years, extensive mountain pine beetle activity and the spread of blister rust has drawn attention to these ecosystems (Logan & Powell 2001; Williams & Liebhold 2002; Carroll et al. 2004; Smith et al. 2006; Logan & Powell 2007). Due to commercial insignificance and a high elevation distribution resulting in minimal beetle activity, the focus of early whitebark pine research was on species life history and autecology (Amman & Schmitz 1988; Jacobs & Weaver 1990; Logan & Powell 2001). Deficient understanding of the factors and interactions influencing disturbance regimes could lead to unfavorable and ineffective management strategies. There is perceived need for quantitative data to explain these complexities (Bebi et al. 2003).

Accidentally introduced to North America a century ago, blister rust has spread and continues to intensify, throughout the range of whitebark pine (Smith et al. 2006).

Throughout the whitebark pine distribution, blister rust is present in 20 to 70% (Schwandt 2006, Tomback 2007).

Although during the 20th century two significant mountain pine beetle events occurred in whitebark pine ecosystems, the extent and intensity of the current beetle outbreak and related mortality in whitebark pine is historically unprecedented. It is important to note that this historical evaluation is made based upon an inherently narrow human time frame of only decades. There is a disparity between this time frame and the broad range of variation in ecosystems shaped by infrequent events (Kendall & Keane 2001; Logan & Powell 2001; McDonald & Hoff 2001; Carroll et al. 2004; Westfall 2005; Gibson 2006; Kulakowski et al. 2006; Schwandt 2006; Gibson et al. 2007). Current research attributes unprecedented beetle activity in high elevation ecosystems to alterations in mountain pine beetle phenology directly related to temperature (Bentz et al. 1991; Logan & Powell 2001).

The largest beetle outbreak documented in whitebark pine in the 20th century extended from southern Canada to Wyoming, began around 1926 and lasted 8-12 years (Ciesla & Furniss 1975; Arno & Hoff 1990; Perkins & Swetnam 1996). Patterns of spread and severity during this outbreak in whitebark pine were similar to those observed previously in lodgepole pine (*Pinus contorta* var. *latifolia* Engle.) (Cole & Amman 1980, Perkins & Swetnam 1996). The 1920s outbreak coincided temporally with a documented drought and was terminated by a prolonged cold winter (Figure 1.1; Finklin 1988; Kipfmueller et al. 2002). Records from ground and aerial survey data indicate a second outbreak, temporally and spatially lesser, in the late 1960s and early 1970s (Parker 1973;

Kipfmueller et al. 2002). This outbreak also coincided with years of precipitation below the long-term mean (Figure 1.1).

Because of the small-scale and infrequent nature of beetle activity in whitebark, susceptibility of whitebark pine to selection by mountain pine beetle is currently unclear. It is unknown how white pine blister rust infection severity, presence of an alternate host, specifically lodgepole pine, or variable whitebark pine density due to diffusion by non-alternate host species or in pure stands influences this species susceptibility to mountain pine beetle.

Documents addressing this situation include the following factors as contributors to current whitebark pine mortality: *i*) a non-native fungal pathogen, white pine blister rust; *ii*) a native forest herbivore, the mountain pine beetle; and *iii*) the current shift in climatic setting toward unprecedented warm temperatures alters the distribution and population dynamics of blister rust and mountain pine beetle, and contributes to whitebark pine drought stress (Figure 1.1). A fourth factor often unsuitably included in this list is whitebark pine loss due to replacement by shade-tolerant conifers. In some whitebark pine stand types, such as mixed conifer, mid-elevation sites, the progression of vegetative succession results in increased density of subalpine fir and Engelmann spruce (*Abies lasiocarpa* Hook. & *Picea engelmanii* Parry.). However, this is a natural process characteristic to and inherent at that site (Campbell & Antos 2003; Walsh 2005).

The following provides a background on whitebark pine and disturbance ecology, and mountain pine beetle and white pine blister rust life history. In addition, this chapter

briefly covers host selection concepts, susceptibility models, ecosystem response, and current prominent management strategies.

WHITEBARK PINE ECOLOGY

Species Description

Whitebark pine is of taxonomical and ecological interest (Tomback et al. 1995). Whitebark is a member of the family Pinaceae, genus *Pinus*, subgenus *Strobus*, and the only North American pine in the subsection *Cembrae*, the nut pines; the other four species in the subsection are Eurasian. Whitebark pine distribution includes subalpine habitat in two zones, the Rocky Mountains from Alberta to Wyoming and the North American coastal range from British Columbia to the Sierra Nevada Mountains in California (Critchfield & Little 1966). This long-lived species occurs in alpine communities in krummholz form, as a dominant species in treeline communities, or as a seral or codominant species in subalpine forests (Arno & Hoff 1990). Whitebark pine commonly survive over 700 years and can persist for 1270 years (Arno & Hoff 1990; Perkins & Swetnam 1996).

Foundation Species Role & Ecosystem Services

Considered commercially insignificant, the value of whitebark pine lies in the realm of aesthetics and biological integrity. This high-elevation, slow growing species occupies cold, windswept sites with poor soil development, water-limitations, and extreme temperatures (Arno & Hoff 1990; Tomback & Linhart 1990). Due to its critical role as both a keystone and foundation species, whitebark pine is a fundamental

component of many high elevation ecosystems in the GYE. A keystone species has an ecological role disproportionately large in comparison to its abundance, and a foundation species is one that defines ecosystem structure, function, and process (Smith & Smith 2001; Tomback et al. 2001a).

The architectural, functional, and physiological characteristics of whitebark pine influence biodiversity and forest structure and process (Ellison et al. 2005). Specifically, these trees maintain hydrological quality by trapping snow, increasing accumulation, and regulating the retention of snowdrifts that generate late-season stream flow (Arno & Hoff 1990; Arno & Weaver 1990; Farnes 1990). These influences are far-reaching and widespread, entire watersheds and impacting agricultural and suburban settings hundreds of miles downstream. In addition, whitebark pine stabilize steep sites, reducing erosion, and snow avalanches (Burroughs & Thomas 1977; Tomback & Kendall 2001). Pioneering, drought and stress tolerate seedlings make whitebark pine key facilitators of regeneration on newly exposed sites or after a disturbance (Arno 1986; Tomback 1986; Tomback 1993; Tomback 2005). Whitebark pine create moist microsites and serve as nurse trees in open areas or ribbon forests, promoting survival and growth of other plants, in particular less hardy conifer species often aggregate around whitebark pine (Lanner 1980; Arno & Weaver 1990; Callaway 1998).

Whitebark pine seeds weigh about 175 milligrams each and are comprised of over 50% lipids, making them one of the most energy-rich vegetative food sources available to many wildlife species (Schmidt & McDonald 1990; Mattson et al. 1992; Lanner & Gilbert 1994). The well-known and charismatic relationship between whitebark pine and

grizzly bear (*Ursus arctos horriblis*) involves storage of cones in middens by red squirrels (*Tamiasciurus hudsonicus*). In late August, grizzlies obtain seeds almost exclusively from squirrel middens, which they search out and excavate. During this time, grizzlies feed on virtually nothing else (Mattson & Reinhart 1994). Grizzlies easily convert the dietary fat available in whitebark pine seeds to adipose tissue critical to survival and reproductive success of the grizzly bear during hibernation (Craighead et al. 1982; Kendall & Arno 1990). In the GYE, grizzly survival, fecundity, and rates of human conflict correlate to whitebark pine seed abundance (Mattson et al. 1992). Many other wildlife species utilize the seeds, including many forest birds, rodents, and black bears (*Ursus americanus*) who climb whitebark pine to obtain cones independently (Lanner & Gilbert 1994).

Although not biologically pertinent whitebark pine, and the alpine ecosystems their majestic form and gnarled character represents, possess tremendous aesthetic value. Whitebark pine define the upper subalpine and embody challenges to survival for backcountry travelers. Whitebark pine thrive on rugged ridges and peaks, places that present conditions so harsh that most other plants and animals are absent. Public concern over declining whitebark pine populations presents public land managers with opportunities to increase awareness of ecology, non-native species control, climate change, and the challenges of forest stewardship. There are currently many active organizations providing education, funding, and political support for whitebark pine restoration efforts.

Germination and Cone Production

Whitebark pine seed germination requires compound stratification by cold temperatures for a minimum of forty-five days (Jacobs & Weaver 1990). Seedling establishment is most successful in openings, adjacent to objects such as rocks or downed wood, where snowmelt is providing moisture, or during years of sufficient early summer precipitation (McCaughey & Schmidt 1990). Recent work has identified an obligate mycorrhizal associate of whitebark pine, critical to survival of newly germinated seedlings (Cripps & Mohatt 2005). In addition, partial shading is essential to seedling survival (Kimmins 1997). Seedlings rapidly develop deep, thick roots improving survival rates, which range from 40 to 60 % for first-year cohorts (Tomback et al. 1993a)

Cone production may commence at twenty to thirty years of age on good sites, but most whitebark pine do not reach maximum cone production until at least sixty to eighty years (Krugmen & Jenkinson 1974). Whitebark pine is monoecious, and development of indehiscent, female ovulate cones takes two years. Upon maturity, two large seeds develop on each cone scale, which are broken open by the Clark's nutcracker (*Nucifraga columbiana* Wilson), which has a long, pointed bill (Tomback 1978). In the GYE, large cone crops occur every three to four years and vary geographically (Morgan & Bunting 1992).

Regeneration Strategies

Whitebark pine exhibit several unique reproductive strategies that facilitate their successional roles in forest structure and function as keystone species, and resilience to disturbance-induced change. In addition, these strategies indicate that whitebark pine

evolved in highly unpredictable and stressful environments. Large, indehiscent, wingless, and thick-coated seeds provide nutrients, allow for rapid initial growth, and are an adaptation to xeric, cold conditions and short growing seasons (Baker 1972). In the *Pinus* genus, only 20 species out of 100 have functionally wingless seeds (Critchfield & Little 1996).

Research on sites burned in the 1988 fires in Yellowstone National Park, revealed that whitebark pine exhibit delayed seed germination for up to eight years due to seed physiology and Clark's nutcracker caching behaviors. This results in a soil seed bank not present in any other *Pinus* species (Tomback et al. 2001b). This reproductive strategy maximizes whitebark pine fitness in the face of unpredictable environmental conditions. Recruitment is occurring continuously, even in years with no cone production or in years following a substantial disturbance, and opportunistically during favorable precipitation events that promote germination (Tomback et al. 2001b; Tomback et al. 2005). Whitebark pine's multi-trunk growth habit is an artifact of nutcracker caching patterns, and this aggregated growth promotes increased germination rates due to cross-pollination, and provides protection and increased nutrient and water acquisition for seedings (Tomback & Linhart 1990).

The Clark's nutcracker is a seed-storing corvid, and primary agent of dispersal of whitebark pine's large wingless seeds. Nutcrackers harvest seeds in late summer and fall, transport them their sublingual pouch and bury them in caches of 1-15 seeds beneath 2 to 3 centimeters of soil (Tomback 1978; Hutchins & Lanner 1982; Tomback 1982). These birds are highly mobile and effective seed dispersers (Tomback & Linhart 1990).

Recently burned areas with dense herbaceous understory are not optimal cache sites (Tomback & Linhart 1990). Rather, nutcrackers prefer to cache seeds on steep south-facing slopes, open rocky sites, under trees or stones and in loose forest litter; they may cover a cache site with an object such as a twig or cone (Mezhenny 1961). A single bird typically caches 20 000 to 40 000, and as many as 98 000 seeds per season. Approximately 40% of cached seeds serve as a food source for adult nutcrackers and their young hatched in late winter, while the remaining unretrieved seeds may germinate in late spring and summer (Tomback 1982).

This mutualistic relationship facilitates rapid recolonization of whitebark pine during secondary succession on disturbed sites or primary succession at timberline. In most whitebark pine stands, successful recruitment depends entirely upon nutcracker caching (Hutchinson & Lanner 1982). This reliance on bird dissemination provides whitebark pine with a pioneering advantage (Tomback & Linhart 1990). They arrive on site sooner than wind-dispersed conifers and exhibit dispersal ranges independent of prevailing winds of up to 22 kilometers from a seed source (Tomback 1982; Tomback et al. 2001b).

The nutcracker has a profound effect on the ecology and evolution of whitebark pine (Hutchinson & Lanner 1982). These unique dispersal patterns result in genetic structure and growth forms different from those of wind-dispersed pines (Furnier et al. 1987; Tomback & Linhart 1990; Tomback et al. 1993b). For example, the common shrubby growth form and multi-branched canopy of whitebark pine is the result of cluster planting by the nutcracker. This growth habitat promotes a “lyrate” crown form and

perching branches available to nutcrackers (Tomback 1978; Lanner 1982; Jacobs & Weaver 1990). In addition, genetic relatedness of trees within clusters is high, yet very low among clusters (Linhart 1990; Tomback 1993b).

Multiple Successional Pathways

Although several successional roles have been characterized, the simplified and widely accepted model of whitebark pine succession is that whitebark pine pioneer post-disturbance sites, then mature and over time succeed to stands of spruce and fir (Keane et al. 1994). This model is insufficient, failing to capture variability among whitebark pine stand types and successional trajectories. Succession cannot be viewed a simple and directional change in species composition based on shade tolerance (Johnson et al. 1994). Complex and multivariate mechanisms such as fecundity, facilitation, competition, species' life history traits, and abiotic conditions play important roles (Fastie 1995; Campbell & Antos 2003).

An examination of post-fire succession in whitebark pine forests in southern British Columbia by Campbell and Antos (2003) quantified the existence and patterns of multiple successional pathways, resulting from interactions between both tree life history traits and disturbance regimes. Using a chronosequence approach, the authors capture successional change over time in multiple types of whitebark pine stands. They address changes in tree species composition and stand structure, and patterns of disturbance based on stand-origin techniques.

Most enlightening are their findings illustrating that whitebark pine play multiple roles in forest succession, as pioneers and as long-lived stress tolerators as seral species

that recruit in stands of all seral stages. Moisture, temperature, and lodgepole pine sapling density were determinants in whitebark pine establishment and persistence. Lodgepole pine sapling density is a key component determining successional pathways (Figure 1.2).

They found that recruitment occurs in late-seral, closed canopy forest and that whitebark pine growing beneath a closed canopy for 150 to 200 years respond to overstory removal. They reveal that whitebark pine are not as shade-intolerant as once believed and never completely out competed by more shade-tolerant species (Arno & Hoff 1990; McCaughley & Schmidt 1990; Campbell & Antos 2003). They equate these multiple trajectories to the life history traits of whitebark pine, specifically its ability to disperse quickly and over a broad range, and to grow slowly and persist under adverse conditions. This study is a quintessential synopsis of the inherent natural variation of forest succession and disturbance-induced change, and illustrates the ineffectiveness of the oversimplification of ecosystem processes.

Role of Fire in Whitebark Pine Ecosystems

Fire plays multiple roles in whitebark pine ecosystems depending on stand structure, microclimate, season of burn, and synoptic climate patterns. Natural fire regimes are highly variable (Campbell & Antos 2003); work on whitebark pine ecosystems suggest fire return intervals that range from 50 to 400 years, and include stand-replacing to mixed-severity fire types (Morgan et al. 1994).

High elevation, dry sites with sparse fuel loading experience small, non-lethal fires (Brown 2000). In these open and patchy whitebark pine stands, fire is restricted to

areas with sufficient fuels and can be crown or surface fire (Brown 2000). Dense subalpine stands of whitebark pine mixed with spruce and fir may experience crown fire or stand-replacing fires of mixed severity. Welsh (2005) found that whitebark pine are often dynamically similar to lodgepole ecosystems, experiencing infrequent, large, high severity stand-replacing crown fires driven by climatic conditions.

Conventional wisdom, rooted in research from ponderosa pine forests of the American Southwest, embraces the idea that human manipulations in the form of 100 years of fire suppression have altered 'natural' fire regimes, and therefore forest structure and function (Covington & Moore 1994). These ideas have ultimately led to the widely embraced, yet erroneous idea that whitebark pine replacement by shade-tolerant species is due to fire suppression, when it is the result of inherent processes associated with forest succession.

Recent findings (Veblen 2003; Baker in prep) suggest that due to field sampling issues fire return intervals are under-estimated, and therefore fire suppression has not altered many forest disturbance regimes. These findings pertain directly to whitebark pine ecosystems. The influence of fire suppression is largely absent in whitebark pine ecosystems due to: *i*) limited human capacity to suppress fire in whitebark pine ecosystems; *ii*) the geographic and edaphic setting and life history traits of whitebark pine; and *iii*) the inherently infrequent nature of fire in whitebark pine.

Romme and Despain (1989) concluded that high elevation forests of the Greater Yellowstone Ecosystem "…were not fundamentally altered during 20th century fire suppression." Because whitebark pine forests develop over hundreds of years, there is an

inherent temporal disjunct between the duration of the fire suppression era and that of forest maturation or fire rotations.

In addition, dendroecological research has shown that subalpine fir has been present may whitebark pine stands for 130 to 300 years, well beyond the time-period that encompasses the fire suppression era in the GYE, and that whitebark pine in subalpine mixed conifer stands are within normative successional status (Larson 2005). Ultimately, 80 years of fire exclusion in the northern Rocky Mountains (Tomback et al. 2001a) did not have an influence on the decline of whitebark pine in remote, high elevation sites.

In addition, ambiguity in the term 'fire-adapted' results in the mistaken reference to whitebark pine as a fire-adapted species. True adaptations to fire are evolutionarily derived physiology traits enabling plants to respond to or tolerate fire, such as serotinous cones, underground rhizomes that resprout, precocious reproduction, thick bark with low conductance, or protective growth habits that prevent crown fire (Carpenter & Recher 1979; Christensen 1985). Whitebark pine do not possess any of these traits.

Whitebark pine do however possess traits such as a soil seed bank, long range dispersal, thick-shelled seeds, stress-tolerant seedlings, and pioneering roles during forest succession. These traits enable them to thrive in unpredictable, harsh, and physiologically stressful environments. However, surface fire easily kills mature whitebark pine due to their relatively thin bark, and seedling establishment and survival are lowest on recently burned seedbeds due to competition by grasses (McCaughley & Schmidt 1990). Although fire plays a key role in shaping the landscape, on an organismal level, whitebark pine is not adapted to direct impacts of fire.

DISTURBANCE ECOLOGY

How will extensive bark beetle mortality influence whitebark pine ecosystem succession, landscape pattern and legacy? The extent and severity of whitebark pine damage must be considered at two spatial scales, alterations to species composition within forests and configuration of the species on the landscape. Scale refers to spatial resolution and extent (Turner et al. 2001). In this study, I quantified patterns on an individual tree- and stand-level. However, the patterns I identified also influence processes at broader spatial scales. Specifically I refer to the impacts of my findings in the Greater Yellowstone landscape, which recognizes a range of ecological systems and processes arranged in space and time (Turner et al. 2001).

A disturbance is a relatively discrete event that induces change and alters the structure and function of a given ecological system (White & Pickett 1985). Defining characteristics of disturbance regimes include return interval, rotation period, size, intensity, extent, rate and pattern of spread, and severity. These regimes characterize spatial and temporal patterns of disturbance and response (Wargo 1995) and vary due to geographic, topographic, and plant community patterns (White & Pickett 1985).

Disturbance events result in change and promote cycling. In the GYE, large-scale disturbances are inherent, characteristic, and central to the development, senescence and rebirth of western forests (Romme et al. 1986; Despain 1990; Aber & Melillo 1991). Stand replacing events, such as bark beetles and fire, may be crucial to the maintenance of some species over their distribution (Samman & Logan 2000). Disturbance on the landscape creates and maintains a spatially and temporally dynamic mosaic of patch

complexity, which enhances recovery, integrity, and biological diversity (White & Pickett 1985; Romme et al. 1986; Turner et al. 2001). This reduces homogeneity, stimulates primary productivity, maintains nutrient and energy cycling, and drives stand dynamics, succession, and species composition and distribution (Romme et al. 1986).

For example, beetle-induced change enhances the complexity and diversity of community resource allocation (Romme et al. 1986). Disturbance regimes are affected by stand characteristics, climate (Veblen et al. 1994), topographical factors (Kramer et al. 2001), disturbance history (Kulakowski & Veblen 2002) and host susceptibility, spatial distribution, and continuity.

Agents of Change

The dominant agents of change in Rocky Mountain coniferous forests are fire, native bark beetles, and pathogens (McCullough et al. 1998). The Rocky Mountains have experienced numerous bark beetle outbreaks of variable size and severity. Forest insects are an integral part of maintaining forest ecosystem characteristics (Baker & Veblen 1990) and outbreaks commonly last from five to twenty years (Safranyik et al. 1989). Periodic outbreaks of bark beetles result in widespread tree mortality and initiate regeneration by increasing light and nutrient availability (Romme et al. 1986; Hadley & Veblen 1993; Veblen et al. 1994).

Such patterns have occurred, and been documented, in lodgepole pine ecosystems (Amman et al. 1977). Conventional wisdom holds that beetle outbreaks occur in lodgepole pine stands when stand age and structure supports mountain pine beetle population increase and synchronous emergence. These continuous stands of mature

lodgepole pine foster large-scale beetle outbreaks (Barclay et al. 2005). This wisdom also supports the premise that dead lodgepole then burn and their serotinous cones release seeds on exposed soil promoting regeneration. This sequence is typical however, the simplification of ecological processes fails to capture inherent variability.

In contrast, beetle outbreaks in whitebark pine ecosystems are less frequent ,and therefore, less understood. As mentioned previously, considerable beetle events were recorded in the 1920s and early 1970s (Despain 1990; Perkins & Swetnam 1996), and currently an outbreak unprecedented in severity and extent is occurring (Logan & Powell 2001; Carroll et al. 2004).

Disturbances do not act in isolation, yet specific and quantitative correlations derived from research are lacking (Knight 1987; Bebi et al. 2003; Kulakowski et al. 2003). Causes of landscape patterns are multivariate interactions among multiple drivers (Turner et al. 2001). In addition, due to the non-native nature of white pine blister rust, impacts by this agent are uncharacteristic of normative disturbance regimes in whitebark pine ecosystems. My work seeks to elucidate potential or existing interactions among whitebark pine, blister rust, beetles, and climate.

Ecosystem Response

Ecosystems are nondeterministic and responsive, influenced by intrinsic and extrinsic factors (Turner et al. 2001). Ecosystem response to pathogens or insects is variable depending on both the traits of the causal agent and species-specific response to the resulting change (Wargo 1995). Because interactions of disturbance agents largely determine subsequent stand composition and successional change, shifts in disturbance

regimes may dramatically alter forest structure (Wargo 1995; McCullough et al. 1998). Plant assemblages that establish following a disturbance-induced change may be different from those prior. The severity and frequency of disturbances and spatial pattern of biotic residuals inherently link patterns of successional change (Pickett et al. 1987; Turner & Dale 1998; Turner et al. 2001; Kimmins 2004). Alterations in climatic conditions may amplify these patterns or changes (Turner et al. 2001).

Characteristic traits of causal agents that influence ecosystem response are similar to those of disturbance regimes, and include the agents: *i*) interactions with abiotic conditions and other causal agents; and *ii*) nativity and life history traits; *iii*) frequency and duration of activity; and *iv*) mechanisms and patterns of spread (Castello et al. 1995).

Species-specific responses influencing the direction and rate of succession following disturbance-induced change include: *i)* response to shifts in limiting resources and subsequent alterations to the composition of plant assemblages; *ii*) resistance of dominant species to change; *iii*) regeneration strategies such as age to sexual maturity and dispersal of propagules; *iv*) relative shade tolerance; *v*) response to competition; *vi*) ability to invade and survive novel conditions; and *vii*) presence and distribution of residuals (Kimmins 2004).

Outcomes of successional change result in a complex variety of stand structures distributed over time and space (Aplet et al. 1998; Turner et al. 2001). The forest components and processes impacted by successional change include: *i*) water and nutrient retention, distribution, and cycling; *ii*) stand density and age; *iii*) patch size and shape; *iv*) tree mortality, establishment and distribution; *v*) understory vegetation

composition; *vi*) tree vigor and phloem thickness; *vii*) soil erosion; and *viii*) coarse wood abundance and distribution (Romme et al. 1986; McCullough et al. 1998; Turner & Dale 1998).

Scale-dependent feedbacks among these components, processes, forest succession, and future disturbances exist (Foster & King 1986; Turner et al. 2001). In addition to alternations in ecosystem services addressed earlier, diminished presence and productivity of whitebark pine will influence treeline dynamics, mixed conifer forest composition and structure, and forest succession.

MOUNTAIN PINE BEETLE ECOLOGY

Life History Traits

As a cyclic source of tree mortality, the mountain pine beetle is a host specific, native insect that resides and reproduces within the subcortical tissues of coniferous trees (Amman & Cole 1983). Aside from emergence and a brief period of dispersal by mature adults, all phases of the beetle life cycle occur beneath the bark of a host tree. The mountain pine beetle has four life stages: egg, larva, pupa, and adult. The female beetle initiates colonization when she enters a host tree and constructs an egg gallery parallel to the tree stem, an adult male follows, mating takes place, and the female lays her eggs. Boring dust comprised of feces, and phloem and xylem fragments accumulates in the galleries (Hopkins 1909; Wood et al. 1966).

All stages of beetle development are highly temperature sensitive (Amman 1985; Bentz et al. 1991; Bentz & Mullins 1999). Typically, eggs are laid in the fall and develop

in 10 to 14 days. During the winter months is the long larval phase, followed by a pupal phase in the spring. Larva and pupa complete their development by feeding on phloem and blue stain fungus spores (Six & Paine 1998) and new adults develop.

Insect abundance decreases with increasing elevation and latitude (Gaston & Williams 1996). Exposure to cold temperature is the largest source of mortality to mountain pine beetle populations. Depending on developmental phase, the lethal temperature range derived from research in lodgepole pine, is between -18° C and - 40°C for 2 to 4 hours (Amman 1973; Safranyik et al. 1974).

However, many factors, such as snow insulation or bark thickness can mitigate this exposure. During the larval phase, in response to decreasing fall temperatures, beetles produce and mediate body tissue glycerol concentration, which regulates cold tolerance (Bentz & Mullins 1999). Mountain pine beetle phenology and seasonality are under direct temperature control (Bentz et al. 1991; Bolstad et al. 1997; Bentz et al. 2001; Logan & Powell 2001; Powell & Logan 2005). Due to a lack of diapause, or an environmentally controlled physiological timing mechanism, there is a direct relationship between the rate of mountain pine beetle larval development and temperature (Logan & Amman 1986; Danks 1987). Emergence occurs when temperatures beneath the bark exceed approximately 20° C (Rasmussen 1974).

Upon emergence, most beetles fly several meters above the ground and disperse widely throughout the forest. Convective winds may carry some beetles as far as 75 kilometers, however only about 3% of emergent beetles exhibit long-range, above canopy-dispersal (Furniss & Furniss 1972; Raffa & Berryman 1980; Safranyik et al.1992;

Jackson & Murphy 2003). Peak emergence typically lasts 7 to 10 days (Safranyik et al. 1975) and each beetle locates a suitable host within two days (Safranyik et al. 1992); however many unusual patterns are currently being observed in the field (Bentz personal communication; Logan personal communication; Bockino personal observation). For example, investigations during the spring of 2007 in the Wind River Range identified multiple age cohorts beneath the bark of whitebark pine (Bentz personal communication). In addition, early season re-emergence of adult beetles and their subsequent infestation of additional host trees during a single season is occurring in the GYE (Bockino personal observation).

Fungal Mutualism

Successful colonization and subsequent reproductive success of mountain pine beetle is dependent upon several fungal mutualists (Six & Paine 1998). In particular, beetles transport the spores of two blue stain fungi (*Ophiostoma clavigerum* and *Ophiostoma montium*) in mycangai, or specialized invaginations of the exoskeleton, and inoculate the host tree as they chew through the bark (Six & Paine 1998; Six 2003). These fungi serve two functions: *i*) rapid penetration into the vascular tissue of the host tree, terminating the tree's defensive resin production (Safranyik et al. 1975), water and nutrient transport and transpiration (Graham 1967), and *ii*) as an important source of nutrients for developing mountain pine beetle pupa (Six & Paine 1998).

Role of Host Monoterpenes

Although host selection behavior involves visual cues, fundamental to colonization and physiology is the interaction between mountain pine beetles and

monoterpenes found in oleoresin of host trees. This is an example of tritrophic chemical communication because a single phytochemical group influences multiple levels of biological organization (Raffa et al. 2005; Seybold et al. 2006). Mountain pine beetles oxidize host monoterpenes to produce attractive and aggregative pheromones to coordinate mass attack (Wood 1982; Seybold et al. 2000). The resulting pheromones elicit responses by beetles inside the tree and as host-locators for those flying in search of a host (Raffa & Berryman 1983). Specifically, mature mountain pine beetles metabolize alpha-Pinene to trans-verbonal (Hughes 1973) aggregation pheromones. As beetle densities increase, gut and gallery inhabiting yeast further metabolize trans-verbonal to the anti-aggregation compound, verbenone (Borden et al. 2003). The quantity of pheromones synthesized is proportional to the quantity of oleoresin in the host tree, which declines with an increase in number of attacks (Raffa & Berryman 1983).

These same molecules comprise an integral part of host tree defense mechanism and, at high concentrations, are toxic to mountain pine beetle eggs, larvae, and adults (Raffa et al. 2005). When mountain pine beetles sever resin ducts of living trees, parenchyma cells break down and mass flow of oleoresin occurs and serves as a physical obstacle to suffocate the beetle. In addition, production of secondary resin with high concentrations of terpene and phenolic compounds serve as toxin defense against the mountain pine beetle (Raffa & Berryman 1983).

Population Ecology

Dendroctonus is Latin for “tree-killer” and unlike many other phytophagus insects, reproductive success of the mountain pine beetle is contingent on the death of

their host (Raffa & Berryman 1983). Most often, beetle populations are in an innocuous, endemic phase in low abundance, residing in a few damaged, stressed, or decadent trees.

However, temporally coincident adult emergence occurs during favorable conditions for beetle establishment, survival, and subsequent population growth which supports the persistence of large, epidemic populations. This coalescence of localized beetle activity is dependent on adaptive seasonality, or synchrony of critical bark beetle phenological events driven directly by temperature (Logan & Bentz 1999; Jenkins et al. 2001; Logan & Powell 2004). The temporal aggregation of numerous beetles on a single tree, in a "mass" attack behavior strategy, enables beetles to collectively overcome tree defensive resin, and potentially toxic monoterpene and phenolic production (Miller & Keen 1960; Safranyik et al. 1975; Raffa 2001). Epidemic populations are resilient to localized mortality and exist at the landscape level. Determinants of population persistence include density-independent factors such as weather events, and stand characteristics and spatial distribution. Density-dependent factors include beetle population density, and intra-specific competition for limited resources such as local habitat and food (Safranyik & Carroll 2005).

Mountain pine beetle exhibit a broad range of aggressiveness in their host selection behavior, depending upon both host characteristics and beetle population dynamics (Raffa & Berryman 1983; Wallin & Raffa 2004). Under endemic conditions, beetles illustrate a selection preference for weakened trees or those with DBH > 8 inches (Preisler & Mitchell 1993; Safranyik & Carroll 2005), while during an epidemic phase beetles are far less discriminating (Evenden et al. 1943; Wood 1963).

Host selection by bark beetles involves many variables including olfactory cues, host tree resistance and nutritional suitability, beetle density, microclimate, and the temporal phase within a beetle outbreak (Amman & Cole 1983; Raffa & Berryman 1983; Preisler & Mitchell 1993; Waring & Six 2005; Campbell and Borden 2006). In addition, tree size and age, and stand density are common factors used to correlate host characteristics to beetle selection (Yoda et al. 1963, Hamilton 1986; Perkins & Roberts 2003).

Relative tree vigor plays a role in beetle host selection patterns and is determined by phloem thickness, sapwood moisture, and resin production (Berryman 1976; Six & Adams in review). In addition, beetle offspring production per square foot is higher in more vigorous trees with thicker phloem. Concurrently, trees with greater vigor produce greater amounts of resin, which reduces beetle production (Reid & Gates 1970). Seemingly contradictory, these findings support the idea that rapid beetle population growth occurs during a temporally discrete opportunity for the beetle. This occurs when a stand of vigorous host trees with thick phloem is experiencing drought or other stress that temporarily reduces resin flow and subsequent defensive capabilities (Berryman 1982).

Host Species Selection

Although virtually all pine species are suitable hosts, the dominant paradigm holds that lodgepole pine are the principal and preferred host of the mountain pine beetle (Ciesla & Furniss 1975; Arno 1986; Arno & Hoff 1990; Bartos & Gibson 1990). The earliest idea of host selection states: “a species which breeds in two or more hosts will

prefer to continue to breed in the host to which it has become adapted" (Hopkins 1916). However, in 1963 Wood discovered this was not always true for Scolytid beetles. Current observations of preferential use of whitebark pine by mountain pine beetle also indicate this is not accurate.

Interestingly, these observations are not entirely novel. Scientists in the 1930s noted host shift and preferential selection behavior by the mountain pine beetle indicating that at certain times both limber and whitebark pine were preferred over lodgepole pine (Hopkins 1916; Evenden 1934; Evenden et al. 1943; Wood 1982). The most common idea held that mountain pine beetle moved from lodgepole pine experiencing beetle outbreaks to whitebark pine in close proximity (Parker 1973). Later reports indicated selection of whitebark pine in the absence of adjacent beetle activity in lodgepole pine (Baker et al. 1971; Bartos & Gibson 1990). As notable changes in landscape patterns and disturbances and observations opposing these reports become evident, the body of research providing data to understand these patterns is becoming increasingly limited in scope.

Susceptibility Models

Prior research of mountain pine beetle outbreaks includes the development of infestation risk and landscape susceptibility predictive models. In 1901, Hopkins developed the host selection idea based entirely on tree diameter and stand density. In 1948, Hopping and Beall showed that tree mortality increases 2-3.5% with each centimeter of tree diameter. For nearly 70 years, these simple methods rated

susceptibility based on tree diameter, stand age and density and failed to incorporate all other site characteristics.

In the 1980s, systems based on site index and stand competition were introduced (Schenk et al. 1980; Anhold & Jenkins 1987). Others rated susceptibility based on host tree growth and vigor (Mahoney 1978; Waring & Pitman 1980). In 1992, Shore and Safranyik developed a more complex rating system incorporating many variables and defining parameters.

However, a recent evaluation of all available susceptibility models indicates a ubiquitous lack of predictive ability by these models for beetle-induced mortality (Bentz et al. 1993). These weaknesses arise from insufficient model input variables and inconsistent definitions for and use of concepts such as susceptibility (Bentz et al. 1993). Today advancing technology promotes inherently complex, and potentially more accurate, risk-rating systems. For example, models developed in 2001 incorporating weather and bark beetle phenology, accurately predicted the extent and severity of the current outbreak in the GYE (Logan & Powell 2004).

WHITE PINE BLISTER RUST

Life History Traits

White pine blister rust is a non-native, fungal pathogen introduced to North America in 1910 likely originating in Siberia and infects five-needle pines (Tainter and Baker 1996; Maloy 1997). Whitebark pine succumbs to blister rust more easily than other five-needle pines, possibly due to increased moisture availability for spores in their

compact crown and clustered fascicles (Bedwell & Childs 1943). In contrast to the cyclic nature of mountain pine beetle activity, blister rust is a continuous source of disturbance.

A member of the Basidiomycota group, this pathogen propagates during a complex, five-stage life cycle (Hoff & Hagle 1990; Hoff 1992; McDonald & Hoff 2001). Two stages occur in cankers on the primary pine host, and three stages occur on the leaves of woody or herbaceous alternate host genera including *Pedicularis, Ribes*, and *Castilleja* (McDonald et al. 2006). Spores are wind dispersed from 300 meters to 3 kilometers, and require humid conditions for survival (McDonald & Hoff 2001). Spores enter through leaf stomata, fungal mycelia colonize living bark and cambial tissue, destroy the water and nutrient transport system, and form cankers or spore producing fruiting bodies (Tainter and Baker 1996; Agrios 1997; McDonald & Hoff 2001). Eventually the pathogen girdles the branches or main bole, resulting in loss of cone-bearing branches and even direct mortality (Tainter and Baker 1996).

Impacts on Whitebark Pine

Because whitebark pine did not evolve with this pathogen, the tree is at a great disadvantage, both physiologically and evolutionarily (Campbell & Antos 2000). Documentation of the extent and severity of infection indicate that blister rust is causing rapid population declines due to mortality and decreased whitebark pine recruitment (Tomback et al. 1995; Kendall & Keane 2001; Van Mantgem et al. 2004). Decreases in recruitment result from the loss of cone production and extensive damage to seedlings and saplings (Tomback et al. 1995).

Similar to the mountain pine beetle, the propagation of this pathogen on the landscape depends upon the spatial pattern and connectivity of host species, which influences subsequent landscape pattern (Holdenrieder et al. 2004). Mean summer precipitation, host tree diameter and elevation are the three principle variables that influence white pine blister rust presence and severity (Smith & Hoffman 2001; Kearns & Jacobi 2007).

Although suggested, the relationship between blister rust induced tree stress and whitebark pine susceptibility to insects has not been quantified (Keane & Arno 1993; Tomback et al. 1995, Campbell & Antos 2000; Kipfmueller et al. 2002; Burns 2006). Manion's (1991) decline-disease spiral provides a conceptual model for the role of pathogens in tree death and supports the idea that multiple stressors compound, increasing tree susceptibility to pathogens or insects.

White Pine Blister Rust Resistance Breeding Program

Each whitebark pine is not equally susceptible, or severely infected with blister rust (Bingham 1972; Bingham 1983). Observations of phenotypically resistant whitebark pine initiated a conservation program in 2001 in the Intermountain West administered by the United States Department of Agriculture Forest Service (Sniezko et al. 2000; Hoff et al. 2001; Mahalovich & Dickerson 2004; McDonald et al. 2004; Schoettle 2004). The program seeks to identify, test, propagate, and out-plant blister rust resistant whitebark pine. Genes that affect the expression of blister rust resistance have been isolated. Resistant alleles condition a hypersensitive response in pine foliar tissue; however, variation in virulence, due to host race formation of white pine blister rust compromises

the ability of trees to develop resistance (Kinloch & Dupper 2002). Premature shedding of infected needles or small diameter stems to inhibit fungal spread occurs in rust resistant individuals (Hoff & Hagle 1990). Currently, screening of seedlings propagated from resistant phenotypes is concurrent with investigations of genetic heritability (Kinloch et al. 1999). Blister rust resistant seedlings have been planted in northwest Montana, and the estimated availability of seedlings for out-planting in the GYE is 2015 (Tomback et al. 2001a).

A Changing Climatic Setting

Shift of Thermally Suitable Habitat

The role of mountain pine beetle as agents of disturbance is normative, yet their population dynamics and distribution are currently shifting due to the effects of changes in climatic conditions (Logan et al. 1995; Logan & Powell 2001; Bale et al. 2002; Williams & Liebhold 2002; Carroll et al. 2004). Concurrent shifts in mountain pine beetle life cycles from maladaptive to adaptive seasonality with population transitions from endemic to epidemic have resulted in intensification of bark beetles within their historic range and unprecedented situations in high elevation ecosystems (Logan & Powell 2001).

All general circulation models project alterations in the spatial and temporal distribution of precipitation, maximum and minimum temperatures by season, snowpack, spring runoff timing, and snow water equivalent (Figure 1.1; Mote et al. 2005; Stahl et al. 2006; IPCC 2007; NOAA 2007). Landscape and stand structure patterns, tree

physiological defenses, and insect development, survival, predator dynamics, and dispersal respond to climate (Aynes & Lombardero 2000). Increased range and intensity of mountain pine beetle eruptive populations will have far-reaching consequences from pinyon pine ecosystems in the desert southwest to forested regions at high elevations and latitudes (Logan et al. 2003).

Conventional wisdom holds that whitebark pine ecosystems were simply too cold for bark beetles (Amman & Schmitz 1988; Logan & Powell 2001; Gedalof 2003). However, in the past 30 years northern Hemisphere warming has resulted in a 7° northward latitudinal shift in climatically suitable habitats for mountain pine beetle (Logan & Powell 2001; Kipfmueller et al. 2002; Carroll et al. 2004). Because high-elevation distributions previously served as an escape strategy from insects or pathogens that require thermally benign habitats for survival and reproductive success, some host species may not be adapted to insects and large-scale beetle outbreaks. In addition, there is a significant disparity between physiological response rates to changing climate by the beetle (typically one year) and their host forests (decades or longer).

Temperature Control of Mountain Pine Beetle Life Cycle

Temperature is the primary abiotic factor affecting poikilothermic species phenology, survival, abundance, and spatial distribution (Bentz & Mullins 1999). The current mountain pine beetle outbreak has developed coincident with an amelioration of extreme winter temperatures (Stahl et al. 2006). Mountain pine beetles require sufficient thermal energy for life cycle completion and there is a direct correlation between temperature and phenologic synchrony, which sustains high population densities, mass

attacks, and epidemic populations (Bentz et al. 1991; Logan & Powell 2001; Bale et al 2002; Logan & Powell 2004; Powell & Logan 2005). Increased temperatures have resulted in a shift from asynchronous, fractional voltinism to synchronous univoltinism and into habitats that, prior to the early 1980s, were thermally unsuitable to mountain pine beetle (Berg 2003; Carroll et al. 2004; Logan & Powell 2007).

Because one natural mechanism that terminates bark beetle outbreaks is exposure of over wintering larvae to lethal temperatures of - 40°C or below, milder winter weather contributes to the magnitude of the current outbreak (Safranyik et al. 1975; Bentz & Mullins 1999; Anon 2003). In addition, seasonal temperature patterns influence the level of cold-hardening, or glycerol production, by mountain pine beetle (Bentz & Mullins 1999).

New research indicates that temperature determines the relative abundance of the two mutualistic fungi associated with mountain pine beetle successful host invasion. Each fungal species has a different thermal optimum, allowing mountain pine beetle to inhabit a broader geographic and climatic range (Six & Bentz 2007). Research indicates that increased warming could exceed the thermal range of *Ophiostoma clavigerum*, resulting in extinction and the loss of a symbiosis. Depending upon the inherent role played by the symbiont prevalent in the altered thermal setting, mountain pine beetle fitness could increase or decrease (Six & Bentz 2007).

Effect of Climate Change on Host Trees

Availability of suitable host trees is the primary biotic factor affecting mountain pine beetle populations. A depletion or lack of host trees is the mechanism, secondary to

lethal temperatures, that slows and eventually terminates an outbreak. Reduced precipitation alters host species water-use efficiency, water stress, and overall vigor (Allen & Breshears 1998; Iverson & Pratsad 2001; Kipfmueller et al. 2002; Neilson et al. 2005). Insects outbreaks may be predisposed in drought stress plant populations (Mattson & Haack 1987). The timing of increased dry years coincides with the initiation of mountain pine beetle population growth and expansion into novel habitats (Figure 1.1 – Panel A; NCDC 2006). The Wyoming Statewide Palmer Hydrological Drought Index (PHDI) is a long-term drought index and indicates multiple and consecutive years below normal precipitation since about 1952 (Figure 1.1 – Panel B; NCDC 2006). "The 1999-2004 drought in the western U.S. will go down in history as one of the most severe droughts in the past 100 years." (NCDC 2006).

However, multiple drivers interact to determine the vulnerability of host trees. For example, research in lodgepole pine systems indicates that stand age, density, aspect and elevation, tree vigor, and drought stress often reflect tree defensive response capacity (Safranyik et al.1975; Thomson & Shrimpton 1984; Shore & Safranyik 1992; Gedalof 2003; Carroll et al. 2004; Guarin & Taylor 2005; Waring & Six 2005). Climatic variables used to construct models for suitability of mountain pine beetle habitat include minimum winter temperatures, average maximum August temperatures, total precipitation April to June, variability of growing season precipitation, and aridity indices (Safranyik et al. 1975). Beetle productivity is lower in senescing, stressed trees due to limited quality and quantity of food resources (Amman 1969; Safranyik et al. 1975; Raffa & Berryman 1987). Phloem thickness determines resource availability, brood

production, and insulation from extreme winter temperatures (Berryman 1982; Amman & Cole 1983; Langor 1989).

In addition to influencing mountain pine beetle populations in whitebark pine ecosystems, climate alters biogeographic patterns of forest species (Romme & Turner 1991). Specifically, elevational and latitudinal shifts in vegetation zones will occur because seasonality of moisture affects recruitment and vegetative composition (Neilson et al. 2005). Whitebark pine in the GYE is near the southern limit of its range (Arno & Hoff 1990). As timberline shifts upward total area will be reduced, and therefore the extent of suitable alpine and whitebark pine habitat decreased (Romme & Turner 1991). This reduction in area may be amplified by limited availability of moisture (IPCC 2007). Disturbance-induced change combined with a shifting climatic context results in altered envelopes in which host tree and mountain pine beetle phenological events occur (Turner 1989; Parmesan 1996; Walther et al. 2002).

CHAPTER TWO: QUANTIFICATION OF MOUNTAIN PINE BEETLE AND WHITE PINE BLISTER RUST INTERACTIONS IN WHITEBARK PINE ECOSYSTEMS

INTRODUCTION

Quantification and documentation of forest dynamics contributes to the understanding of changing disturbance regimes influenced by factors such as non-native species and altered climatic conditions. Collectively disturbance, resulting change, and subsequent succession are key contributors intricately linked to complex spatial configurations on the landscape (Turner et al. 2001). These patterns result in a mosaic of seral stages, ecosystem function, and species diversity (Reiners & Lang 1979; White 1979; Turner et al. 2001). Shifts in these disturbance regimes may dramatically alter landscape structure and ecosystem function (Turner et al. 2001).

Currently whitebark pine ecosystems within the GYE are afflicted with historically unprecedented epidemic-level populations of mountain pine beetle and high incidence of white pine blister rust both of which are continuing to spread (Kendall & Keane 2001; Logan & Powell 2001; McDonald & Hoff 2001; Carroll et al. 2004; Westfall 2005; Gibson 2006; Schwandt 2006; Gibson et al. 2007). Blister rust and bark beetle impacts combined with the effect of recent warming on beetle population dynamics (Logan & Powell 2001; Bale et al. 2002; Williams & Liebhold 2002) place this species in a precarious state (Zeglen 2002).

This ecologically important conifer species is currently experiencing very high levels of mortality over its entire range. In the northern Rocky Mountains, whitebark

pine mortality rates are as high as 90% (Kendall 1994; Smith & Hoffman 2000; Newcomb 2003; Tomback 2007). In the Interior Columbia Basin, whitebark pine populations have declined by at least 45% (Keane 2001). The GYE Whitebark Pine Monitoring Working Group Annual Report and data from the 2006 United States Department of Agriculture Forest Health and Protection aerial survey in the GYE, indicated that approximately 41% of whitebark pine-dominated forest stands contained some level of mountain pine beetle caused mortality, and 81% were infected with white pine blister rust (Gibson 2006; Schwartz et al. 2007).

The intensity, severity, duration, and extent of current mountain pine beetle activity in these systems are quickly outpacing my understanding of whitebark pine ecosystem processes (Ayres & Lombardero 2000). Understanding these dynamics has become vital to the conservation of this critical and charismatic high elevation conifer (Perkins & Roberts 2003; Waring & Six 2005; Schwartz et al. 2007). Interactions among beetles, blister rust, and tree- and stand-level response in these ecosystems will determine future stand structure, composition, function, successional trajectories, disturbance regimes, energy and nutrient fluxes, and ecosystem services (Tomback & Kendall 2001; Schwandt 2006). Drawing upon current unprecedented field conditions, my work seeks to elucidate potential or existing interactions among inherent characteristics of whitebark pine, white pine blister rust, and mountain pine beetle host selection patterns.

Whitebark Pine Ecology

Whitebark pine is of taxonomical, ecological, and socioeconomic interest (Tomback et al. 1995). Whitebark pine is a member of the family Pinaceae, genus *Pinus*,

subgenus *Strobus*, and subsection *Cembra*, one of five stone pines worldwide (Critchfield & Little 1966). Although commercially insignificant, the value of whitebark pine rests in the realm of aesthetics, biological integrity, and ecosystem services. This slow growing, long-lived pine is often the only conifer species capable of establishment and survival on cold, harsh sites with poorly developed soil, high winds, and extreme temperatures (Arno 1986; Arno & Hoff 1990; Keane & Arno 1993).

Often referred to as a keystone and foundation species, whitebark pine is a fundamental component of many high elevation ecosystems in the GYE and exhibits its influence at multiple scales throughout the western United States and Canada (Tomback et al 2001a). Ecosystem theory defines a keystone species as one that exerts influences, often indirectly, disproportionate to its relative abundance or biomass (Paine 1995). A foundation species is one that defines ecosystem structure, function, and process (Smith & Smith 2001; Tomback et al. 2001a). Central to their ecosystem roles are the far-reaching impacts of whitebark pine on watershed quality by regulating snow accumulation, redistribution, retention, spring melt and run-off, and soil erosion on steep sites (Arno & Weaver 1990). These influences affect agricultural lands and urban communities hundreds of miles away. Whitebark pine facilitate regeneration following disturbance, influencing community composition, structure, and succession (Arno & Hoff 1986; Farnes 1990; Tomback & Linhart 1990; Tomback et al. 2001a; Weaver 2001).

Every three to five years, heavy cone crops produce abundant lipid-rich seeds which are an essential vegetative food source for some wildlife species, including the endangered grizzly bear (*Ursus arctos horriblis* Ord) (Krugman & Jenkinson 1974;

Schmidt & McDonald 1990; Mattson et al.1994). The Clark's nutcracker is the primary dispersal vector for the wingless seeds and depends directly on whitebark pine seeds; nutcracker-pine interdependence is a nearly obligate mutualism (Tomback 1982; Tomback & Linhart 1990; Lanner 1996). Nutcrackers extract seeds from cones and cache thousands throughout the landscape, transporting seeds several hundred meters up to over 12 kilometers (Hutchins & Lanner 1982). Fundamental to whitebark pine regeneration and population ecology, nutcrackers drive whitebark pine geographical distribution, genetic structure, and pioneer role on recently disturbed sites (Weaver & Dale, 1974; Lanner 1980; Tomback et al. 1982; Tomback & Linhart 1990; Tomback et al.1995). Whitebark pine seeds provide an energy-rich food source for nutcrackers over wintering and courting in forests below the subalpine zone, and nestlings hatched in early spring (Tomback 1978).

Mountain Pine Beetle Ecology

Mountain pine beetle are host specific, native insects that reproduce within the subcortical region of coniferous trees (Wood 1963). Mountain pine beetle populations exhibit cyclic patterns of growth and decline, generally increasing to epidemic population levels every 30 to 40 years (Perkins & Swetnam 1996; Kipfuemeller et al. 2002).

Unlike many other phytophagus insects, reproductive success of mountain pine beetle is contingent on the death of their host (Berryman 1972; Safranyik et al. 1975). Successful host mortality by these insects is attributable to two mechanisms. First, in mutualistic relationships, beetles vector microorganisms which rapidly invade the xylem tissue of the host tree which in turn disrupts defensive resin production (Berryman 1969;

Safranyik et al. 1975), water and nutrient transport, and transpiration (Graham 1967). Second, mountain pine beetle utilizes a mass attack strategy to overcome host tree defenses. Simultaneous colonization of host trees by thousands of beetles involves synchronous emergence and chemically controlled pheromone signals (Safranyik et al. 1975; Raffa & Berryman 1983).

Mountain pine beetle host selection behavior is variable and depends upon host characteristics, climatic conditions, and beetle population dynamics (Raffa & Berryman 1983; Wallin & Raffa 2004). These dynamics are poorly understood in whitebark pine ecosystems.

White Pine Blister Rust Ecology

In contrast to mountain pine beetle, white pine blister rust is a non-native pathogen introduced to North America in 1910, likely of Asian origin, and a continuous source of disturbance rather than cyclic (Miekle 1943; Hunt 2003). Mycelium from this fungus penetrate living bark and cambial tissue, destroy the water and nutrient transport system and form cankers or spore producing fruiting bodies called aecia (Agrios 1997). Rust is devastating five-needle pine populations throughout the Rocky Mountains, and the GYE is an area of greatest concern (Smith & Hoffman 2000). Throughout whitebark pine's range infection levels range from 70-100%, in the early 2000s mean mortality due to blister rust was 35% and mean infection was 66% (Kendall & Keane 2001; Kinloch 2003). Blister rust infection rates and distribution are continuing to increase.

Long-term, blister rust is considered the most damaging agent to whitebark pine, decreasing recruitment due to loss of cone production and extensive damage to seedlings

and saplings (Tomback et al.1995; McDonald & Hoff 2001). Because whitebark pine did not evolve with this pathogen, the conifer species is at a disadvantage, both physiologically and evolutionarily (Campbell & Antos 2000).

STUDY APPROACH

An interaction between white pine blister rust presence and whitebark pine susceptibility to mountain pine beetle has been suggested (Keane & Arno 1993; Kegley et al. 2004; Burns 2006), but quantified by only a single study (Six & Adams in review), and observed during the first year of a repeat survey (Schwandt & Kegley 2004). The interaction has potential to hasten the decline of whitebark pine (Manion 1991; Tomback et al. 1995; Campbell & Antos 2000). I based my research on the timely opportunity to improve the understanding of disturbance interactions in whitebark pine ecosystems within a framework of their imminent and perilous situation.

This study addresses the variability of individual host tree condition, with the *a priori* assumption that all mature whitebark pine trees greater than 15 cm diameter at breast height (DBH) are equally susceptible to being selected as a host to the mountain pine beetle. If this assumption is insufficient, once identified, these patterns will enhance our understanding of the relationships among beetle host selection, individual tree characteristics, and the spatial and temporal spread of mountain pine beetle outbreaks on the landscape (Coops et al. in review).

Objectives & Hypotheses

My specific objectives include quantification of: (*i*) the spatial extent and severity of mountain pine beetle activity and white pine blister rust infection in whitebark pine in the GYE, *(ii)* whitebark pine mortality and cone presence in the GYE, (*iii*) the interaction between individual whitebark pine tree-level white pine blister rust severity and positive selection as a host by the mountain pine beetle, *(iv)* preferential host selection of whitebark pine over lodgepole pine, and (*v*) associations among tree diameter, beetle entrance site density, whitebark pine stand density, non-alternate host conifer species density, and site factors to mountain pine beetle host selection. Finally, I this research will result in the development of a model of host selection probability for my study sites.

I anticipate, in comparison to 2005 and 2006 surveys, increased severity, and extent of both white pine blister rust infection and mountain pine beetle occurrence and resulting mortality, and decreased cone presence in the GYE. I postulate that there is a positive relationship between white pine blister rust severity and beetle host selection, because of decreased whitebark pine vigor and physiological capability to induce defensive mechanisms with increased rust severity (Keane et al. 1994; Tomback et al. 1995). I also postulate that the mountain pine beetle will preferentially select whitebark pine as a host tree over lodgepole pine in stands where the two species are mixed and codominant. Observations of the current outbreak have indicated this host selection pattern (Bentz, personal communication; Bockino, personal observation; Renkin, personal communication). Recent work has documented this preferential host selection in another five-needled stone pine ecosystem, limber pine (*Pinus flexilus*; Dean 2007). I

also suggest that both stand overstory structure, specifically species composition and tree density, may play a role in patterns of host selection due to olfactory and visually guided beetle host choice (Zhang 2001). Finally, I suggest the complexity of mountain pine beetle host selection in whitebark pine ecosystems involves multiple predictor variables and interactions. These relationships may be dissimilar from those observed in lodgepole pine systems.

METHODS

Study Site Overview

The GYE straddles the continental divide in the northern segment of the Central Rocky Mountains and encompasses portions of southwestern Montana, northwestern Wyoming, and eastern Idaho. Two national parks, Grand Teton and Yellowstone, portions of seven national forests, three National Wildlife Refuges, and Bureau of Land Management, state, and private properties lie within this extensive region. This 7.5 million hectare core of protected federal and private land (Clark & Minta 1994) is one of the largest remaining intact ecosystems in the northern temperate zone (Keiter & Boyce 1991). Originally defined as the range of the Yellowstone grizzly bear (Craighead 1991), this ecosystem contains a rich variety of flora, fauna and rugged mountain ecosystems, and is the origin of three major continental river systems and 60 percent of the earth's geothermal features (Keiter & Boyce 1991). The striking gradients in local climate, elevation, and soil characteristics are the foundation for the vegetative mosaic in the GYE

(Glick et al. 1991). The GYE represents one of the most extensive whitebark pine populations in the lower 48 states (Figure 2.1; Critchfield & Little 1966).

The climate characterized by warm, dry summers and long, cold winters with continuous snow pack and mean temperatures below freezing is influenced by pacific, polar, and continental weather systems (Despain 1990). The growing season is two to three months at high elevation whitebark pine sites. Current research in the GYE reports influential changes in the traditional climatic setting. Since the late 1970s, mean minimum winter temperatures have been increasing, spring snowmelt is occurring earlier, and precipitation received in the form of snow is decreasing congruently with an increase in rain events (Mote et al. 2005; Stahl et al. 2006; NCDC 2006; IPCC 2007). These changes influence population dynamics of bark beetles and blister rust, host tree vigor, and disturbance regimes (Tomback et al. 1995; Ayres & Lombardero 2000; Logan & Powell 2001; Kipfmueller et al. 2002; Carroll et al. 2004).

Site Selection

This study focused on the conifer communities found in the upper subalpine and timberline zones where whitebark pine are dominant on dry, exposed sites and on mesic sites where whitebark pine are codominant with Engelmann spruce and subalpine fir. During the summer of 2006, I chose four study sites to investigate the patterns and geographic variability of mountain pine beetle host selection within whitebark pine stands in the GYE. Sample sites within the GYE were determined based on biophysical characteristics (Table 2.1). Site selection was based on: *i*) the presence of current mountain pine beetle activity identified through the use of Forest Health Protection aerial

surveys (Figure 2.2); *ii*) overstory conifer species composition; *iii*) the presence of whitepine blister rust symptoms; and *iv*) little to no evidence of direct human manipulation of forest structure, such as timber harvest. To minimize the influence of topography, elevation, and aspect on my dataset and final model, I targeted areas that were relatively homogeneous for these variables.

Site selection resulted in the differentiation of two types of sites: *i*) three 'white pine blister rust' sites characterized by the presence of blister rust and a single mountain pine beetle host, whitebark pine; and *ii*) a 'host species' site characterized by the presence of two tree species which host the mountain pine beetle, whitebark pine with very low to absent blister rust symptoms, and lodgepole pine. I identified three total 'white pine blister rust' sites, one at each Breccia Peak, Mount Leidy, and Teewinot, and a single 'host species' site at Sylvan Pass. Hereafter I will refer to these sites as 'white pine blister rust' or host species' sites.

White Pine Blister Rust Sites

As mentioned above, I identified three 'white pine blister rust' sites – Breccia Peak, Mount Leidy, and Teewinot. At each site, I further delineated two stand types based on overstory tree species composition. The first stand type, referred to hereafter as pure whitebark pine (PURE), was distinguished by the presence of whitebark pine as the dominant canopy species in an abundance of ≥ 90% of total basal area. In these stands, subalpine fir and/or Engelmann spruce were present in the understory or ≤ 10% of total basal area in the overstory. I selected these stands to determine the role of whitebark pine blister rust and tree density in individual tree selection as a host to the mountain pine

beetle. A stand is a spatially continuous aggregate of trees and associated vegetation with similar structure and climatic conditions, but does not exclude topographic and microsite variability (Hocker 1979; Oliver & Larson 1990).

The second stand type, referred to hereafter as non-alternate host mix (NHMIX), was distinguished by canopy composition of whitebark pine with subalpine fir and/or Engelmann spruce. The latter two species represent tree species that are not hosts to the mountain pine beetle. In these stands, whitebark pine comprised at least 20%, and no greater than 80%, of the canopy tree total basal area. I selected these stands to determine if a "diffusion-effect" by the presence of non-alternate host species, resulting in lower densities of and therefore greater distances between whitebark pine, plays a role in the susceptibility of an individual whitebark pine to selection by the mountain pine beetle.

Host Species Site

I identified a single site at Sylvan Pass, where whitebark pine and lodgepole pine were codominant. I used this site to determine the role of host species in selection patterns by the mountain pine beetle, referred to hereafter as alternate host mix (AHMIX). The canopy in these stands was comprised of codominant whitebark pine and lodgepole pine with negligible presence of subalpine fir, Douglas fir, and/or Engelmann spruce.

Temporal Variation in Mountain Pine Beetle Population Phase

The mountain pine beetle was present on all my study sites; however, a temporally driven range of mountain pine beetle population phase existed among sites, due to the large spatial extent of the GYE, and variation in topographic, climatic, and

geologic attributes among sites. In the field, this temporal variation was evident in the proportions of whitebark pine at each site that were dead, red-needled or green-needled. In addition, local ecologists have observed the temporal spread and increased intensity of mountain pine beetle disturbance in the GYE (Logan & Powell 2001; Gibson 2006; Renkin personal communication). Sylvan Pass represents the site with the oldest beetle outbreak, which began approximately 10 years ago in 1997. The approximate outbreak initiation on Teewinot was 2001, on Breccia Peak 2002, and finally 2003 on Mount Leidy, where mountain pine beetle populations most recently transitioned to an epidemic phase (Renkin, personal communication; Bockino, personal observation).

Data Collection

At my three 'white pine blister rust' sites – Breccia Peak, Mount Leidy, and Teewinot – twenty-four plots were examined in each of two stand types, pure whitebark pine and whitebark pine mixed with subalpine fir and Engelmann spruce (n = 144 plots). At my 'host species' site, Sylvan Pass, twenty-four plots were examined in a single stand type, where whitebark pine and lodgepole pine were codominant (n = 24 plots). To minimize the influences of edaphic factors, I initially delineated stands by substrate parent material, slope, aspect, and elevation. I based subsequent stand identification on overstory species composition, as mentioned above. Within each stand, I identified polygons that were homogenous in regard to forest structure and species composition using digital vegetation maps and observations made in the field.

I distributed plots randomly within each polygon to capture the natural variability due to the effects of microsites, disturbance history, or regeneration patterns. Within my

chosen polygon, I established a random starting point and transect azimuth. I followed the transect from the random starting point until encountering a single whitebark pine with mountain pine beetle activity within 30 meters of the transect trajectory. This whitebark pine served as plot center. Subsequent plots were a minimum of 50 meters from the initial plot, along the transect azimuth to the next whitebark pine with mountain pine beetle activity. Data recorded at each plot center included UTM coordinates determined using a GPS (Nad 83, Zone 12), elevation, slope, aspect, and topographic position.

Due to the multitrunk or clustered growth habitat of whitebark pine, I used variable radius plot techniques to determine which trees were included in each plot (Bitterlich 1984; Lesser et al.1994; Marshall et al. 2004). Angle-point sampling achieves greater precision than plot sampling when used in stands with clumped tree distribution patterns (Oderwald 1981). All trees greater than 15 cm DBH were included in the plot, as determined by a Laser Technology RD 1000 Criterion electronic relaskop set at a metric basal area factor of 2.0. I recorded the following data for each tree: species, DBH, live or dead status, cone presence or absence, average pitch tube density, crown color, and blister rust severity (modified from Six & Newcomb 2005 – see below), where applicable. I tallied trees with stems that forked below breast height separately. From this data tree density (trees per hectare; TPH), and individual tree (m^2) and stand basal area (ms^2/ha) were calculated (Husch et al. 2003).

Indicators of Mountain Pine Beetle Host Selection

I characterized host selection by mountain pine beetle with the following indicators of mountain pine beetle activity the presence of: *i*) pitch tubes, which are mixtures of tree resin and beetle-produced boring dust; *ii*) boring dust in bark crevices particularly around root collar of tree; *iii*) entrance holes with inconspicuous pitch tubes; small (≈2 mm diameter) emergence holes; and *iv*) beetles actively chewing into bark (Safranyik et al. 1974).

I represent mountain pine beetle entrance site density by the number of pitch tubes per 900 cm^2 on the bole of each whitebark pine. Four categories were established: zero, 1-5, 6-10, and >10 pitch tubes per 900 cm^2. I counted beetle entrance sites in two 30 x 30 cm quadrats at tree DBH on opposite sides of each tree. On trees with no apparent pitch tubes remaining due to loss of bark, I estimated the number of beetle entrance sites using galleries located on the bole of the tree in the xylem tissue. This method serves as an index for the density of mountain pine beetle entrance sites per tree, but does not provide information on attack success, brood production, fecundity, tree defensive response, or mortality. My work on National Park Service land prohibited destructive sampling or bark peeling, therefore I could not verify mountain pine beetle establishment and brood success. Herafter, I refer to any sign of mountain pine beetle activity to as 'host selection'.

Crown Needle Color

I used crown needle color as an indicator of the temporal sequence of attack to determine host selection preferences. The rate of needle fade can vary with local climate,

elevation, tree condition, and genetics. However crown needle color has been shown to be a valid and reliable index to the sequence of host tree selection, when trees from the same location are compared to one another within a single time period (Wear et al. 1964; Belluschi & Johnson 1969; Amman & Cole 1969; Safranyik 2004; Wulder et al. 2004; Wulder et al. 2005; Wulder et al. 2006). Immediately following selection as a host, tree foliage remains green and indicators of attack are pitch tubes and boring dust. The first visible sign of impact is a change in foliage color from green to greenish-yellow that usually begins in the top of the crown (Figure 2.3). Generally, foliage fades from green to yellow to red over the spring and summer following selection as a host (Amman 1982; Henigman et al. 1999; Coops et al. in review). The leaves gradually desiccate and pigment molecules break down; initially the green chlorophyll pigment molecules are lost, then yellow carotenes and red anthocyanins (Hill et al. 1967). Slowly, the needles drop until the tree is completely defoliated. Twelve months after selection as a host, over 90% of killed trees will have red needles. Three years after selection, most trees will have lost all their needles (BC Ministry of Forests 1995).

Blister Rust Severity

Modeled after Six & Newcomb's (2005) severity rating system, visual estimates of white pine blister rust severity were determined for each tree. Scores for the crown and bole were determined separately. Visible rust symptoms used in this study include: *i*) branch flagging (yellow, red, gray needles, or bare tips on live branches); *ii*) rodent chewing in association with a small portion of a branch or the bole; roughened, dead bark, often with resinous, visible orange cankers often evident on young stem; and *iii*)

branch tissue with thin, smooth bark, swollen sections of a branch, or white aecial blisters that produce orange-colored aeciospores (Hoff 1992).

An ocular search for individual rust symptoms, with binoculars, was limited to three minutes for the crown and three minutes for the bole, or a total of six minutes maximum. I conducted this search on multiple sides of each tree. I assigned one of the three following severity scores to the crown and bole of each tree, separately:

Severity Code	Number of Detectable Cankers
0	0
1	1 to 3
2	> 3

Categorizing cankers by their relative location is important because bole cankers often kill the entire tree or spread to the crown. Crown cankers are not an immediate threat to tree survival, however, they result in significant losses of cone-bearing branches (Campbell & Antos 2000, Smith & Hoffman 2000, & Zeglen 2002). By combining bole and crown scores, this system also provides a total whole tree blister rust severity rating, which ranges from 0 to a maximum of 4. Although this system differentiated between crown and bole rust severity, it provides no information on vertical or horizontal distribution within the tree. Data collected on rust severity provided estimates of rust incidence and severity within a stand and for individual trees.

Cone Presence

I performed ocular estimates of cone presence on both live and dead whitebark pine. I defined cone presence by the occurrence of either first or second year ovulate

cones or cone skeletons from cone crops of previous years. I estimated cone presence concurrent with my ocular search of each tree for blister rust symptoms.

STATISTICAL ANALYSES

Null Hypothesis

The *a priori* assumption of all data analyses states that each individual whitebark pine or lodgepole pine greater than 15cm DBH, in each stand or pool of data, was equally likely to be selected as a host tree by the mountain pine beetle.

Chi-Square Testing

I used two-dimensional chi-square tests of independence to determine statistical significance of the differences between two variables for a variety of host tree characteristics (SAS 2006). The first variable was bivariate and defined as a whitebark pine selected as a host to mountain pine beetle compared to whitebark pine not selected. Depending upon the tree characteristic of interest, my second variable had up to six categories. These tests corroborate relationships among variables, and the strength, direction, and shape of the associations identified.

Chi-square analyses compare observed frequencies to expected frequencies which were derived from my sample statistics, based on a model of complete independence between mountain pine beetle host selection and the whitebark pine variables I tested. I generated 'host selection frequency ratios' by comparing the frequencies observed in my sample to the expected frequencies.

Chi-square analyses assume a normal distribution of sample frequencies about the expected population parameter value, within any category. For chi-square tests with expected cell frequencies less than 1.0, which indicates an asymmetric or non-normal distribution, I pooled observed frequencies for these cells in order to meet the minimum. For example, abundance of trees sampled in the largest diameter categories was relatively low. Therefore, I pooled trees with dbh of 75 to 135 cm into single category so that their expected cell frequency was at least 1.0.

Habitat Use-Availability Selection Ratio

A habitat use-availability selection ratio (HSR) is the ratio of the use of some habitat in question to the availability of that same habitat. In this study, I defined habitat by two host characteristics of interest – tree species (whitebark or lodgepole pine), and blister rust severity. These ratios provided a metric of relative use by mountain pine beetle for a specified host characteristic or habitat, which allows detection of preferentially selected habitats (Manly et al. 1972; Manly et al. 2002; Calenge & Dufour 2006). Habitat use-availability selection ratios were calculated for each plot, based on plot-specific tree composition. Therefore, HSRs account for the influence of stand density, species composition, outbreak intensity, and temporal sequence of beetle activity on an individual tree (Gara & Coster 1968). I inferred habitat (host tree characteristic) preferences through disproportional use of dissimilar habitats over others (Aebischer et al. 1993).

I used dissimilar bivariate (habitat A and habitat B) individual whitebark pine host characteristics to test which habitat is preferred by the mountain pine beetle (Manly et al.

1993, Manly et al. 2002). I calculated a habitat use-availability selection ratio by determining the frequency of observations of mountain pine beetle presence in habitat A (i.e., lodgepole pine) compared to the frequency of observations in habitat B (i.e., whitebark pine). Ultimately, I calculated relative habitat use-availability selection preference by scaling absolute HSRs to the relative availability of whitebark pine with the desired characteristic.

For plots at 'white pine blister rust' sites, I compared habitat use-availability selection by mountain pine beetle based on individual whitebark pine blister rust severity. Based on severity patterns observed in the field and revealed by my data, I compressed whole tree blister rust severity ratings into two categories: light (0-1) and heavy (2-4). For each plot at my 'host species' site, I compared the use of whitebark pine and lodgepole pine to their availability.

Compression of whole tree blister rust severity categories could result in the placement of an individual tree in the heavy blister rust category that was phenotypically symptomatic in only the crown or bole. However, this corroborates with researched blister rust epidemiology and subsequent impacts on individual whitebark pine that indicate trees with more than one or two cankers rapidly succumb to severe infection (Smith & Hoffman 2000; Kinloch 2003; Six & Newcomb 2005). In addition, trees with bole rust commonly experience significant crown damage by fungal mycelia resulting in top-kill and the loss of most cone bearing branches (Kinloch 2003).

I calculated habitat use-availability selection ratios using the equation:

$$\frac{(\text{\# preferred host attacked} \div \text{total attacked})}{(\text{\# preferred host available} \div \text{total available})} \qquad \textit{Equation 1}$$

For each site, I tested mean habitat use-availability selection ratios (HSR) against selection ratios of non-preference (1.0) using one-group t-tests (SAS 2006). I plotted HSRs against the relative abundance of the preferred host, and applied a logarithmic curve, to detect trends in habitat use-availability selection strength, and as verification that habitat use-availability selection preferences detected were not occurring simply due to relative abundance.

Logistic Regression – Selection Probability Function

A bivariate, discrete response variable (selected as host by mountain pine or not selected) was regressed against multiple tree and stand predictor variables (Minitab 2007). This yields the probability of use or selection of a resource unit, which in this study was an individual whitebark pine. The logistic regression model presented here has a dependent variable which was transformed into a logit variable, calculated as the natural logarithm (*ln*) of the probability of a certain event occurring (p), and was then divided by the probability of no event ($p-1$). The logit is a special case of a link function in a generalized linear model (Hosmer & Lemeshow 2000).

The *ln* transforms a straight-line relationship to the logistic distribution. Therefore, the log of the odds of selection by mountain pine beetle as a function of the independent variable can expressed as the logit:

$$logit = ln\ [p/(1-p)] = b_0 + b_1x_1 + b_2x_2 + ...+ b_nx \qquad \textit{Equation 2}$$

where $x_1, x_2 ....x_n$ were independent variables and $b_0, b_1....b_n$ were coefficients determined in the logistic regression process.

Next, I back transformed the model to generate probabilities of selection of individual whitebark as a host by mountain pine beetle as:

$$p = 1/[1 + e^{-(b0 + b1x1 + b2x2 + \ldots + bnxn)}] \qquad \textit{Equation 3}$$

Stand- and tree-level metrics used to develop this model were taken from both stand types (PURE & NHMIX) at my 'white pine blister rust sites' – Breccia Peak, Mount Leidy, and Teewinot. I chose these metrics, or potential predictors, to investigate my initial questions and quantify the relationships among tree characteristics and host selection by the mountain pine beetle.

For my analysis, each tree with a suite of characteristics, was a replicate. I created dummy variables to transform continuous independent variables to categorical for diameter at breast height, study site, rust severity, and stand composition. For DBH, I used the midpoint of each category to create a continuous variable and therefore a smooth line.

Because logistic regression calculates changes in the logit scale, not the dependent itself, as in ordinary least squares, the dependent variable or error terms need not be normally distributed or linearly related, variances need not be homogeneous, and independent variables do not need to be bounded or interval (Rice 1994; Peng & Harry 2002). This study exceeds the minimum number of observations per parameter in the model (Peduzzi et al. 1996).

I fit a logistic regression model to the pooled data set using a manual, backward best subsets selection method. I based the inclusion and exclusion of independent variables and interaction terms on the Wald statistic, which tests each independent

variable against the null hypothesis that the coefficient associated with that variable was zero (Hosmer & Lemeshow 2000). Minitab imposes a restriction that the main effects must remain in the model when their cross product, or interaction, is in the model (Minitab 2007). I used a log-likelihood test, which is the deviance without any independent variables in the model minus the deviance with all independent variables in the model, to test the null hypothesis that all slopes were zero. I used Pearson's chi-square test for goodness-of-fit to determine how well the model fit my data.

RESULTS

White Pine Blister Rust Site Conditions Summary

I summarized data from all sites to obtain proportions of whitebark pine that were dead, blister rust symptomatic, selected as host trees by the mountain pine beetle, afflicted with both rust and beetles, and cone producing (Table 2.2). Data inclusive of all whitebark sampled at sites with blister rust, Breccia Peak, Mount Leidy, and Teewinot (total n = 1787) revealed that: 45% were dead; 83% of whitebark pine were symptomatic for blister rust; 81% had crown rust; 49% had bole rust; 67% were selected as a host by the mountain pine beetle; 61% were afflicted by both rust and beetles; and 49% had cones or cone skeletons from the prior year. When I included data from Sylvan Pass (all whitebark, including those with no rust, total n = 1947) mean whitebark pine mortality increased to 52% (range 33-79%), and the proportion selected by mountain pine beetle increased to 69% (range 50-84%).

Among sites, whitebark pine mortality was lowest at Teewinot PURE (33%) and greatest and oldest at Sylvan Pass AHMIX (79%). The proportion of whitebark pine selected as host trees by mountain pine beetle was lowest at Teewinot PURE (50%) and greatest at Sylvan Pass AHMIX (84%). In comparison, both mortality and beetle selection were lower in lodgepole pine than whitebark pine at Sylvan Pass. Cone presence in whitebark pine ranged from 24-68% and mean cone presence was slightly higher (56%) when whitebark pine data from Sylvan Pass was included.

Host Tree Species Site Conditions Summary

At my single 'host species' site I observed the greatest proportion of whitebark pine that were dead (79%) and selected as hosts by mountain pine beetle (84%). In comparison, host selection by mountain pine beetle in lodgepole pine was 65% and mortality, only 50%. Cones were present on only 24% of whitebark sampled, and on 93% of lodgepole sampled (Table 2.2).

Blister Rust Severity Summary

At 'white pine blister rust' sites, blister rust severity ratings range from no rust (0.0) to a maximum whole tree severity rating of 4.0 (Table 2.3). Among all sites, I observed that blister rust was more abundant and severe on branches found in crowns among all sampled whitebark pine (Table 2.3). For whitebark pine sampled at 'white pine blister rust sites' ($n = 1787$), mean crown rust severity was 1.32 (range 1.14-1.52), which was greater than mean bole severity of 0.73 (range 0.38-1.18). This difference was statistically significant ($t = 31.37$; $p < 0.0001$). Between stand types, mean crown

and bole rust was greater on individual whitebark pine found in NHMIX stands, except where there was no difference at Mount Leidy.

Mean crown rust contribution toward the whole tree rust severity rating was 64 % (range 61-75%), and inversely, bole rust contributed the remaining 36% (range 25-39%). The relative contribution of crown rust was greatest at Breccia Peak PURE (75%). Between stand types, the relative contribution of crown rust between stand types was greatest in PURE stands (65-75%).

For the subset of whitebark pine selected by the mountain pine beetle (n = 1203), mean whole tree rust for trees selected as a hosts by the mountain pine beetle (2.39, range 1.69-3.28) which was nearly twice as severe as those trees that were not selected (1.34, range 0.79-2.01). Rust severity for trees selected as hosts was greatest at Teewinot PURE (3.28). In addition, the mean rust for whitebark pine selected as host trees (2.39) was greater than the mean whole tree rust for all whitebark (2.04). These differences were statistically significant (Table 2.3; $p<0.0001$).

Host Selection Frequency Positively Related to Rust Severity

Among 'white pine blister rust' sites, there was a recurrent pattern of host selection by mountain pine beetle in relation to blister rust severity. The proportion of trees selected, and the disparity between those selected as hosts and those not selected by mountain pine beetle, increases with whole tree blister rust severity (Figure 2.4).

Using chi-square analyses, I tested the pattern identified in Figure 2.4, and found that mountain pine beetle host selection frequency ratios were statistically different among individual whole tree rust severity categories (Table 2.4). I calculated host

selection frequency ratios for each rust severity category, based on my observed frequency of individual whitebark pine not selected compared to those selected as a host by mountain pine beetle (Table 2.4).

In all cases, blister rust severity amplifies the frequency ratio of individual whitebark pine not selected to those trees selected as hosts by the mountain pine beetle. All observed frequency ratios for rust categories 2-4 exceeded the expected ratio calculated by SAS (2006) based on a chi-square model of complete independence, except for Mount Leidy PURE. This reveals an increase in selection intensity for whitebark pine with heavy blister rust. For light rust categories, mountain pine beetle selected fewer than expected whitebark pine, while for heavy rust categories the opposite was true. All tests for independence were highly significant ($p<0.0001$), providing strong evidence that mountain pine beetle host selection differs by rust severity category.

I also used frequency ratios to assess the strength and direction of host selection (Table 2.4). For example, selection strength was greatest at Breccia Peak, in PURE and NHMIX stands, where host selection frequency ratios were 1:23 and 1:51, respectively. This denotes that at Breccia Peak PURE for individual trees with blister rust severity of 4.0, there were 23 whitebark pine selected as host trees for each that was not selected. I compared this to an expected host selection frequency ratio of 1: 4.5. In NHMIX stands, observed host selection frequency of trees with whole tree rust severity 4.0 was 51 times greater than trees with light rust severity. Similar associations, in both strength and direction existed at Mount Leidy and Teewinot. While significant, the selection intensity observed at Teewinot was lower than at Breccia Peak and Mount Leidy (Table 2.4).

Host Selection Frequency Depends on Tree Species

Data from my 'host species' site at Sylvan Pass indicated that whitebark pine were selected by the mountain pine beetle first, and continue to be selected in greater proportions than lodgepole pine (Figure 2.5). I determined this by comparing host selection frequency ratios of available lodgepole pine to whitebark pine, using crown needle color as a surrogate for time. Between both *Pinus* species that host the mountain pine beetle, proportionately more whitebark pine had red, yellow, or no needles compared to lodgepole pine. Conversely, proportionately more lodgepole pine were green-needled than were whitebark pine (Figure 2.5).

I tested this pattern using chi-square analyses to determine host selection frequency ratios (Table 2.5; $p > 0.0001$). I found that mountain pine beetle host selection frequency ratios were statistically different between lodgepole pine and whitebark pine among crown needle color categories. This reveals that mountain pine beetle host selection differed between these two species, and that whitebark pine were more frequently selected throughout the outbreak. When compared to lodgepole pine, there were nearly twice as many whitebark bark pine had red, yellow, or needles (1:1.75), and less than half the expected whitebark pine were live with green needles (1:0.43). This means that for each lodgepole pine selected as a host, 1.75 whitebark pine were selected. Conversely, for every two green-needled or not selected lodgepole pine, one whitebark pine was observed (Table 2.5).

Individual Whitebark Pine Characteristics by Rust Severity

The distribution of whitebark pine sampled in this study among the five categories of whole tree rust severity was relatively equal, ranging from 17.2-21.9% per category (Table 2.6). This was not true when crown and bole rust were assessed separately, indicating that severe crown rust was more prevalent than bole rust. For example, greater than half of the whitebark pine sampled (51.1%) had severe crown rust, while 23.3% had severe bole rust. In contrast, 50.6 % of trees had no bole rust symptoms and 19.4% had no crown rust symptoms (Table 2.6).

The disproportionate distribution of whitebark pine selected as hosts to mountain pine beetle by whole tree rust category provides the opportunity to determine host selection patterns. For example, only 8.7% of available whitebark with no rust were selected, while 29.7% of those with severe whole tree rust (category 4) were selected as hosts by mountain pine beetle. I also found that the distribution of whitebark pine selected by mountain pine beetle was disproportionate among bole and crown rust categories.

I compared several other whitebark pine characteristics such as mean tree diameter and pitch tube density to whole tree, bole, and crown rust severity. For whitebark pine symptomatic for rust at 'white pine blister rust' sites, the mean pitch tube density per 900 cm^2 was 5.28. Pitch tube density by rust category ranged from 3.3 to 6.7 per 900 cm^2, from light to heavy rust severity, respectively. Mean tree diameter was lowest for trees with no rust (33.6) and increased with rust severity (43.4 for category 4).

Mean diameter was greater for whitebark selected as host trees (41.8 cm) by mountain pine beetle than that of those not selected (36.3 cm).

First or second year ovulate cones, or cone skeletons from a prior cone crop, were present on 49 % of whitebark pine sampled at 'white pine blister rust' sites (n = 1787). When evaluated by rust severity category, cone presence decreased dramatically with greater rust severity. For trees with no rust symptoms, cone presence was high (79%), while only 33% of whitebark pine with heavy rust bore cones.

Mountain Pine Beetle Entrance Site Density

Chi-square tests of data from 'white pine blister rust' sites provided evidence that greater rust severity was associated with increased mountain pine beetle entrance site density (Table 2.7). Among sites with rust symptoms present, in both stand types, the observed frequency ratio of trees with light rust to heavy rust decreased with pitch tube density per 900 cm^2, and conversely increased for whitebark pine with no pitch tubes, or those not selected by the beetle (Table 2.7).

Among sites, observed ratios of whitebark pine with light rust to those with heavy rust were consistently greater than expected for pitch tube densities 1-10 per 900 cm^2. For example, at Teewinot NHMIX an observed ratio of 1:16.5 was compared to an expected ratio of 1:1.72. This means that for each tree with 6-10 pitch tubes per 900 cm^2 and light rust, I observed 16 trees with heavy rust (Table 2.7).

These relationships were strongest for trees with moderate pitch tubes densities. At all sites, in both stand types, for whitebark pine with no rust pitch tube density was less than expected ($p<0.0001$). Although at some sites the frequency ratios for trees with

>10 pitch tubes per 900 cm^2 exceeded expected, there was a notable decrease in strength (Table 2.7).

Rust Severity Depends on Diameter at Breast Height

I compared the frequency of whitebark pine with light rust severity (categories 0-1) to those with heavy rust severity (categories 2-4) by DBH category (Table 2.8). I tested all whitebark pine from 'white pine blister rust' sites collectively and found a significant relationship between rust severity and DBH ($n = 1787$; $p<0.0001$). For all whitebark in stands with blister rust, I observed more than expected whitebark pine with heavy rust in diameter categories >35 cm. I assessed the strength of this relationship by comparing the range of observed frequency ratios (1:1.9-1: 3.2) to an expected frequency ratio of 1:1.6, calculated by chi-square analyses.

The relationship between rust severity and tree diameter was similar among all sites, with the exception of Teewinot PURE, where blister rust severity and diameter were independent (Table 2.8; $p = 0.8821$). In general, diameters greater than 36 cm had greater rust severity. However, the strength of the relationship was variable among sites.

Mountain Pine Beetle Host Selection Relationship to DBH Was Variable

My analyses illustrate the variable nature of host selection patterns associated with tree diameter (Table 2.9). Observed host selection frequencies for DBH categories compared to expected frequencies, calculated by chi-square analyses, were variable and inconsistent. For example, at Breccia Peak NHMIX and Mount Leidy PURE, chi-square tests indicated that host selection was independent of diameter ($p = 0.2331$; $p = 0.5132$). Results at Breccia Peak NHMIX were in sharp contrast to Breccia Peak PURE, with

highly significant diameter and host selection associations consistent with pooled data. I saw the opposite pattern at Mount Leidy, where in PURE stands host selection was weakly dependent on diameter, while in NHMIX stands, host selection was dependent upon tree diameter (Table 2.9).

Tests of pooled data (n = 1947) revealed that observed selection frequencies of whitebark pine with DBH >36 cm were greater than expected (Table 2.9). I illustrated the strength of these relationships by host selection frequency ratios, which range from 1: 2.9 to 1:3.6. I compared these selection frequency ratios to an expected ratio of 1:2.2, which indicated that for each whitebark pine not selected as a host tree in a particular diameter category I expect 2.2 selected as a host tree. Therefore, in all diameter categories >36 cm, more whitebark pine than expected were selected as host trees by the mountain pine beetle.

Selection Frequency Independent of Whitebark Pine Density in NHMIX Stands

Chi-square analyses indicated that mountain pine beetle host selection frequency ratios were independent of the density (TPH) of whitebark pine relative to non-alternate host species, subalpine fir, and Engelmann spruce, in NHMIX stands at Breccia Peak and Mount Leidy (Table 2.10). For Teewinot, the chi-square test was significant, but no cell contributed >3.841, indicating that the differences between the observed and expected frequency ratios were subtle.

Selection Frequency Depends on Whitebark Pine Density in PURE Stands

Contrary to patterns seen in NHMIX stands, mountain pine beetle host selection differed by whitebark pine density in PURE stands (Table 2.11). The strength of

selection preference by the mountain pine beetle was variable. For example, selection strength was weak at Teewinot for whitebark pine in stands of 401-500 TPH where the observed host selection frequency ratio of 1:1.1 was compared to an expected ratio of 1:0.96. In contrast, at Breccia Peak for whitebark pine in stands of 301-400 TPH, the observed host selection frequency ratio was 1:17. This denotes that for each individual whitebark pine not selected as a host tree in the 301-400 TPH category, there were 17 selected as a host tree. I compared this to an expected host selection frequency ratio of 1: 4.4. Selection strength was also strong at Mount Leidy for whitebark pine in stands of 301-400 TPH where the observed host selection frequency ratio was 1:13 and expected was 1:2.8.

My data revealed that selection as a host by mountain pine beetle was more likely for an individual whitebark pine in stands of moderate densities, 300-600 TPH. Observed host selection frequencies ratios were less than expected for whitebark pine found in stands with the lowest (≤100 TPH) or high stand densities (>600 TPH).

Habitat Use-Availability Ratios: Tree Species

I calculated HSRs from the frequency of whitebark pine selected as hosts by mountain pine beetle relative to the alternate host, lodgepole pine, and the availability of each species at each plot (Table 2.12; n = 24). Whitebark pine was significantly and preferentially selected as a host tree over lodgepole pine (HSR = 1.281, SE = 0.06, $p<0.001$). I found that mountain pine beetle selected whitebark pine over lodgepole as their preferred habitat, on a local spatial scale, when I integrated plot-level species composition, density, and temporal sequence of selection (Table 2.12).

Habitat Use-Availability Ratios: White Pine Blister Rust Severity

For each plot at Breccia Peak, Teewinot, and Mount Leidy, I derived habitat use-availability ratios (HSRs) from the frequency of whitebark pine selected as host trees by mountain pine beetle with heavy rust compared to those with light rust, relative to the availability of these two rust categories (Table 2.12). There was variability in HSRs among individual sites; at Breccia Peak and Teewinot mean HSRs were greater in PURE stands. At Mount Leidy the mean HSR was greater in NHMIX stands. Data pooled by stand type resulted in mean HSRs greater in PURE (1.334, SE = 0.09) than NHMIX (1.239, SE = 0.05) stands. Pooled HSR data for all plots from 'white pine blister rust' sites (n = 143) provided empirical evidence of preferential host selection by mountain pine beetle of whitebark pine with heavy rust (mean HSR = 1.287, SE = 0.05).

Regardless of data compilation patterns, all plot-level HSRs revealed significant preferential selection. Among sites, directional one group t-tests indicated that mean HSRs were significantly greater than 1.0 ($p < 0.001$), with the strength of selection preference ranging from 1.109 to 1.452 (Table 2.12). When I account for plot level species composition, temporal sequence of beetle selection, and habitat availability I find that mountain pine beetle preferentially select trees with heavy blister rust.

Habitat Use-Availability & Relative Abundance: Blister Rust

Scatter plots with fitted logarithmic curves for all plots at Breccia Peak, Mount Leidy, and Teewinot indicated a negative relationship between habitat use-availability selection ratios (HSR) and the relative abundance of trees with heavy rust available (Figure 2.6). The majority of HSRs were greater than 1.0 (HSR =1.0 indicates no

preferential selection) and selection strength was greatest when there were fewer trees with heavy rust available. This evidence demonstrates a preferential pattern of host selection for whitebark pine with heavy rust. Host selection strength decreases as the relative abundance of whitebark pine increases toward 100%, indicating a saturation phenomenon. The discrete upper border on the data cloud is an artifact of the graphical representation of a ratio. These were plots where the mountain pine beetle selected all the whitebark pine available with heavy rust, and although available none with light rust.

Habitat Use-Availability & Relative Abundance: Tree Species

At Sylvan Pass, I plotted HSRs against the relative abundance of whitebark pine to verify that selection preferences were not due to the relative abundance of the preferred host (Figure 2.7). I found that there was not a relationship between preferential habitat selection for whitebark pine and its relative abundance compared to lodgepole pine. In addition, the majority of the HSR were greater than one, indicating preferential selection. Once again, this illustrates a pattern of preferential selection by mountain pine beetle for a specific host – whitebark pine.

Multivariate Probability of Selection Function: By Site

Results of a manual, backward stepwise regression identified three independent variables, three interactions terms among the main effects, and one adjusted (squared) term (Figure 2.8; Table 2.13; Table 2.14). The parameter estimates and fit statistics of these variables (Table 2.14) revealed that rust severity, stand type (NHMIX or PURE), and DBH were highly significant ($p<0.0001$) in predicting the selection of an individual whitebark pine as a host by mountain pine beetle.

I evaluated model plausibility from a biological perspective and then used fit-statistics to assess model robustness. Goodness-of-fit tests based on Pearson's residuals denote adequate model fit ($\chi 2 = 86.3$, df = 84, $p = 0.41$). According to concordant pairs 55% of variation in my data was explained by the model (Somers' D = 0.55). The null hypothesis that the true slope was zero was rejected by the log-likelihood test (G = 381.1; df = 10; $p<0.0001$), and significant interactions occurred among stand type, DBH, and rust severity. This indicates that a sole tree- or stand-variable is an invalid predictor of selection by mountain pine beetle.

On the whole, among all three sites there was an high degree of correspondence. Selection probability was most similar between Breccia Peak and Mount Leidy ($p = 0.121$), while Teewinot was less similar ($p<0.0001$; Figure 2.8; Table 2.14). The principal and recurrent configuration was that blister rust severity plays a greater role than stand type, site, or tree diameter; the probability of selection as a host was greatest for trees with heavy rust and lowest for those with light rust.

Among sites, the probability of selection for trees with heavy rust ranges from 0.40 to 0.95 and from 0.10 to 0.70 for those with light rust. Minimum selection probability was greatest at Breccia Peak (0.25) moderate at Mount Leidy (0.18), and lowest at Teewinot (0.10). Parallel to these trends, maximum selection probability was greatest at Breccia Peak (0.94) and Mount Leidy (0.91), and lowest at Teewinot (0.82).

Multivariate Probability of Selection Function: Single Model

Because variability in selection probability among sites was low, I removed study site from my regression and built a global function based on DBH, stand type, and rust

severity (Table 2.15; Figure 2.9). I refer to this as the 'main model' from here forward. Similar fit-statistics as above denote adequate model robustness including: Pearson's residuals ($\chi 2 = 26.4$, df = 26, p = 0.60); concordant pairs (Somers' D = 0.44); and log-likelihood test (G = 242.69; df = 6; $p<0.0001$). Once again, significant interactions occurred among stand type, DBH, and rust severity.

Examination of this regression revealed several relationships and illustrated the multifaceted and interactive nature of mountain pine beetle selection (Figure 2.9). Once again, blister rust severity plays a greater role than stand type, site, or tree diameter; the probability of selection as a host was greater for trees with heavy rust (0.6 to 0.93) than those with light rust (0.2 to 0.65).

Except for trees with heavy rust in NHMIX stands, host selection probability was greatest for a range of tree diameters approximately 45 to 100 cm. This range corresponded to those diameter categories where the observed frequency of selection as a host exceeded expected (Table 2.9).

Finally, host selection probability varied conversely with stand type; at smaller diameters, host selection probability was greatest for trees in PURE stands. This relationship switched at larger tree diameters, where trees in NHMIX stands had greater probability of selection as a host to mountain pine beetle. These findings complement my preceding analyses (Table 2.4; Table 2.9), and provided further evidence of the fundamental role blister rust plays in mountain pine host selection.

DISCUSSION

The Role of White Pine Blister Rust

In support of my hypotheses, my results reveal a positive relationship between blister rust severity and mountain pine beetle selection on both stand- and tree-levels for whitebark pine. These findings provide an illustration of the interaction dynamics between the mountain pine beetle and white pine blister rust as agents of change. In addition, habitat use-availability selection ratio analyses illustrate that mountain beetles are preferentially selecting whitebark pine with severe blister rust infection, regardless of the relative abundance of their preferred host. The mean rust severity of all whitebark pine selected as host trees by the beetle was nearly twice as great as that of trees not selected. To my knowledge, this was the first empirical study of these relationships in the GYE.

My results correspond directly with two studies reporting that whitebark pine exhibiting greater blister rust severity were more likely to be selected by the mountain pine beetle (Kegley et al. 2004; Six & Adams in review). Initial observations from a revisit survey also found beetles appeared to prefer whitebark pine with severe blister rust, although later observations were unclear (Schwandt & Kegley 2004). Aside from these two studies, previous research with which to compare my results is not available.

My study also demonstrates that rust severity was greater on larger diameter whitebark pine. This corresponds with findings from research conducted on a closely related five-needle pine species, limber pine (*Pinus flexilus* James), relating increased

whitepine blister rust infection with greater tree diameter (Hunt 1983; Campbell & Antos 2000; Conklin 2004; Kearns & Jacobi 2007).

There was also a significant and positive relationship between beetle entrance site density and rust severity. Research on intraspecific competition beneath the bark of a single host tree during outbreaks has revealed beetle densities are limited within an exhaustible food and breeding resource (Bentz et al. 1996). My data captures the association between rust severity and entrance site density, and corroborates with research regarding the termination of mountain pine beetle colonization due to intraspecific competition that begins to occur beyond beetle densities of approximately 80 entrance sites per m^2 of bark (Raffa & Berryman 1983).

I observed a significant and negative relationship between cone presence and blister rust severity. Over 75% of trees with little to no rust symptoms were cone-producing. This was in stark contrast to those trees with heavy rust, of which only one-third were cone-producing. In addition, my data indicated that crown rust was nearly twice as severe as bole rust. This finding provides an explanation for strength of the relationship between rust severity and reduced cone production. For example, the impact of crown rust is greatest on cone-bearing branches. The reduction in cone production due to blister rust damage will decrease recruitment rates, seed availability for dispersal by the Clark's nutcracker, and subsequent subalpine forest and treeline pattern and process (McKinney & Tomback 2007; Resler & Tomback in press).

Role of Host Species

My findings also support my initial idea that, contrary to historic patterns, whitebark pine has been the target host from the beginning of the current mountain pine beetle outbreak. This finding is congruent with studies of mixed stands of limber pine and lodgepole pine in the Medicine Bow National Forest in southeast Wyoming (Dean 2007). In addition, similar patterns are being observed in stands of codominant lodgepole pine and whitebark pine in the northern Wind River Range (Bentz, personal communication; Bockino personal observation).

Stand Overstory Species Composition

In support of my hypothesis that stand overstory species composition and tree density influence the patterns of host selection, I found mortality and blister rust infection rates were slightly lower on whitebark pine found in pure stands. My data revealed a positive relationship between the density of whitebark pine in pure stands and host selection, for a range of whitebark pine density from roughly 300 to 600 per hectare. These densities may provide optimum thermal habitat and host species availability. For example, thermal conditions in pure stands may contribute to beetle development and survival because these stands tend to be less dense resulting in greater incident solar radiation per tree and higher subcortical temperatures (Bartos & Amman 1989).

Fundamental factors influencing host tree vigor in lodgepole pine ecosystems include stand density, and tree size and age (Amman et al. 1977; Cole & Amman 1980; Berryman 1982; Hamilton 1986; Schmid & Amman 1992; Shore & Safranyik 1992). Variation in the chemical and visual characteristics between these stand types and

densities present the mountain pine beetle with dissimilar environments in which they make habitat choices (Zhang 2001; Seybold et al. 2006).

Contrary to my original hypothesis, the presence of non-host trees does not result in a host diffusion effect. My data indicated that there was not a relationship between relative density of whitebark pine in mixed stands of Engelmann spruce and subalpine fir and mountain pine beetle selection. Mountain pine beetle are able to disperse sufficient distances (30 m to 20 km) within or between stands (Furniss & Furniss 1972; Raffa 1980).

Stand type and density influence cone production; I found greatest cone production in pure stands. Open sites often characteristic of pure stands encourage the growth of whitebark pine with broad and spreading crown form. This "lyrate" growth habit results in greater abundance of cone bearing branches (Tomback 1978; Lanner 1980; Lanner 1982).

Multiple Whitebark Pine Characteristics Influence Beetle Selection

My data exhibit complex relationships between tree characteristics and beetle selection in support of my global hypothesis that multiple variables influence mountain pine beetle selection. Multiple logistic regression analyses indicated that a single variable, or tree characteristic, was not mutually exclusive and therefore inappropriate as a sole predictor of mountain pine beetle selection. Consideration of suites of variables and their interactions is fundamental to evaluation of selection probability. My initial univariate analyses, however, provided a framework for later multivariate analyses. In

addition, it is important to address individual host tree characteristics to determine the strength and direction of relationships and to clarify previous research.

For example, my findings conflict with the conventional premise that mountain pine beetle host selection is based predominantly on tree DBH (Cole & Amman 1969; Amman et al. 1977; Mahoney 1978). My findings illustrate that the range of tree diameters preferred by the mountain pine beetle varies with both stand composition and blister rust severity and reinforce my hypothesis that host selection relationships are multifaceted.

I derived the models of selection probability presented in this study from data collected in the GYE. Site-specific models indicated that selection probability at Teewinot was slightly different from Breccia Peak and Mount Leidy. This pattern may be partially due to the similarity in abiotic context, specifically parent material origin, topography, aspect, and precipitation patterns between Breccia Peak and Mount Leidy compared to Teewinot.

When I removed site from my analyses to produce my main model, the initial relationships identified remained significant. Common patterns among sites were evident, although the predictive ability of this model in disparate geographic locations is variable. Variation in elevation, topography, soils, disturbance history, and climatic patterns may limit this model's breadth of geographic applicability. I plan to validate this model in the future at additional sites in the GYE, utilizing data provided by the GYE Interagency Grizzly Bear Coordinating Team.

An additional caveat includes the potential source of distortion in my model due to dichotomizing blister rust severity, an inherently continuous variable. However, as mentioned earlier, the epidemiology and virulence of white pine blister rust supports my binary separation between whitebark pine with light rust, and those with heavy rust.

Potential Explanatory Mechanisms

Although this study reveals many significant relationships among disturbance agents, host tree characteristics, and stand structure, many of the mechanisms driving these interactions are currently unknown. The majority of my initial understanding of mountain pine beetle host selection patterns was based on research performed in lodgepole pine ecosystems. Explanations of my findings derived from those ideas may not be applicable for several reasons. Recent work outlined in the following review of the potential explanatory mechanisms suggests that in whitebark pine ecosystems, beetle population dynamics, host nutritional and chemical defense status, and the role of thermal and climatic factors, are distinctive.

In western North America, mountain pine beetle reproduce beneath the bark of 13 native and several non-native *Pinus* species. Research has shown that each of these species presents the beetle with a slightly different environment (McKnight 1979; Sturgeon & Mitton 1986). Phloem nutritional, chemical, and defense status is dissimilar between soft or haploxylone pines, such as whitebark and limber pine and hard or diploxylone pines, such as lodgepole (Mirov 1967; Langor 1990). These differences may be qualitative, such as variable nitrogen content or phenols for oxidation and energetic provisions (Langor 1990). Research of nutritional variations among pines indicates that

soft pines are more suitable to mountain pine beetle reproduction and development (Amman 1984; Langor 1989; Langer 1990).

On a species-level, whitebark pine may allow for greater beetle population growth due to greater nutrient availability in their phloem than is in lodgepole pine (Amman 1984). Research documenting differences between mountain pine beetle offspring found greater development rates, brood size and fecundity, weight, nitrogen, and fat content of those emerging from limber pine than those from lodgepole pine (Langer 1990; Cerezke 1995; Dean 2007). Quantitative variation in thermal insulation and abundance of habitat may also exist (Langor 1989; Langor 1990; Dean 2007). These differences may be relevant to whitebark pine and notable on an individual tree level, within a single *Pinus* species. For example, the nutritional and chemical defense status of a whitebark pine with heavy blister rust may be different from one with no blister rust.

The role of host resistance is also fundamental to understanding mountain pine beetle selection patterns. Research clearly supports the idea that drought and disease compromise host tree vigor, which leads to reduced tree resistance to attack by mountain pine beetle (Cates & Alexander 1982; Mattson & Haack 1987; Lorio 1993). More recently, a single study in Montana, found a significant negative relationship between sapwood moisture content and blister rust severity, suggesting a reduction in tree defense capabilities (Six & Adams in review).

Differences in host tree vigor may also be related to the presence and severity of white pine blister rust (Manion 1991; Tomback et al. 1995). Anatomical and cellular responses by trees infected with blister rust result in energetically costly processes. For

example, cortical parenchyma and phloem polyphenolic parenchyma cells divide to inhibit fungal colonization (Hoff et al. 2001; Hudgins et al. 2004). In addition, phenolic compound production is increased and concentrated around mycelial masses to kill or inactivate fungal hyphae (Hunter 1974; Beckman 2000). There is a potential feedback between altered or increased phenolic compounds and mountain pine beetle host colonization and population dynamics (Raffa et al. 2005; Seybold et al. 2006). The chemical composition of a tree responding to severe blister rust may provide the mountain pine beetle with greater quantity, quality or variety of phenolic groups that serve as metabolic precursors to their aggregation and breeding pheromone system (Hudgins et al. 2005). Chemical defenses in pines are constitutive and inducible (Raffa et al. 2005; Seybold et al. 2006), suggesting that these defenses are limited. Perhaps whitebark pine responding to invasion by blister rust have less chemical resources available for defensive reactions to mountain pine beetle colonization.

Chemical variation and resin production between conifer species has also been documented (McKnight 1979; Critchfield 1986). The variation between tree species phenolic compounds may relate to the ability of the mountain pine beetle to overcome the defenses of the host tree (Raffa & Berryman 1983). This is a likely factor explaining the host selection preference by mountain pine beetle for whitebark pine. For example, in whitebark pine the ratio of 3-carene (aggregation compound) to terpinolene (toxic phenols) was about 10:1 compared to a range from 20:1 to 15:1 in lodgepole pine (Smith 2000). In addition, alpha-pinene concentrations are significantly lower in whitebark pine than lodgepole pine (Smith 2000). The chemical composition of an individual tree

influences beetle pheromone development and aggregation behavior, growth rates, and survival, which as mentioned above are different between whitebark pine and lodgepole pine (Raffa & Berryman 1983; Langor 1990; Raffa et al. 2005).

Finally, and potentially the most fundamental explanation, is that the current and changing climatic setting is substantially different from historic conditions, and directly alters the life history traits of mountain pine beetle, blister rust, and their interactions (Bentz et al. 1991; Ayres & Lombardero 2000; Logan & Powell 2001, Carroll et al. 2004; Mote et al. 2005; Stahl et al. 2006). Specifically, temperature increases in high elevation habitats promote the proliferation of mountain pine beetle populations into areas previously thermally unsuitable (Logan & Powell 2001; Carroll et al. 2004). These increases have resulted in intensification of bark beetles within their historic distribution (Logan & Powell 2001).

Mountain pine beetle are well-adapted for immediate and opportunistic response to changes in climatic conditions, due to the lack of a diapause phase in their life history (Bentz et al. 1991; Powell et al. 2000; Logan & Powell 2001; Powell & Logan 2005). A dramatic illustration of the thermally opportunistic nature of the mountain pine beetle is the increase in the proportion of univoltine synchronous mountain pine beetle brood, survivorship, and greater cold tolerance, due to increases in mean minimum temperatures since the 1980s (Bentz et al. 2004). Univoltinism is directly related to outbreak intensity and mountain pine beetle host colonization success (Logan & Powell 2003; Logan & Powell 2007).

Field observations in the Intermountain West suggest unprecedented patterns of mountain pine beetle range expansion on the landscape (Renkin personal communication; Logan & Bentz 1999; Logan & Powell 2001; Carroll et al. 2004; Logan & Powell 2007; Gibson 2006). In response to these circumstances, several veteran entomologists have initiated projects directed at the quantification of these novel observations. These studies will evaluate alterations in beetle phenology characterized by multiple host colonization and brood production by a single adult beetle. This appears to be occurring when an adult beetle over winters beneath the bark, re-emerges early the following spring to colonization an additional whitebark pine. This means in a single flight season, there are multiple cohorts of mountain pine beetle colonizing host trees (Bentz, personal communication). My study provides critical information to the global understanding of the present situation in whitebark pine ecosystems.

A Changing Disturbance Regime: Blister Rust and Mountain Pine Beetle in Concert

Understanding disturbance interactions within a disturbance-adapted ecosystem is fundamental to understanding population dynamics and therefore species longevity and future status and conservation (Turner et al. 2001). Large-scale mountain pine beetle outbreaks are inherent and historic in lodgepole ecosystems (Taylor & Carroll 2003). However, dendroecological assessments of subalpine ecosystems indicate that these events in whitebark pine were rare (Perkins & Swetnam 1996). Historic evasion of bark beetles by the high elevation distribution of whitebark pine ecosystems may suggest an evolutionary lack of defense mechanisms against mountain pine beetle by whitebark pine (Amman & Schmitz 1988; Logan & Powell 2001). In addition, the impacts of non-native

blister rust are uncharacteristic of normative disturbance regimes in whitebark pine ecosystems.

Mountain pine beetle, blister rust, and climate change act in concert. The relationship between white pine blister rust severity and incidence of selection by the mountain pine beetle found in this study indicates that these two agents of change interact to alter the intensity, rate, frequency, severity, and extent of the disturbances presently occurring in whitebark pine ecosystems. Severe blister rust may function to alter the threshold conditions that result in the transition of mountain pine beetle population levels from an endemic to epidemic phase. Concurrently, habitats thermally favorable to bark beetle life history have expanded to encompass a greater proportion of the distribution of whitebark pine (Logan & Bentz 1999; Logan & Powell 2001; Carroll et al. 2004). These interactions will enhance whitebark pine mortality, widespread population decline, and the alter whitebark pine demographics and the ecological processes to which these trees are critical (Schmidt & McDonald 1990; Ayres & Lombardero 2000; Logan & Powell 2001; Tomback et al. 2001a; Bale et al. 2002).

Variation in stand conditions, and resulting heterogeneity, determine the pattern of connectivity and extent of susceptible trees and stands on the landscape (Safranyik 1978; Wood 1982; Raffa & Berryman1986; Bentz et al. 1996). This subsequently affects the pattern of spread and success of mountain pine beetle and blister rust on the landscape. For example, widespread and severe blister rust infection rates may lead to increased availability of whitebark pine with decreased vigor on the landscape (Ayres & Lombardero 2000). Because disturbance is scale-dependent, landscape perspective is

inherently vital because pathogens and insects propagate according to landscape structure, connectivity, and abiotic environment (Turner et al. 2001; Holdenrieder et al. 2004; Barclay et al. 2005).

Rust Resistance on the Landscape

My work reveals that on an individual tree-level, the interaction between blister rust and mountain pine beetle serves to increase the selection probability. Although austere, when considered on a broader landscape-scale this interaction may support the "natural selection stand approach" proposed by Hoff et al. (1994). This idea reflects the potential for the interaction between mountain pine beetle and white pine blister rust to alter the genetic composition of whitebark pine populations remaining on the landscape. This alteration can occur rapidly, in as little as 50 years or one generation exposed to selection (Hoff et al. 1994).

Inherently, in the absence of a beetle outbreak, the proportion of seeds from blister rust resistant trees available for recruitment will slowly increase (Hoff et al. 1994; McKinney & Tomback 2007). Due to top-kill and mortality to cone-bearing branches by blister rust, fewer seeds from whitebark pine with greater rust severity will be available for caching by the nutcracker and subsequent germination. Differential survival occurs among individual whitebark pine due to blister rust (McKinney & Tomback 2007; Schoettle & Sniezko 2007).

However, due to the interaction between blister rust and beetles, the rate of change in the proportion of banked seeds from rust resistant whitebark pine available for recruitment will increase during mountain pine beetle outbreaks. By selecting and killing

whitebark pine with greater rust severity, in time mountain pine beetle host selection patterns will reduce the number of trees with severe rust available to recruit into subsequent populations.

This process will occur more quickly in the presence of the interaction between blister rust and beetle selection (Figure 2.10). Like blister rust, the mountain pine beetle cause differential survival of individual whitebark pine. The accelerated rate of change in the proportion of whitebark pine in the population with severe rust, may exhibit an initial delay as the result of the distinguishing reproductive strategies of whitebark pine. Due to delayed germination and soil seed banking strategies characteristic of whitebark pine, seeds from whitebark pine produced prior to the selective action of the mountain pine beetle during the current outbreak, are presently in the seed bank. An additional influence on the rate of change is reduced seed availability, due to blister rust damage, for nutcracker caching (McKinney & Tomback 2007).

As the Intermountain West rust resistance breeding and restoration program continues to grow (Mahalovich & Dickerson 2004), this idea may become more important. In essence, host selection patterns exhibited by the mountain pine beetle, interacting with blister rust, may assist managers in their efforts to increase the proportion of whitebark pine with less severe blister rust on the landscape. As regulators of ecosystem processes, mountain pine beetles are allies for management of whitebark pine in their present situation.

Implications of the Decline of a Foundation Species

As both a foundation and keystone species occupying alpine and northern latitudinal habitats, where changes in climatic conditions and vegetative structure are occurring (Romme & Turner 1991; Beniston et al. 1996; Parmesan 1996; Walther et al. 2002) whitebark pine will become increasingly significant as a "barometer of change". In particular, simulated vegetation change in the GYE project diminished whitebark pine range in response to climate change (Bartlein et al. 1997). Directional or differential selection on a keystone species will produce a ripple effect on biodiversity and ecosystem function. This trophic cascade will result in changes in ecosystem services such as key grizzly bear habitat component and watershed quality regulation, forest succession, and alpine vegetation biogeography (Mattson et al. 1987; Callaway 1998; Tomback et al. 2001a; Schoettle 2004).

Whitebark pine ecosystem response and degree of resilience to alterations to the frequency and severity of disturbances will have profound effects on successional trajectories, stand composition and structure, landscape patterns, and future disturbance regimes (Romme & Turner 1991; Dale et al. 2002). As mentioned above, the combined effects of rust and beetles vary with the scale. On a stand-, ecosystem-, or landscape-level, as biogenic disturbance agents, mountain pine beetle and white pine blister rust influence autogenic and allogenic succession. This will result in altered patterns of ecosystem development and function, landscape structure and vegetative community composition (Kimmins 2004). In addition, mechanisms of allogenic succession respond

to alterations in climatic setting, which influences the biotic components of succession (Kimmins 2004).

Whitebark pine occur in many community types depending on abiotic conditions such as moisture and temperature (Pfister et al. 1977), and biotic mechanisms such as dispersal and germination success. Recent work on successional trajectories of whitebark pine stands describe a broad range of successional roles filled by whitebark pine, and this range includes the well-documented early pioneer and climax roles, but also reveals a significant late-seral, shade tolerant role (Campbell et al. 2003). In addition, whitebark pine reproductive strategies enhance their ability to disperse, colonize and persist on harsh sites (Tomback & Linhart 1990; Tomback et al. 1993a; Tomback et al. 2001a). For example, at the highest elevations krummholz whitebark pine facilitate timberline community expansion through creation of protected microclimates (Callaway 1998; Resler & Tomback in press). In lower subalpine habitat types, whitebark pine is codominant with subalpine fir, lodgepole pine, and Engelmann spruce (Pfister et al. 1977).

The future distribution and abundance of whitebark pine on the landscape will reflect the inherent successional roles of whitebark pine, combined with the effects of the current blister rust and beetle disturbance. Limited propagule availability due to blister rust impacts on seed production may decrease future colonization rates (Resler & Tomback in press). In mixed conifer stands, where whitebark pine is seral, beetle caused mortality may release suppressed whitebark pine and promote increased growth rates (Mattson & Addy 1975; Veblen et al. 1991). Current disturbances may promote this

response in the GYE, as many stands contain several understory cohorts of whitebark pine (Bockino, personal observation).

Resilience on the Landscape

A broad range of successional roles and reproductive strategies is an indication of the resilience of the whitebark pine as a species. Whitebark pine exhibit several traits that indicate that they evolved in highly unpredictable and stressful environments (Tomback & Linhart 1990). Large, indehiscent, wingless, and thick-coated seeds provide nutrients, allow for rapid initial growth, and are an adaptation to xeric, cold conditions and short growing seasons (Baker 1972; Tomback & Linhart 1990). Furthermore, these seeds are stored in soil seed banks for up to eight years. Recruitment can occur continuously, even during years with no cone production and following severe disturbance events (Tomback 2001). Reliance on bird dissemination provides whitebark pine with a pioneering advantage and a larger dispersal range (Tomback et al. 1990). Whitebark pine's multi-trunk growth habit is not only a relic of nutcracker caching patterns, but because aggregated growth may provide protection, increased nutrient and water acquisition, and increased germination rates due to cross-pollination (Linhart & Tomback 1985; Tomback & Linhart 1990).

The relative importance of certain variables and processes may shift with changes in disturbance regimes and climate. I must consider these disturbances within a hierarchical framework of scale (Turner et al. 2001). The elimination and fragmentation of localized populations of whitebark pine is eminent, yet residual or legacy populations, propagule availability and distribution on landscape play a vital role of large-scale

patterns of persistence (Turner & Dale 1998). It is plausible that whitebark pine will survive as a species in a mosaic of patches of different ages and a spatial configuration dissimilar from the present.

Further Research

My research has served to elucidate and quantify several relevant areas of whitebark pine ecology previously not well understood. However, many subject areas of interest and importance remain. I can explain only a portion of host tree selection patterns by mountain pine beetle by the variables tested in this study. It is likely that I did not measure or identify all the biological factors associated with selection. I suggest analyses of the variation of the following traits between whitebark pine and lodgepole pine: *i*) phloem nutritional quality and quantity; *ii*) phenolic compounds available for pheromones production; *iii*) mountain pine beetle productivity and survivorship, and both brood and individual beetle size and nitrogen composition; and *iv*) chemical defense systems. In addition, understanding of multiple successional pathways in varying whitebark pine stand types and the genetic composition of whitebark pine populations prior to and following mountain pine beetle outbreaks are vital to proper management strategies. Finally, an examination of the effect of blister rust on beetle physiology or population dynamics would augment my findings.

CONCLUSIONS

It is clear that whitebark pine in the GYE are in a precarious state. As anticipated, for whitebark pine within my study sites, rates of mortality and rust infection are higher

than prior surveys; roughly half of all individuals sampled were dead, excluding the most recently selected green-needled whitebark pine which, when they die, will increase mortality to over two-thirds. Greater than 75% were infected with blister rust, nearly two-thirds were afflicted with both mountain pine beetle and white pine blister rust, and only half were producing cones. These rates correspond with findings in other areas within the distribution of this conifer species (Campbell & Antos 2000; Zeglen 2003; Gibson 2006; Gibson et al. 2007; Schwartz 2007).

Through this work, I met my primary goal to elucidate potential or existing interactions among whitebark pine, blister rust, beetles, and climate. This study reveals that severe blister rust increases individual whitebark pine probability of selection by mountain pine beetle. I also illustrate that due to interactions among variables, selection probability must be evaluated with multiple tree- or stand-characteristics.

In addition, during the current outbreak, whitebark pine rather than lodgepole pine is the host species preferred by the mountain pine beetle. Concurrently, climate change has resulted in the expansion of habitats thermally favorable to bark beetle reproductive success in whitebark pine ecosystems.

This research suggests that the interactions of blister rust and the mountain pine beetle will enhance whitebark pine mortality, population decline, and alter the ecological functions and processes to which these trees are critical. However, the interaction between white pine blister rust and mountain pine beetle selection patterns is a selective force altering the degree of rust resistance in subsequent generations of whitebark pine.

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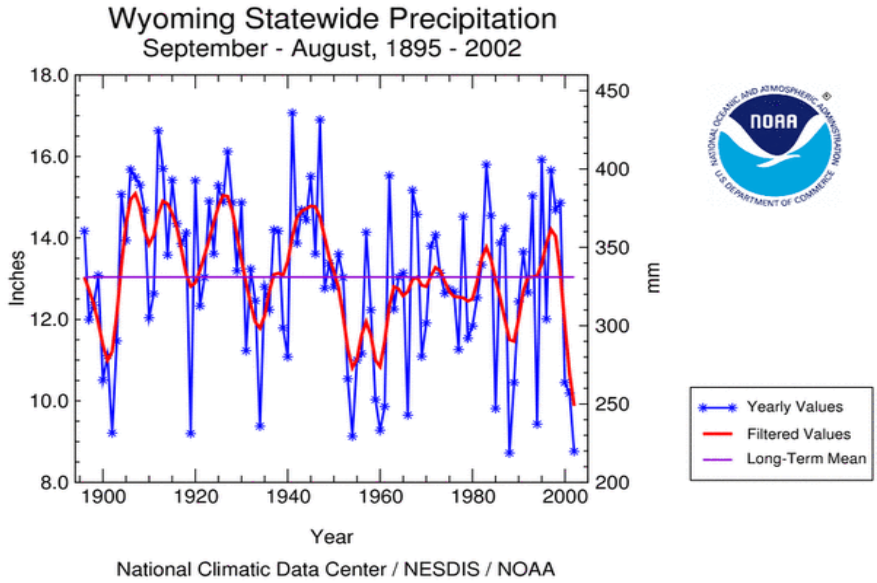
FIGURES

Figure 1.1. Wyoming climatic setting (reprinted - National Climatic Data Center 2002).
Panel A: Years were yearly and fitted values fall below long-term mean correspond to mountain pine beetle activity.
Panel B: Wyoming Statewide Palmer Hydrological Drought Index (PHDI) is a long-term drought index and indicates multiple and consecutive years below normal precipitation since about 1952.

A.



B.

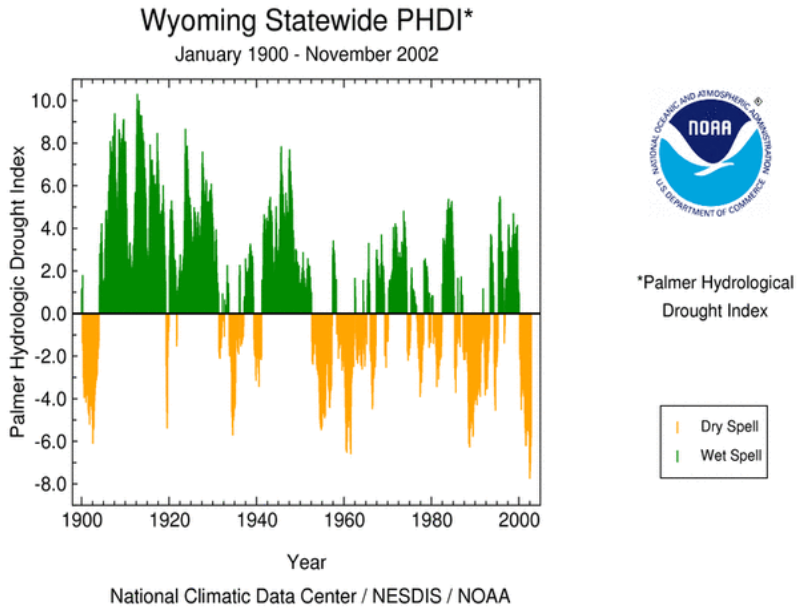


Figure 1.2. Representation of relative tree dominance for two pathways of post-fire succession in whitebark pine forest. Abundant lodgepole pine in early successional stages define Pathway 1. Sparse or absent lodgepole pine define Pathway 2. Grey shading indicates the range of stand-replacing fire return intervals reported in the literature (Reprinted – Campbell & Antos 2003).

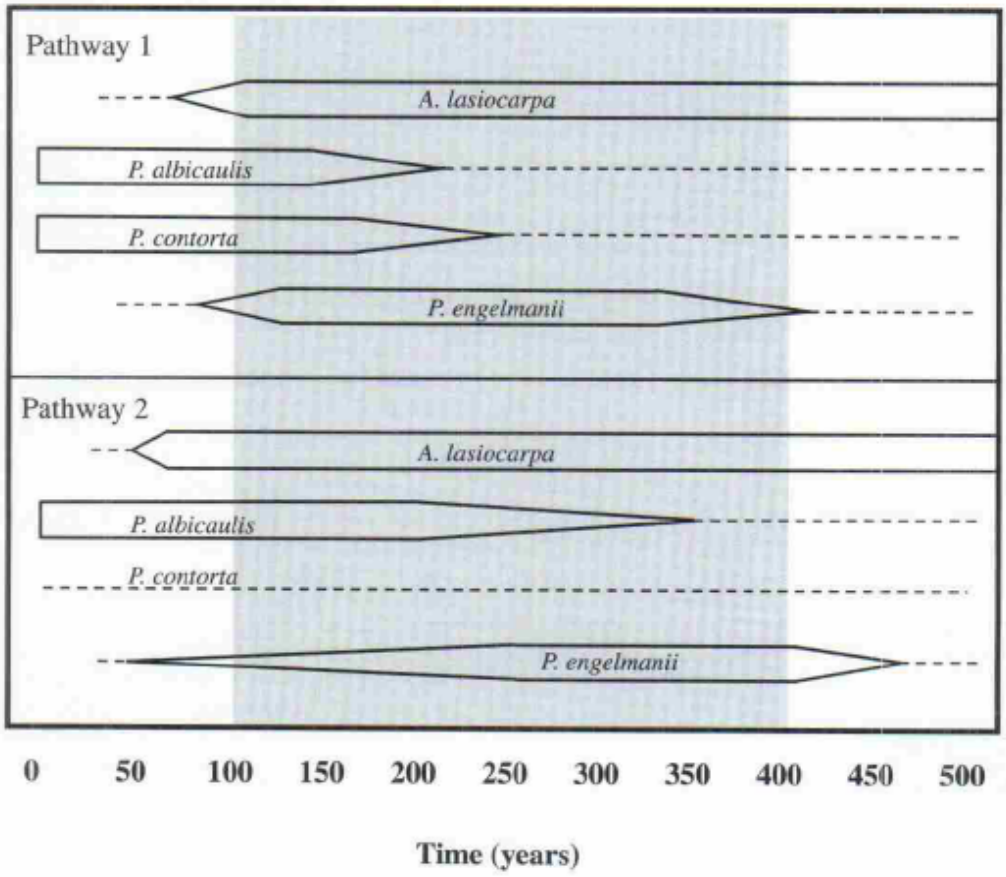


Figure 2.1. Whitebark pine distribution (USGS 1999) and site locations in Greater Yellowstone Ecosystem for data collected May-August 2006.

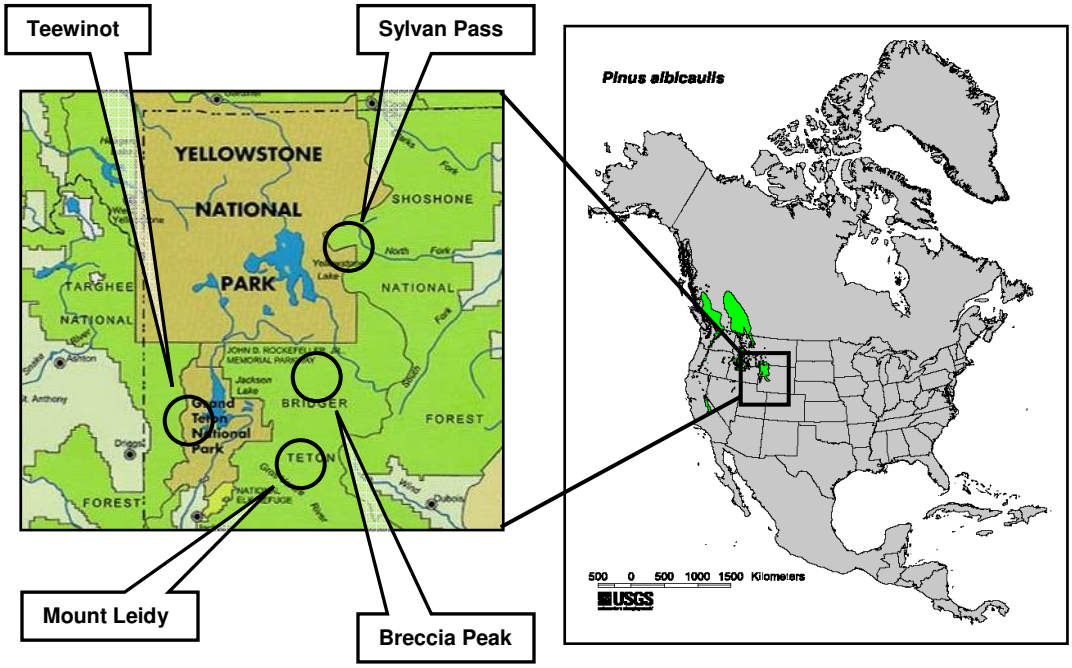


Figure 2.2. Forest Health Protection (FHP) Aerial Detection Survey data 2000-2006. Delineated polygons indicate whitebark pine detected annually as new red-needled from fixed wing planes. These surveys provide an index to change over time, spatial extent, and distribution. Within each polygon is a range of whitebark pine mortality. They do not provide empirical evidence of severity and intensity of mortality within a polygon. FHP does not survey all areas, due to smoke or cloud cover or funding restrictions, even though mountain pine beetle may be active in those areas.

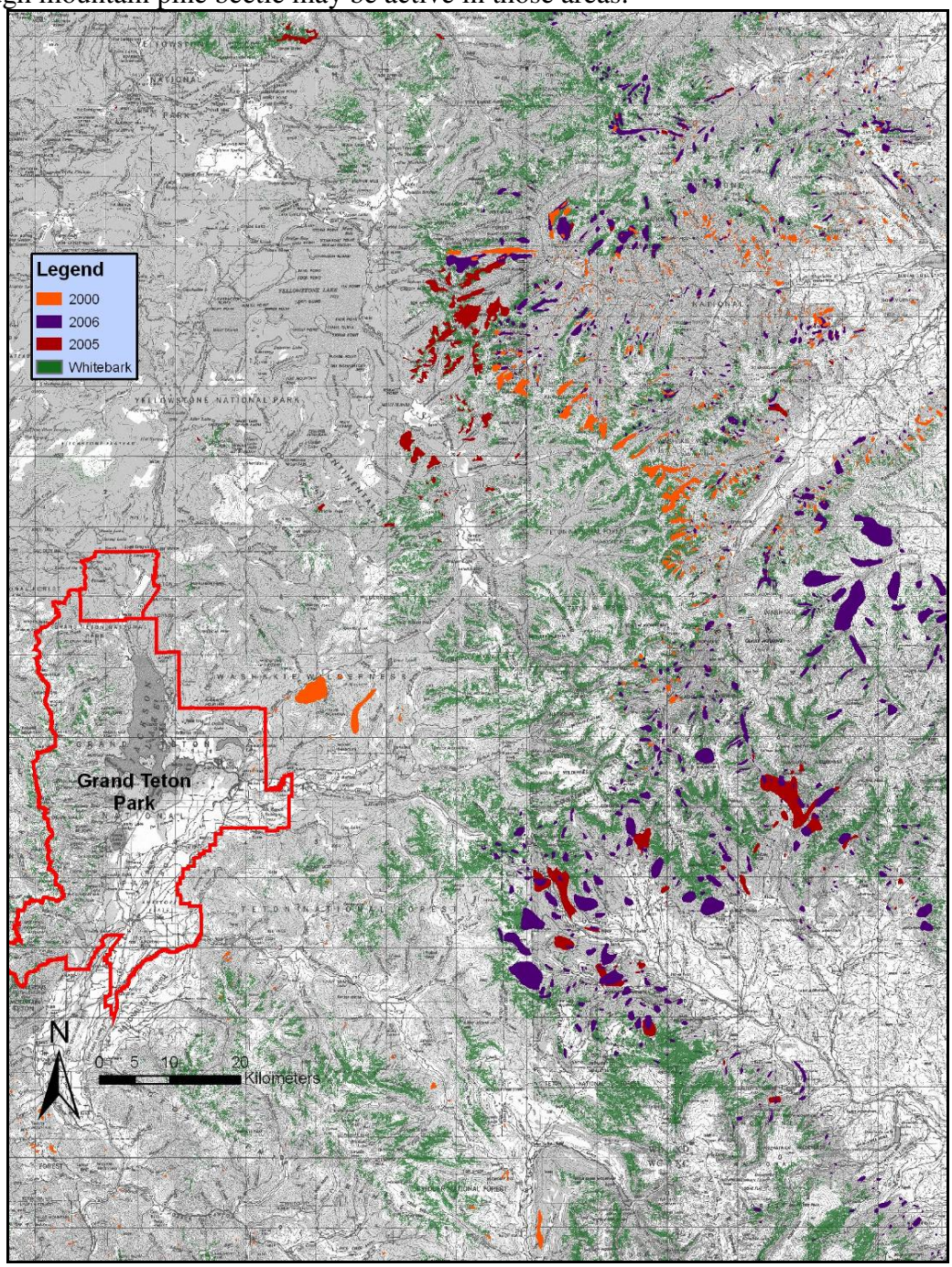


Figure 2.3. Crown needle color classification as a surrogate for temporal sequence of host selection by mountain pine beetle. (reprinted from Oregon Department of Forestry, 2005). We modified this classification to include four categories: green, yellow, red, and gray (no needles). We excluded gray "ghost" whitebark pine with no bark from data analysis, due their age they were likely mountain pine beetle mortality from the epidemic in the 1970s.

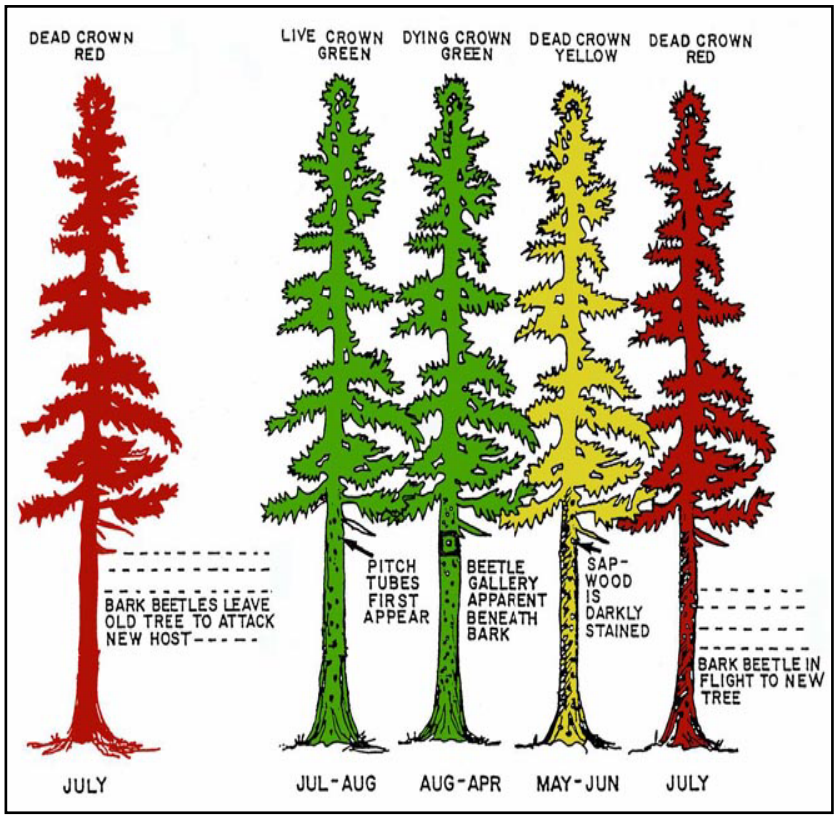


Figure 2.4. Percent of available whitebark pine selected as hosts by mountain pine beetle. MPB host selection by rust severity category (0-4) and stand type (PURE, NHMIX). Error bars indicate a 95% confidence interval. Shaded bars are whitebark pine selected by MPB, open are not selected.

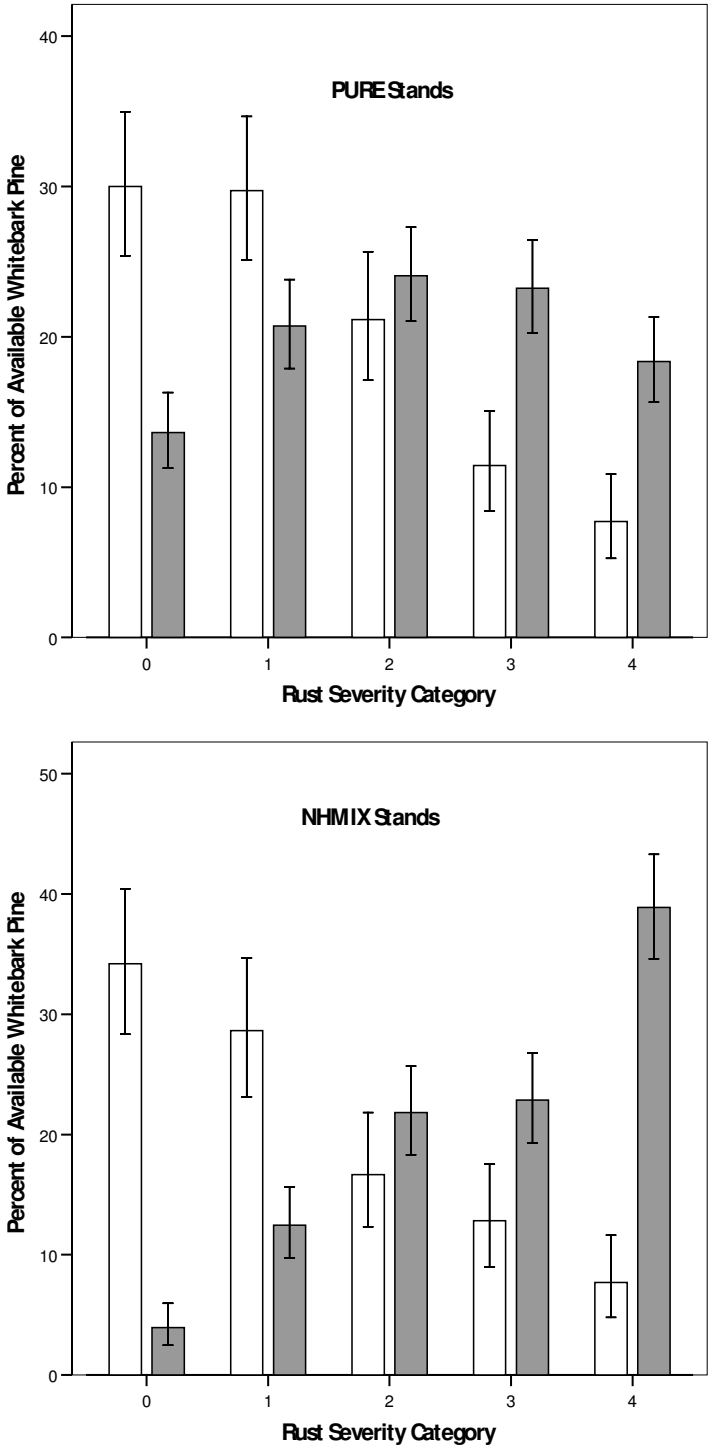


Figure 2.5. Temporal host selection by mountain pine beetle of percent available lodgepole pine and whitebark pine. We used crown needle color as a surrogate for time. Trees with red/yellow or no needles were selected as host trees first, and those with green needles were selected last or not at all. Error bars indicate a 95% confidence interval. Shaded bars are lodgepole pine, open whitebark pine.

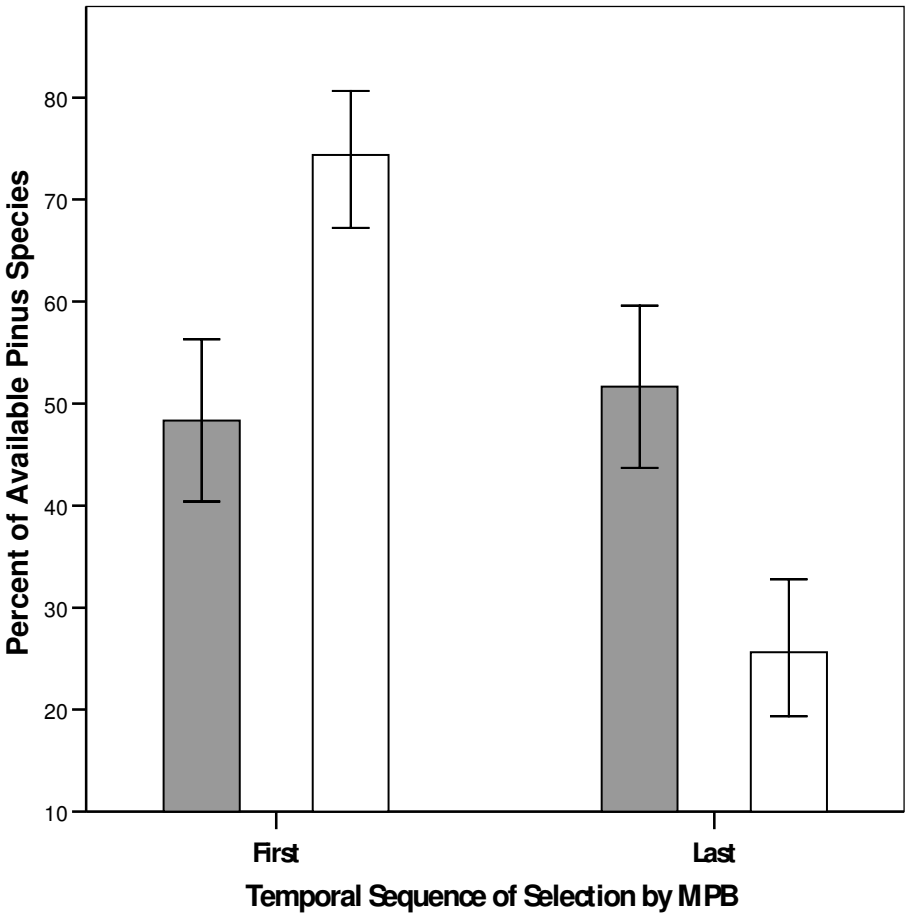


Figure 2.6. Habitat use-availability selection ratios for 'white pine blister rust' sites plotted against the relative abundance of whitebark pine with the preferred host/habitat characteristic of heavy blister rust (whole tree rust severity 2-4) for all plots at Breccia Peak, Mount Leidy and Teewinot (total plots, n = 143). Logarithmic curve overlaid to illustrate decrease in HSR strength with increase in the availability of preferred host/habitat.

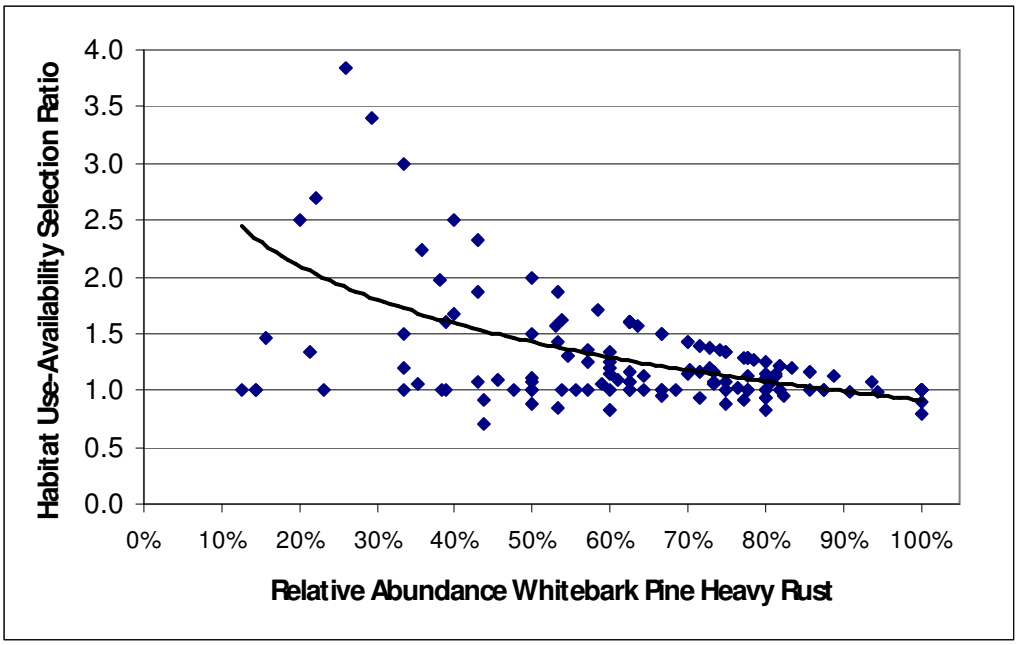


Figure 2.7. Habitat use-availability selection ratios for 'host species" sites of lodgepole pine compared to whitebark pine plotted against the relative abundance of whitebark pine. The preferred host/habitat tree identified by directional t-test (n = 24).

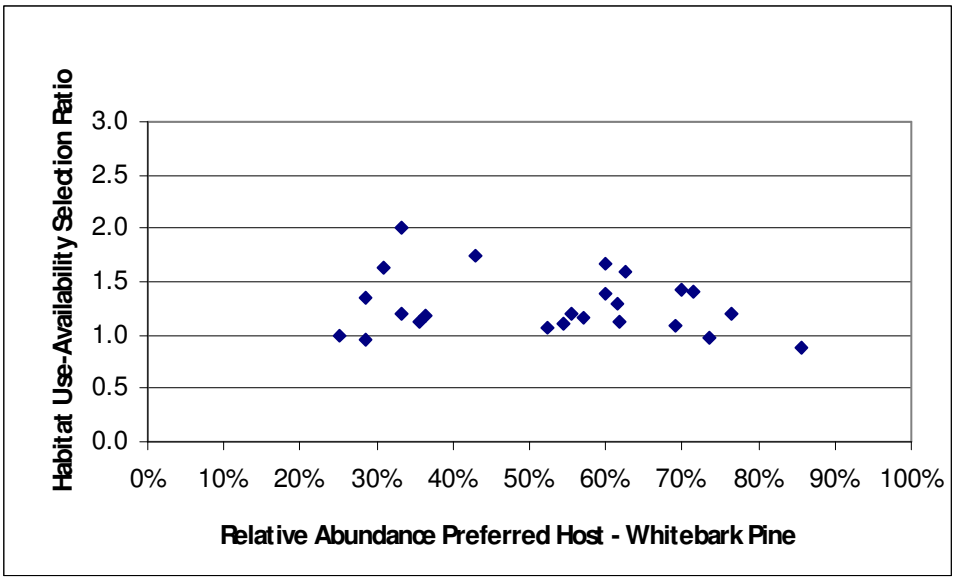


Figure 2.8. Site-specific model – multiple logistic regression selection probability function derived using a manual, backward, best subsets selection method based on the Wald statistic. Individual whitebark pine host selection is a function of study site (Breccia Peak, is the reference location), stand type (NHMIX or PURE), tree diameter, and whole tree blister rust severity.

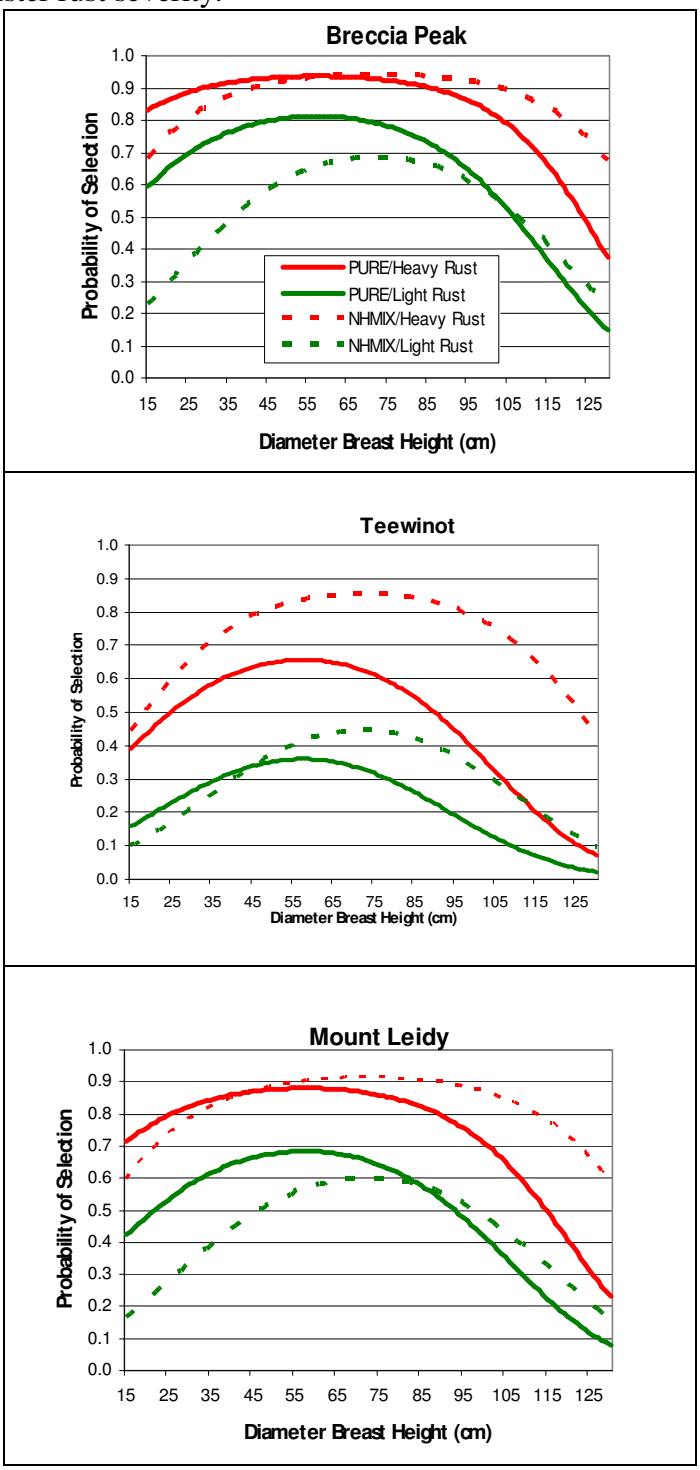


Figure 2.9. Main model – multiple logistic regression selection probability function derived using a manual, backward best subsets selection method based on the Wald statistic. Selection probability is for an individual whitebark pine with study site removed from model.

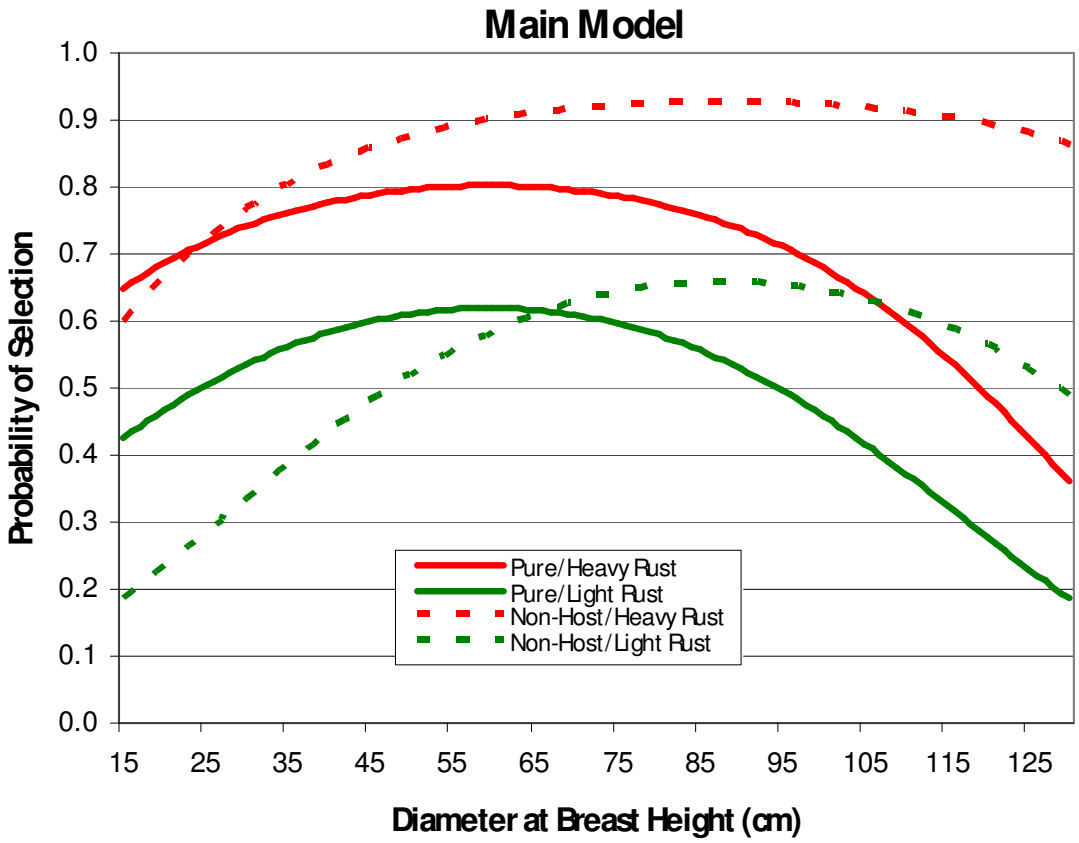
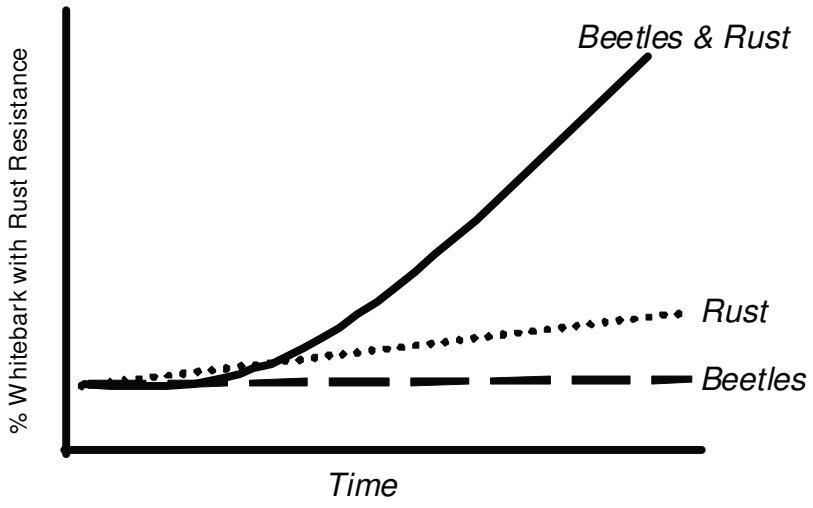


Figure 2.10. Conceptual diagram – rust resistance on the landscape. The proportion of whitebark pine on the landscape with rust resistance over time related to different agents of change.



TABLES

Table 2.1. Site attributes of sampled whitebark pine within GYE. PURE stands have ≥ 80% whitebark pine. NHMIX are comprised of whitebark pine with subalpine fir, and Engelmann spruce. AHMIX are comprised of whitebark with lodgepole, Engelmann spruce, and subalpine fir. Site order corresponds to the relative stage of the mountain pine beetle epidemic. The epidemic is oldest at Sylvan Pass and most recent at Mount Leidy.

Stand Type (by site)	Number of Plots	Elevation (meters)	Aspect	Substrate Origin	Blister Rust Symptoms	Mountain Pine Beetle	Jurisdiction
Sylvan Pass				Volcanic	Low/Absent	Present	Yellowstone NP
AHMIX	24	2608-2766	170-254°				
Breccia Peak				Volcanic	Present	Present	Bridger-Teton NF
PURE	24	2981-3151	160-270°				
NHMIX	23	2851-2990	110-270°				
Teewinot				Crystalline	Present	Present	Grand Teton NP
PURE	24	2748-2984	50-165°				
NHMIX	24	2568-2788	50-145°				
Mount Leidy				Sedimentary	Present	Present	Bridger-Teton NF
PURE	24	2815-2919	150-260°				
NHMIX	24	2764-2887	350-70°				

Table 2.2. Site conditions during June-August 2006 field season for study sites in GYE. White pine blister rust totals (symptoms, crown, or bole) for GYE exclude Sylvan Pass 'host species' site, due to negligible rust in whitebark pine in mature overstory. LP = lodgepole pine (not a host to blister rust), WB = whitebark pine, and X = non applicable field. Values in bold are means.

Stand Type (by site)	Number Trees Sampled	Proportion of Trees						
		Dead	Blister Rust Symptomatic	Crown Rust Present	Bole Rust Present	Selected by MPB	MPB & Rust	Cones Present
Sylvan Pass								
LP	149	50	X	X	X	65	X	93
WB	164	79	0	0	0	84	X	24
Breccia Peak								
PURE	293	39	76	74	29	82	67	68
NHMIX	226	65	89	87	58	77	75	55
Teewinot								
PURE	392	33	86	85	45	50	47	65
NHMIX	204	62	92	89	73	66	64	38
Mount Leidy								
PURE	385	45	79	76	51	74	63	42
NHMIX	287	41	79	77	52	61	57	31
All WB-Rust Sites	**1787**	**45**	**83**	**81**	**49**	**67**	**62**	**49**
Mean All WB	**1947**	**52**	X	X	X	**69**	**56**	**56**

Table 2.3. Blister rust severity for 'white pine blister rust sites' by location on individual tree, and in comparison to mountain pine beetle host selection. Maximum possible severity rating for crown or bole, separately is 2.0. Maximum whole tree severity rating is 4.0. Summary statistics are for all whitebark pine sampled at 'white pine blister rust sites' (n = 1787). Subset of whitebark pine selected as host by beetle, n = 1203.

Stand Type (by site)	Crown	Bole	Whole Tree	Crown Rust: Whole Tree	Whole Tree (Selected as Host)	Whole Tree (Not-selected as Host)	Significance Between Whole Tree Rust - Selected/Not Selected
Breccia Peak							
PURE	1.14	0.38	1.52	0.75	1.69	0.79	t = -6.63; p<0.0001
NHMIX	1.42	0.85	2.27	0.63	2.67	1.08	t = 9.31; p<0.0001
Teewinot							
PURE	1.39	0.65	2.04	0.68	3.28	1.68	t = -5.53; p<0.0001
NHMIX	1.52	1.18	2.70	0.66	3.11	2.01	t = -5.49; p<0.0001
Mount Leidy							
PURE	1.27	0.70	1.97	0.65	2.28	1.11	t = -8.46; p<0.0001
NHMIX	1.25	0.81	2.06	0.61	2.78	1.02	t = 12.16; p<0.0001
Mean – All WB Rust Sites	***1.32***	***0.73***	***2.04***	***0.64***	***2.39***	***1.34***	t = 16.39; p<0.0001
	Significance t =31.37; p<0.0001						

Table 2.4. Mountain pine beetle host selection frequency ratios by whole tree rust severity for 'white pine blister rust' sites (n = 1787). Rust severity categories where observed ratios exceed expected ratios are in bold.

Site	Whole Tree Rust Severity	PURE MPB Selection Frequency Ratio†	NHMIX MPB Selection Frequency Ratio†	PURE χ^{2}††	NHMIX χ^{2}††
Breccia Peak		Expected = 1 : 4.50	Expected = 1 : 3.50	25.94	63.74
	0	1 : 1.90	1 : 0.40	p<0.0001	p<0.0001
	1	1 : 3.80	1 : 1.40		
	2	**1 : 6.50**	**1 : 4.50**		
	3	**1 : 38.0**	**1: 11.8**		
	4	**1 : 23.0**	**1: 51.0**		
Teewinot		Expected = 1 : 0.98	Expected = 1 : 1.90	36.22	36.81
	0	1 : 0.28	1 : 0.30	p<0.0001	p<0.0001
	1	1 : 0.57	1 : 0.50		
	2	**1 : 1.30**	**1 : 3.00**		
	3	**1 : 1.60**	**1 : 2.00**		
	4	**1 : 2.00**	**1 : 4.60**		
Mount Leidy		Expected = 1 : 2.50	Expected = 1 : 1.50	54.43	95.54
	0	1 : 1.08	1 : 0.20	p<0.0001	p<0.0001
	1	1 : 1.70	1 : 0.83		
	2	1 : 2.40	**1 : 1.70**		
	3	**1 : 11.3**	**1 : 3.20**		
	4	**1 : 16.0**	**1 : 23.6**		
All WB with Rust		MPB Selection Frequency Ratio†	χ^{2}††		
		Expected = 1 : 2.06	231.89		
	0	1 : 0.63	p<0.0001		
	1	1 : 1.30			
	2	**1 : 2.30**			
	3	**1 : 4.04**			
	4	**1 : 7.56**			

†We calculated host selection frequency ratios (not selected : selected) by dividing the observed number of whitebark pine selected as hosts by the MPB by the observed number of whitebark pine not selected. We calculated this ratio for each blister rust severity category (0-4).

††Pearson's chi-square calculates expected ratios based on the null hypothesis that MPB host selection is independent of blister rust severity.

Table 2.5. Mountain pine beetle host selection frequency ratios of lodgepole pine compared to whitebark pine (n = 313). Categories where observed host selection frequencies differ from expected are in bold. Deviation from expected is bidirectional. When the observed frequency ratio is less than expected, lodgepole pine were selected more frequently than whitebark pine. Conversely, when the observed ratio exceed the expected, whitebark pine were selected more frequently than lodgepole pine.

Site	Crown Needle Color	*Pinus* Species Frequency Ratio (LP:WB)[†]	NHMIX $\chi^{2\dagger\dagger}$
Sylvan Pass		Expected = 1 : 1.07	30.46
	red/yellow	**1 : 1.75**	p<0.0001
	green	**1 : 0.43**	

[†]We calculated tree species host selection frequency ratios (lodgepole pine : whitebark) by dividing the observed number of whitebark pine selected as hosts by mountain pine beetle by the observed number of lodgepole pine selected. We calculated this ratio for each crown needle color category. Crown needle color is our surrogate for the temporal sequence of host selection by mountain pine beetle

[††]Pearson's chi-square calculates expected ratios based on the null hypothesis that *Pinus* host species is independent of crown needle color, or time.

Table 2.6. Summary data for 'white pine blister rust' sites (n = 1787). Individual whitebark pine characteristics by whole tree rust severity category, mean whitebark diameter breast height, mountain pine beetle selection, pitch tube density, and cone presence/absence.

Whole Tree Rust	% Total WB	DBH (cm)	% Selected by MPB	Pitch Tube Density (900 cm2)	% Cones Present
0	17.2	33.6	8.7	3.3	79
1	21.3	37.8	17.1	4.6	71
2	21.9	41.6	21.1	5.6	62
3	19.3	42.7	23.4	6.0	48
4	20.4	43.4	29.7	6.7	33
Bole Rust					
0	50.6	38.1	54.1	4.5	75
1	26.1	41.8	77.8	5.9	48
2	23.3	42.2	60.3	6.3	34
Crown Rust					
0	19.4	33.6	40.1	3.2	74
1	29.4	38.0	62.3	4.8	66
2	51.1	43.6	80.3	6.2	48
Sample Mean	X	41.8 Selected 36.3 Not Selected	67.3	5.28	49

Table 2.7. Rust severity frequency ratios by pitch tube density for all whitebark in 'white pine blister rust' sites (n = 1787). Pitch tube density categories where observed frequencies exceeded expected are in bold.

Site	Pitch Tubes Per 900 cm^2	PURE Rust Severity Frequency Ratio†	NHMIX Rust Severity Frequency Ratio†	PURE $\chi^{2\dagger\dagger}$	NHMIX $\chi^{2\dagger\dagger}$
Breccia Peak		Expected = 1: 0.88	Expected = 1: 2.27	17.95	52.71
	0	1: 0.26	1: 0.42	p<0.0001	p<0.0001
	1-5	**1: 0.95**	**1: 5.00**		
	6-10	**1: 1.21**	**1: 5.58**		
	>10	**1: 1.10**	**1: 2.46**		
Teewinot		Expected = 1: 1.67	Expected = 1: 1.72	25.87	114.78
	0	1: 1.01	1: 1.19	p<0.0001	p<0.0001
	1-5	**1: 2.75**	**1: 5.20**		
	6-10	**1: 3.20**	**1: 16.5**		
	>10	**1: 5.00**	1: 0.04		
Mount Leidy		Expected = 1: 1.49	Expected = 1: 1.52	58.13	76.21
	0	1: 0.52	1: 0.43	p<0.0001	p<0.0001
	1-5	**1: 1.50**	**1: 1.87**		
	6-10	**1: 4.06**	**1: 5.80**		
	>10	1: 1.09	**1: 4.80**		

	Pitch Tubes Per 900 cm^2	Rust Severity Frequency Ratio†	$\chi^{2\dagger\dagger}$
All WB in Stands with Rust		Expected = 1: 1.6	98.39
	0	1: 0.65	p<0.0001
	1-5	**1: 2.38**	
	6-10	**1: 3.42**	
	>10	1: 1.57	

†We calculated rust severity frequency ratios (whitebark pine with light rust : whitebark pine with heavy rust) by dividing the observed number of whitebark pine with heavy rust (2-4) by the observed number of whitebark pine with light rust (0-1) for each pitch tube density category.

††Pearson's chi-square calculates expected ratios based on the null hypothesis that the ratio of whitebark pine with light rust : heavy rust was independent of pitch tube density.

Table 2. 8. Rust severity frequency ratios by whitebark pine diameter for all whitebark in 'white pine blister rust' sites (n = 1787). Diameter categories where observed ratios exceed expected are in bold.

Site	DBH (cm)	PURE Rust Severity Frequency Ratio†	NHMIX Rust Severity Frequency Ratio†	PURE χ^{2}††	NHMIX χ^{2}††
Breccia Peak		Expected = 1: 0.88	Expected = 1: 2.4	41.26	21.83
	15-25	1: 0.3	1: 1.1	p<0.0001	p=0.0006
	26-35	1: 0.5	1: 1.4		
	36-45	**1: 1.1**	1: 1.6		
	46-55	**1: 2.1**	**1: 5.0**		
	56-65	**1: 1.1**	**1: 26**		
	>65	**1: 6.0**	**1: 3.8**		
Teewinot		Expected = 1: 1.5	Expected = 1: 1.5	25.29	39.86
	15-25	1: 0.7	1: 0.6	p=0.8821*	p=0.0121
	26-35	1: 0.9	1: 1.4		
	36-45	**1: 1.7**	**1: 3.4**		
	46-55	**1: 2.6**	**1: 5.0**		
	56-65	**1: 4.2**	**1: 14**		
	>65	**1: 3.4**	**1: 4**		
Mount Leidy		Expected = 1: 1.7	Expected = 1: 3.5	1.753	14.61
	15-25	1: 1.6	1: 0.5	p<0.0001	p<0.0001
	26-35	1: 1.5	1: 2.6		
	36-45	1: 1.7	**1: 5.2**		
	46-55	**1: 1.9**	**1: 6.4**		
	56-65	**1: 2.1**	1: 2.8		
	>65	1: 1.1	**1: 5.0**		

	DBH (cm)	Rust Severity Frequency Ratio†	χ^{2}††
All WB in Stands with Rust			
		Expected = 1: 1.6	109.7
	15-25	1: 0.7	p<0.0001
	26-35	1: 1.2	
	36-45	**1: 1.9**	
	46-55	**1: 2.9**	
	56-65	**1: 3.3**	
	>65	**1: 3.2**	

†Ratios (whitebark pine with light rust : whitebark pine with heavy rust) were calculated by dividing the observed number of whitebark pine with heavy rust severity (2-4) by the observed number of whitebark pine with light rust severity (0-1) for each diameter category.

††We calculated expected ratios based on Pearson's chi-square test of the null hypothesis that the ratio of whitebark pine with heavy rust : light rust was independent of whitebark pine diameter.

*Pearson's chi-square test of the model is not significant, we accept the null hypothesis that host selection by mountain pine beetle is independent of DBH.

Table 2.9. Mountain pine beetle host selection frequency ratios by whitebark pine diameter (DBH). Diameter categories where observed ratios meet or exceed expected are in bold.

Site	DBH (cm)	PURE MPB Host Selection Frequency Ratio†	NHMIX MPB Host Selection Frequency Ratio†	PURE χ^{2}††	NHMIX χ^{2}††
Breccia Peak		Expected = 1: 4.5	Expected = 1: 3.5	42.02	8.069
	15-25	1: 1.2	**1: 4.0**	p<0.0001	p=0.2331*
	26-35	1: 3.3	1: 1.9		
	36-45	**1: 14.0**	1: 2.9		
	46-55	**1: 21.5**	**1: 4.3**		
	56-65	**1: 5.7**	**1: 8.0**		
	>65	**1: 6.0**	**1: 7.0**		
Mount Leidy		Expected = 1: 0.9	Expected = 1: 1.2	5.242	16.70
	15-25	1: 0.8	1: 0.5	p=0.5132*	p=0.0104
	26-35	1: 0.8	**1: 1.3**		
	36-45	**1: 1.2**	**1: 1.2**		
	46-55	**1: 0.9**	**1: 1.8**		
	56-65	**1: 0.9**	**1: 1.3**		
	>65	**1: 1.8**	**1: 1.2**		
Teewinot		Expected = 1: 2.8	Expected = 1: 1.6	13.79	56.70
	15-25	1: 1.6	1: 0.5	p=0.0321	p<0.0001
	26-35	1: 2.3	**1: 1.9**		
	36-45	**1: 4.0**	**1: 3.1**		
	46-55	**1: 6.3**	**1: 9.0**		
	56-65	**1: 4.2**	**1: 14.0**		
	>65	**1: 2.1**	**1: 4.0**		

	DBH (cm)	MPB Host Selection Frequency Ratio†	χ^{2}††
	All WB	Expected = 1: 2.2	93.27
	15-25	1: 0.9	p<0.0001
	26-35	1: 1.7	
	36-45	**1: 2.9**	
	46-55	**1: 3.6**	
	56-65	**1: 3.6**	
	>65	**1: 3.5**	

†Mountain pine beetle host selection frequency ratios (not selected by MPB : selected by MPB) were calculated by dividing the observed number of selected whitebark pine by the observed number of unselected whitebark pine for each DBH category (n = 1947).
†† We calculated expected ratios based on Pearson's chi-square test of the null hypothesis that the host selection frequency ratio of whitebark pine not selected : selected was independent of DBH.
*Pearson's chi-square test of the model is not significant, we accept the null hypothesis that host selection by mountain pine beetle is independent of DBH.

Table 2.10. Host selection frequency ratios by relative density whitebark pine in NHMIX stands. Relative density categories where the observed frequency ratios exceed expected and chi-square tests are significant are in bold.

NHMIX Site	Relative Density Whitebark	MPB Host Selection Frequency Ratio	$\chi^{2\dagger\dagger}$	Significance
Breccia Peak		Expected = 1: 3.4	2.41	0.3002
	≤ 0.35	1: 2.6		
	0.36 – 0.65	1: 3.1		
	0.66 – 0.85	1: 5.4		
Teewinot		Expected = 1: 1.9	6.91	0.0316*
	≤ 0.35	**1: 2.3**		
	0.36 – 0.65	**1: 2.4**		
	0.66 – 0.85	1: 1.0		
Mount Leidy		Expected = 1: 1.5	1.72	0.4221
	≤ 0.35	1: 2.5		
	0.36 – 0.65	1: 1.4		
	0.66 – 0.85	1: 1.6		

† We calculated mountain pine beetle host selection frequency ratios (not selected by MPB : selected by MPB) by dividing the observed number of selected whitebark pine as a host by the observed number whitebark pine not selected for each relative abundance category.

††We calculated expected ratios based on Pearson's chi-square test of the null hypothesis that host selection frequency ratios are independent of relative density of whitebark.

*Among relative density categories, no cell has >3.841 $\chi 2$ contribution. This indicates that the differences in attack ratios among density categories at Teewinot are only subtle.

Table 2.11. Host selection frequency ratios by stand density whitebark pine in PURE stands. Whitebark pine density categories where the observed frequency ratio exceeds the expected is in bold.

PURE Site	WB Per Hectare	MPB Host Selection Frequency Ratio	$\chi^{2\dagger\dagger}$	Significance
Breccia Peak		Expected = 1: 4.4	54.50	p<0.0001
	≤100	1: 0.4		
	100-200	**1: 10.4**		
	201-300	1: 3.7		
	301-400	**1: 17.0**		
	401-500	**1: 7.3**		
	501-600	1: 0.67		
	>600	1: 2.2		
Teewinot		Expected = 1: 0.96	20.38	p=0.0004
	≤100	X		
	100-200	X		
	201-300	1: 0.8		
	301-400	1: 0.6		
	401-500	**1: 1.1**		
	501-600	**1: 10.5**		
	>600	1: 0.9		
Mount Leidy		Expected = 1: 2.8	13.45	p=0.0195
	≤100	X		
	100-200	1: 2.5		
	201-300	1: 2.5		
	301-400	**1: 13.0**		
	401-500	**1: 3.4**		
	501-600	**1: 9.5**		
	>600	1: 2.2		

†Mountain pine beetle host selection frequency ratios (not selected by MPB : selected by MPB) were calculated by dividing the observed number of selected whitebark pine by the observed number of unselected whitebark pine for each stand density category.

††We calculated expected ratios based on Pearson's chi-square test of the null hypothesis that the ratio of selected to unselected whitebark pine was independent of relative density of whitebark.

Table 2.12. Habitat use-availability selection ratios (used habitat characteristic: available habitat characteristic) was calculated for each plot to detect preferential habitat selection by mountain pine beetle. Habitat use-availability selection ratios (HSRs) in bold indicate significant deviation from 1.0 and preferential selection by MPB, assessed by a directional t-test ($\alpha = 0.05$).

Stand Type (by site)	# Plots	Directional one group t-test					
		Host/Habitat Characteristic	Dichotomous Host Characteristic Categories	Mean HSR†	SE of Mean	t-value	Significance *
Sylvan Pass							
AHMIX	24	Species	WB / LP	**1.281**	0.0574	4.89	p< 0.0001
Breccia Peak							
PURE	24	Rust Severity	Light / Heavy	**1.452**	0.2520	1.79	p=0.04
NHMIX	23	Rust Severity	Light / Heavy	**1.213**	0.0780	2.72	p=0.01
Teewinot							
PURE	24	Rust Severity	Light / Heavy	**1.292**	0.0889	3.28	p=0.002
NHMIX	24	Rust Severity	Light / Heavy	**1.109**	0.4356	2.49	p=0.01
Mount Leidy							
PURE	24	Rust Severity	Light / Heavy	**1.258**	0.1277	2.02	p=0.03
NHMIX	24	Rust Severity	Light / Heavy	**1.395**	0.1390	2.87	p=0.004
All Plots With Rust	143	Rust Severity	Light / Heavy	**1.287**	0.0567	5.06	p<0.0001
PURE	72	Rust Severity	Light / Heavy	**1.334**	0.0978	3.41	p=0.01
NHMIX	71	Rust Severity	Light / Heavy	**1.239**	0.0568	4.20	p<0.0001

†Ratios were calculated for each plot which calibrates the HSR to account for the host/habitat habitat composition at each plot.

*Null hypothesis: HSR – 1.0 = 0.0 tested against alternate hypothesis: HSR– 1.0 ≠ 0.0. Rust severity is a dichotomous habitat characteristic defined by whole tree rust severity: heavy rust (2-4) and light rust (0-1).

Table 2.13. Definitions of independent variables used to build our logistic regression selection probability function. Reference location is Breccia Peak.

Variable	Variable Type	Range of Values	Description
Study Site	Categorical	1 – 3	Breccia Peak, Mount Leidy, or Teewinot
Stand Type	Binary	0 – 1	NHMIX or PURE over story tree species composition
DBH	Continuous	10–130 cm	Tree diameter at breast height
Rust Severity	Binary	0 – 1	Whole tree rust severity (light rust = 0,1; heavy rust = 2-4)

Table 2.14. Site Specific parameters and fit statistics used in best subsets logistic regression procedure. Reference location is Breccia Peak. Pearson's goodness of fit test: $\chi 2 = 86.35$, df= 84, p = 0.41. DBH^2 term accounts for mountain pine beetle selection preference for mid-range tree diameters.

Variable	Coefficient (α)	SE Coefficient	Wald χ^2	Significance
Constant	-2.38758	0.434710	-5.49	< 0.0001
Rust Severity	1.98419	0.195118	10.17	< 0.0001
Stand Type	1.85460	0.429068	4.32	< 0.0001
DBH	0.0876168	0.014738	5.94	< 0.0001
DBH^2	-0.0006070	0.000142	-4.27	< 0.0001
Stand Type * DBH	-0.0179631	0.008939	-2.01	0.044
Stand Type * Rust	-0.760664	0.246974	-3.08	0.002
Teewinot	-0.916511	0.251537	-3.64	< 0.0001
Mount Leidy	-0.377325	0.243416	-1.55	0.121
Teewinot * Stand Type	-1.04454	0.320838	-3.26	0.001
Mount Leidy * Stand Type	-0.314706	0.316450	-0.99	0.320

Table 2.15. Global model parameters and fit statistics used in best subsets logistic regression procedure. Pearson's goodness of fit test: $\chi 2 = 26.40$, df =26, p = 0.60. DBH^2 term accounts for mountain pine beetle selection preference for mid-range tree diameters.

Variable	Coefficient (α)	SE Coefficient	Wald χ^2	Significance
Constant	-2.418220	0.353826	-6.83	< 0.0001
Rust Severity	1.872690	0.187714	9.98	< 0.0001
Stand Type	1.504390	0.339604	4.43	< 0.0001
DBH	0.069685	0.013559	5.14	< 0.0001
DBH^2	-0.000395	0.000133	-2.97	0.003
Stand Type * DBH	-0.022660	0.008374	-2.71	0.007
Stand Type * Rust	-0.958375	0.231945	-4.13	< 0.0001