Geospatial Variation of an Invasive Forest Disease and the Effects on Treeline Dynamics in the Rocky Mountains

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Geospatial and Environmental Analysis

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October 2, 2013
Blacksburg, Virginia

Keywords: Treeline, Whitebark Pine, *Pinus albicaulis*, Blister Rust, Rocky Mountains, spatial pattern, GIS, GPS, DEM, Agent-Based Model

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ABSTRACT

Whitebark pine is an important keystone and foundation species in western North American mountain ranges, and facilitates tree island development in Rocky Mountain treelines. The manifestation of white pine blister rust in the cold and dry treelines of the Rockies, and the subsequent infection and mortality of whitebark pines raises questions as to how these extreme environments harbor the invasive disease, and what the consequences may be for treeline dynamics. This dissertation research comprises three studies that investigate abiotic factors influential for blister rust infection in treeline whitebark pines, how disease coupled with changing climate may affect whitebark pine treeline dynamics, and the connection between treeline spatial patterns and disease. The first study examined the spatial variation of blister rust infection in two whitebark pine treeline communities, and potential topographic correlates. Using geospatial and field approaches to generate high resolution terrain models of treeline landscapes, microtopography associated with solar radiation and moisture were found most influential to blister rust infection in treeline whitebark pines. Using field-based observations from sampled treeline communities, the second study developed an agent-based model to examine the effects of disease and climate on treeline pattern and process. Treeline dynamics were simulated under five hypothetical scenarios to assess changes in tree spatial patterns and populations. Blister rust-induced loss of whitebark pines resulted in a decline of facilitative processes, and an overall negative treeline response to disease—despite the beneficial effects of climate amelioration. The objective of the third study was to explore whether spatial patterns of tree proximity, size, and growth infer disease patterns. Comparing spatial patterns of tree characteristics between diseased and undiseased treeline communities, I found that trees growing near trees with larger stem diameters, and larger tree islands, tended to have more blister rust cankers, and displayed clustered spatial patterns. Undiseased treeline patterns revealed near neighbors smaller in stem diameter and tree island size, and were randomly dispersed. Blister rust diseased whitebark pines reveal spatial autocorrelation, despite the complex blister rust disease life cycle. Overall, findings from this dissertation reveal the implications of invasive disease on sensitive treeline ecotones dependent on a keystone species.

Acknowledgements

The journey toward the doctorate is a challenging endeavor. It is full of hurdles and setbacks, which are somehow compensated by the gratification of accomplishment to help make the push further. To the many people who provided mentorship and support to me through the process, and helped me make this push—thank you.

My dissertation research was primarily supported by a National Science Foundation Geography and Spatial Sciences Program grant (808548) awarded to Dr. Lynn Resler, Dr. Diana Tomback, and Dr. George Malanson. I feel fortunate that I had the opportunity to work with these research experts in treeline ecosystems, in such beautiful and scenic mountain landscapes, and to have them as coauthors on papers—it has made me a better writer.

I express much thanks to my committee members: to my advisor Lynn Resler, whose knowledge and experience guided my efforts throughout the PhD process; to George Malanson, his expertise in agent-based modeling and feedback processes provided an invaluable resource ("good stuff Maynard!"); and to Steve Prisley and Bill Carstensen, who helped me hash out ideas for the geospatial and statistical components of my research, and above all provided their support, encouragement, and trust in my accomplishments. Thank you.

Sharing the trials and tribulations of being a graduate student with my fellow PhD graduate students, both in the VT Geography Department and outside, was an important outlet and they made the experience so much more fun. In particular, Candice Luebbering, Arvind Bhuta, Melanie Stine, Jess Walker, Baojuan Zheng, and Tammy Parece—I appreciate your friendship and support as we worked towards the PhD. And to Jim Campbell, even though our office was at the far end of the building and end of the hallway, you always stopped by to visit us in the GEA office—thanks for lending your insight over the years.

A special thanks to my fellow band members, music fed my soul—long live the Septapüs! And to Sinking Creek Pottery, working clay into art kept me balanced.

Most importantly, I am so thankful for the immeasurable support from my family and friends. I especially owe a heartfelt thanks to my husband John McKenna, who has patiently endured the ups and downs of my journey toward the doctorate—I love you.

Attribution

My coauthors for chapters 3 and 4 consist of my advisory committee, co-principal investigator for the supporting research grant, and colleague. A brief description of their contributions towards each chapter is outlined below.

Chapter 3: Topographic Influences on the Distribution of White Pine Blister Rust in *Pinus albicaulis* Treeline Communities

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Chapter 4: Feedbacks, disease, and climate influences on whitebark pine treeline dynamics: An agent-based treeline model.

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Chapter 1: Introduction

The subject of introduced species has become a major conservation and environmental concern within the fields of biogeography, invasion biology, and landscape pathology, (Simberloff, 2004). Second to habitat loss (Wilcove et al., 1998), introduced invasive species are a major threat to native species (Simberloff, 2004). Whitebark pine (*Pinus albicaulis*), a native foundation and keystone species of the western mountains of the U.S. and southwest Canada (Kendall and Arno, 1990; McCaughey and Schmidt, 1990; Tomback et al., 1995; Murray et al., 2000; Ellison et al., 2005), is being threatened by a non-native disease, white pine blister rust. The introduction of the exotic fungal pathogen, *Cronartium ribicola*, which causes white pine blister rust in five-needled white pines (Hoff and Hagle, 1990; Tomback et al., 1995), has spread throughout the range of whitebark pine. Despite research suggesting the spread of blister rust is limited to mild and moist climates (Van Arsdel et al., 1956), blister rust has reached the cold and dry upper limits of the alpine treeline ecotone (ATE) east of the Continental Divide in the Rocky Mountains (Resler and Tomback, 2008). Due to the viability of blister rust in the cold and dry climates of the ATE, blister rust is killing whitebark pine, a frequent initiator of tree islands (Resler, 2004; Resler and Tomback, 2008). The mortality of whitebark pine is likely to have serious landscape consequences across the ATE in the context of climate change. The decline of this important keystone species due to blister rust will likely impact the community structure and formation of tree islands in the ATE, potentially skewing interpretations of treeline response as a bioclimatic indicator of climate change (Tomback and Resler, 2007; Schrag et al., 2008).

Whitebark pine plays a fundamental role as a keystone and foundation species in high elevation forests of western North American mountains (Kendall and Arno, 1990; McCaughey and Schmidt, 1990; Murray et al., 2000; Tomback et al., 2001; Ellison et al., 2005). It is a keystone species in regards to the numerous ecosystem services it provides relative to its abundance (Paine, 1995), and a foundation species by modulating environments and stabilizing ecosystem processes that promote forest structure (Ellison et al., 2005). Its seeds provide a high-energy food source that red squirrels, Clark's nutcracker, and grizzly bears favor (Kendall and Arno, 1990). The pine also provides canopy shelter for wildlife (such as Clark's nutcrackers, red squirrel, and grizzly bears) (Kendall and Arno, 1990).

In the alpine treeline ecotone, krummholz whitebark pine facilitates other conifer species (Blakeslee, 2012) that usually results in the establishment of tree islands (Resler, 2004), and its roots and canopy help stabilize slopes and preserve snowpack (Arno and Hoff, 1989). The unique keystone relationship between whitebark pine and Clark's nutcracker enable the regeneration of whitebark pine in high elevation sites across the ATE landscape (Tomback and Linhart, 1990; Tomback et al., 1995), typically providing the foundation for tree islands in treeline systems where whitebark pine dominates (particularly in northern Montana treelines). However, since the introduction of white pine blister rust to North America in the early 1900s, there has been a decline in populations of whitebark pine nearly range-wide (Kendall and Arno, 1990).

White pine blister rust is a devastating disease of five-needled white pines, of which whitebark pine is highly susceptible (Hoff et al., 1980; Hoff and Hagle, 1990; Tomback et al., 1995). While other disturbances such as fire suppression and mountain pine beetle infestations have contributed to whitebark pine's decline (Kendall and Arno, 1990; Keane and Arno, 1993), more than 90% of whitebark pine mortality is due to blister rust. Mortality is particularly evident in the northwestern portion of whitebark pine's range, with the highest percentage of tree mortality occurring in the northern Rocky Mountains of, Montana (Kendall and Arno, 1990;

Keane et al., 1994; Smith et al., 2008). Its prevalence has been linked to mild, moist climates (Van Arsdel et al., 1956), and researchers have suggested dry and cold environments hinder the blister rust life cycle and its transmission (Campbell and Antos, 2000). However, recent research has shown that blister rust is capable of completing its life cycle and transmitting the disease in the dry and cold environments of the ATE, east of Continental Divide (Tomback and Resler, 2007; Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013).

SIGNIFICANCE

Non-native (exotic) invasive species are those organisms that have been successfully introduced and naturalized into a new region, become readily abundant within a community, and interact in such a way that typically results in competition or other negative impacts to native species (Simberloff, 2004; Sax et al., 2005; Vellend et al., 2007). Introduced invasive species have contributed to huge environmental and economic loss costing the U.S. $120 billion dollars every year (Pimentel et al., 2005). Many studies have examined the spread of invasive species (With, 2002; Daehler, 2005; Van Kleunen and Fischer, 2009), their evolutionary traits attributed to their invasive success (Whitney and Gabler, 2008), and their impacts on native species. There has been a growing trend towards creating predictive models of invasive species distribution patterns and linking exotic disease to a warming climate (Van Mantgem et al., 2009; Evans and Finkral, 2010).

One of the devastating outcomes of invasive species is their influence in altering ecosystem function within a community, and the resulting transformations on the landscape (Westbrooks, 1998), which is a problem with invasive plants as well as invasive disease (Tomback and Resler, 2007; Van Mantgem et al., 2009; Evans and Finkral, 2010). From an understanding of the climatic niche of whitebark pine forest communities (Rehfeldt et al., 2006), whitebark pine should advance beyond the current ATE position under current climate warming trends. Under these warming trends, forest encroachment to higher elevations should result from the dispersal (Hutchins and Lanner, 1982; Tomback, 1982), propagation, and establishment of whitebark pine in the Rocky Mountains (Callaway, 1998; Resler, 2004; Maher and Germino, 2006). However, blister rust-induced mortality of this keystone species is likely to disrupt ecosystem function of many ecosystems, ranging from the subalpine to alpine (Tomback and Resler, 2007; McKinney et al., 2009; McKinney and Fiedler, 2010). In alpine treeline ecosystems, the impacts from blister rust will likely cause decreased propagation of whitebark pine, and therefore, decreased facilitation and establishment of tree islands within the ATE. Though treeline position may serve, at least in some locations, as a bioclimatic indicator of climate change (Körner and Paulsen, 2004; Harsch et al., 2009; Hoch and Körner, 2009; Harsch and Bader, 2011), blister rust-induced mortality of whitebark pine may confound interpretations of changing treelines—treelines that are not only responding to a changing climate, but also to a disease-altered ecosystem (Tomback and Resler, 2007).

There is a gap in the literature involving spatially and ecologically complex systems (Agrawal et al., 2007; Urban et al., 2008; Urban et al., 2012) especially within the context of invasive disease impacts on treeline ecosystems, and ecotones in general. Urban et al. (2008, 2012) indicated there is a paucity of research involving spatially and ecologically complex studies, particularly in metacommunities—stressing the need for more research in this area. This study will contribute to research in spatially and ecologically complex systems of metacommunities—and the complexities, patterns, and processes of whitebark pine treeline communities provide fine examples of this framework. The ATE represents both a spatially (through form and pattern), and ecologically (through function) complex ecosystem, where multiple species interact for coexistence and survival in a stressful abiotic environment. Feedbacks among disease, climate, and vegetation further complicate the dynamics occurring in the ATE. A few studies have investigated the impacts of blister rust on the ATE landscape (Tomback and Resler, 2007; Resler and Tomback, 2008; Smith et al., 2011) and have formed the foundation for this research.

OBJECTIVES

The purpose of this research is to examine the effects of, and factors influencing, exotic disease on a keystone and foundation species integral in the alpine treeline ecotone. My research goals are to investigate the presence and intensity of white pine blister rust disease among treeline whitebark pine, and to examine the effects of white pine blister rust on whitebark pine treeline communities in the Rocky Mountains. Specifically, I investigate whitebark pine at treelines near its southern, middle, and northern distributional range in the Beartooth Plateau (southern) and Glacier National Park (middle) of Montana, U.S.A., and in Banff National Park (northern) in Alberta, Canada.

There are three manuscript chapters in this dissertation, which are also prepared and submitted to peer-reviewed journals. The main objectives of these chapters are to: 1) explore the geographic variation of blister rust incidence among treeline whitebark pine with differing topographic and environmental variables, 2) simulate treeline dynamics using an agent-based model in order to explore the potential effects of climate change, blister rust disease, and these combined effects on whitebark pine communities in the ATE landscape, and 3) examine spatial patterns of neighboring whitebark pine trees and tree islands in relation to size, growth habit, and disease characteristics at three different latitudinal treelines.

This dissertation research combines landscape ecology and forest pathology to examine pathogenic influences on landscape spatial patterns, as well as the connectivity and influence of landscape patterns on disease manifestation (Legendre and Fortin, 1989; Holdenrieder et al., 2004; Lundquist, 2005; Ellis et al., 2010). To examine spatial pattern and pathogenic influences, I investigate the incidence and intensity of blister rust in treeline whitebark pine ecosystems at three latitudes in the Rocky Mountains, east of the Continental Divide. Chapter 3 examines the environmental and topographic variables that influence blister rust disease on treeline whitebark pine. Using field observations of the sampled disease-altered ATE landscapes, and research findings from the literature, Chapter 4 involves simulations of treeline dynamics to explore the effects of blister rust disease and the combined effects of disease and climate change on treeline whitebark pine communities. Chapter 5 explores the spatial patterns of treeline whitebark pine, and the notion that spatial proximity and growth/health characteristics of the tree may provide inference to disease pattern. Each chapter provides insight to the research questions: (Chapter 3) “What are the disease-influencing topographic factors and do they vary geographically?”, (Chapter 4) “How do whitebark pine-dominated treeline communities respond to blister rust disease, and how does treeline respond to disease with a warming climate?”, and (Chapter 5) “Do the spatial patterns of whitebark pine treelines and their characteristics correlate to disease incidence and pattern?” Research findings from these three studies contribute much-needed information on sensitive ecosystems dependent on a keystone and foundation species, and reveal the implications of an introduced invasive disease on the spatially and ecologically complex processes that drive whitebark pine treelines.

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Chapter 2: Literature Review

THE ALPINE TREELINE ECOTONE AND THE ROLE OF WHITEBARK PINE IN TREELINE FORMATION

The alpine treeline ecotone (ATE) is a transition zone from the upper limit of the closed contiguous forest, tall trees closely spaced together in subalpine forest, and alpine (treeless) tundra, resulting in a patchy forest mosaic (Hansen-Bristow et al., 1988; Rochefort et al., 1994; Holtmeier, 2009). This transition zone connects patches of forest at the highest elevations, with the lower elevational closed forest (Körner, 1998). While anthropogenic influences (i.e., logging, controlled-burning, livestock grazing) and natural disturbances (avalanches, landslides, lightning-induced fire) can also play a role in shaping the treeline limit (Körner, 1998; Körner and Paulsen, 2004; Holtmeier, 2009), the characteristics of climatically-driven and weather-sculpted treeline are discussed here.

“Treeline” is not actually a line, but a physiological threshold—an ecotone shaped by environmental, biological, spatial, and temporal processes (Holtmeier, 2009). Frost damage, winter desiccation, and strong winds are common causes of treeline formation in temperate-zones (Körner, 1998). At the ATE tree growth is limited along an environmental gradient and results in a transition from upright to dwarfed trees, and subsequently, to alpine plants (Stevens and Fox, 1991). Wind and snow cover strongly influence the growth and shape of krummholz (wind-stunted and deformed [Holtmeier, 2009]) trees in the alpine (Daly, 1984), and the low-lying growth habit of these trees provides a survival advantage in these high elevation ecosystems. Upright trees, having increased canopy exposure to atmospheric elements and colder soil surrounding their root zones, are exposed to the harsh climates of the ATE more so than are the low-lying shrubs, forbs, and grasses (Körner and Paulsen, 2004). As a result, trees growing in the ATE are stressed due to the harsh winters experienced at these elevations (Hansen-Bristow et al., 1988).

With increasing elevation (and wind exposure and cold temperatures), trees become increasingly stunted and deformed, and often grow sheltered in the lee of a rock, topographic shelter, or other vegetation (Marr, 1977; Benedict, 1984; Hotmeier and Broll, 2010). Periglacial land features such as patterned ground formed from freeze-thaw processes often provide shelters suitable for seedling establishment (Butler and Malanson, 1989; Butler et al., 2004). If enough viable seeds successfully germinate and grow under the protection of these shelters, or spread through vegetative layering, a dense clumping of krummholz trees can occur, typically growing leeward (away from the wind), and forming dense clusters of tree islands (Marr, 1977; Arno and Hammerly, 1984; Resler, 2004; Holtmeier, 2009; Holtmeier and Broll, 2010). Generally, trees growing within tree islands have increased moisture availability (in terms of soil moisture and reduced evapotranspiration loss), and more protection from wind and cold temperatures than if growing individually and isolated (Holtmeier and Broll, 1992). Tree islands often form by the initial establishment of a hardy conifer individual, capable of withstanding the cold and windy climates of the ATE on its own (Habeck, 1969). Less cold- and wind-tolerant conifers may establish in the lee of the hardy conifer; these less hardy individuals are often shade-tolerant species that benefit under the shelter of the lead tree island initiator (Arno and Hammerly, 1984; Arno and Weaver, 1990).

Research has shown that in the northern Rocky Mountains, east of the Continental Divide, whitebark pine is a frequent initiator of tree island colonies at treelines (Resler, 2004; Resler and Tomback, 2008). This process directly relates to the pine’s dependence upon avian dispersal. Whitebark pine seed is dispersed to the upper limits of treeline by its coevolutionary counterpart, the Clark’s nutcracker (*Nucifraga columbiana*) (Hutchins and Lanner, 1982; Tomback, 1982). These birds collect seeds from whitebark pine cones in their throat pouch and have been known to travel long distances (distances up to 12.5 km between source tree and seed cache site have been documented) to cache seeds in storage sites. They typically store 1-15 seeds per cache in order to harvest this food source (Hutchins and Lanner, 1982; Tomback, 1982). These cache sites are usually located in loose substrate on exposed slopes above treeline, in meadows, or within burned sites. The nutcracker has an impressive memory capacity of its seed cache locations, using natural features as landmarks such as logs, rocks, or the base of trees to cache seeds (Tomback, 1982; Tomback et al., 1990; Hutchins, 1990). If any of the seeds are not harvested, and whitebark pine successfully germinates and grows within the tundra, other tree species may benefit. Shade-tolerant conifer species such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) may successfully establish under whitebark pine’s protection from less-than-ideal abiotic conditions (Callaway, 1998), resulting in the formation of tree islands (Habeck, 1969; Arno and Hammerly, 1984; Holtmeier, 2009). Under current climate conditions, conifer species such as subalpine fir, Engelmann spruce, alpine larch (*Larix lyallii*), lodgepole pine (*Pinus contorta*), and whitebark pine compete for survival in the ATE, yet they also form a mutualism in tree island patches through facilitation (Habeck, 1969; Arno and Hammerly, 1984). Unlike lower elevations where conditions are not as harsh and species compete for growth, facilitation in high elevation forests near treeline enables these species to coexist in the same habitat (Callaway, 1998).

TREELINE WHITEBARK PINE AND BLISTER RUST

Whitebark pine populations are on the decline range-wide due to numerous ecosystem disturbances primarily caused by anthropogenic influences (Larson, 2011). Mountain pine beetle infestations and fire suppression practices have contributed to considerable declines of this important species (Kendall and Arno, 1990; Keane and Arno, 1993). However, blister rust, which is caused by the introduced pathogen *Cronartium ribicola* (Kendall and Arno, 1990; Keane et al., 1994), accounts for more than 90% of whitebark pine mortality within its northwest range, particularly within the northern U.S. Rocky Mountains (Hoff and Hagle, 1990; Tomback and Achuff, 2010). Though white pine blister rust affects all five-needled white pines, whitebark pine is highly susceptible to infection (Hoff et al., 1980).

Blister rust, which is native to Eurasia, was accidentally introduced to western North America in 1910 by way of boat-transported, disease-infected eastern white pine nursery stock delivered from France (Hoff and Hagle, 1990). Within a span of just 13 years, the fungal disease spread from the point of introduction in Vancouver British Columbia, all the way to eastern Washington and Idaho infecting most of the range of western white pine and much of the whitebark pine range (Hoff and Hagle, 1990). With a complex life cycle involving five different stages of spore development, blister rust requires transmission between a white pine host and an alternate host. The list of alternate host plants include *Ribes* spp. (many varieties of currants and gooseberries) which have long been known as susceptible to blister rust (Spaulding and Gravatt, 1917), and two other species recently documented as *C. ribicola* infectious, sickletop lousewort (*Pedicularis racemosa*), and scarlet paintbrush (*Castilleja miniata*) (McDonald et al., 2006). Blister rust was originally thought to be limited to mild and moist climates (Van Arsdel et al., 1956), however, this disease appears to be a problem wherever host and alternate host plants can grow (Kinloch, 2003), including cold and dry environments of subalpine forests (Hoff and Hagle, 1990) and the alpine treeline ecotone (Resler and Tomback, 2008; Smith et al., 2011).

TREELINE PROCESSES IN WHITEBARK PINE ECOSYSTEMS

Whitebark pine ecosystems within the alpine treeline ecotone are the result of a multitude of population and community ecological phenomena and processes. Indirect/direct effects, feedbacks, adaptation, facilitation, mutualism, succession, diffuse coevolution, colonization, niche theory, and metacommunities (Tilman, 1985; Bruno et al., 2003; Strauss et al., 2005; Baumeister and Callaway, 2006; Urban et al., 2008) are all important concepts for explaining the formation of treeline whitebark pine communities. Within the context of landscape ecology, not one but many, of these mechanisms are acting in unison to create the patchy landscape of the ATE. To understand how these ecological mechanisms play out across the ATE landscape, one must first understand the conditions under which trees grow in the ATE, and the disturbances that affect the ecosystem processes that form them.

Indirect/Direct Effects

Indirect and direct effects have an important role in natural systems. Definitions of these ecological terms are the following: direct effects result from the interactions between two species; and indirect effects involve an intermediary species in which one species affects a second species indirectly by way of a third or intermediary species. Indirect effects do not result from direct physical interaction, and occur in multi-species communities. In complex multi-species communities indirect effects must be considered (Wootton, 1994a, b), especially within the ATE, where multiple interactions among species are occurring.

The spatial patterns of whitebark pine above treeline are directly affected by the seed-dispersal and harvesting habits of the Clark's nutcracker (e.g., Tomback, 2001). Clark's nutcracker acts as a facultative mutualist by dispersing and potentially regenerating whitebark pine, and whitebark pine is obligately dependent on Clark's nutcracker for dispersal of its heavy wingless seeds (McKinney et al., 2009). During a successful cone crop when food supplies are plentiful, the nutcracker may not harvest all seed caches. Any remaining unharvested seeds in these cache sites may successfully germinate into individual or clusters of seedlings, which in turn, indirectly effect the formation of tree islands due to the establishment and facilitation of whitebark pine. The beneficial facilitative effects that whitebark pine has on other conifer species (i.e., providing shelter and ameliorating cold and windy conditions [Resler, 2005]), result in the mosaic of tree patches in the alpine treeline ecotone.

Blister rust disease plays a major role in indirect/direct effects on ATE ecosystem processes. While it is not perceived that human activity directly transports blister rust within a forested ecosystem (aside from the initial introduction of this exotic pathogen to North America), it may influence the growth of alternate host species. For example, with regards to the alternate host plant *Ribes* spp., indirect effects of human-caused disturbances such as fire can encourage *Ribes* spp. seed germination. *Ribes* spp. have extremely tough seed coats that can remain dormant for hundreds of years until a disturbance (such as fire) stimulates germination. Human-induced (and natural) fire disturbances can indirectly increase these alternate host plant populations, potentially promoting blister rust disease development in whitebark pine ecosystems where fire plays an important role (Hoff and Hagle, 1990).

In another manner, human-induced changes to forest ecosystems can directly and indirectly affect plant-animal interactions in terms of producer/consumer relationships, resulting in forest successional changes that further reduce producer populations. One such study (McKinney and Fiedler, 2010) examines the relationship between a producer (whitebark pine) and its consumer the red tree squirrel (*Tamiasciurus hudsonicus).* The study reveals the indirect effects of blister rust-induced mortality of whitebark pine on seed predator behavior of the red tree squirrel. In Rocky Mountain subalpine forests where whitebark pine forests are successionally replaced by mixed conifer forests (largely due to blister rust mortality), seed consumption of the opportunistic red squirrel increase. Findings from this study hypothesized that increased seed predator behavior of the red squirrel would further compound the decline of its producer by inhibiting the potential for regenerative seed-dispersal by Clark's nutcracker.

Positive Feedbacks

Positive feedbacks amplify a response (DeAngelis et al., 1986), and can cause acceleration or spatial extension in natural systems (Wiens and Moss, 2005). Positive feedbacks are especially apparent in vegetation ecosystems, such as the ATE. Positive plant interactions (which include facultative and obligate facilitations, and mutualisms) can result in positive feedbacks and are defined as the interactions between two or more plant species in a community, resulting in a positive effect on at least one of the community species. Positive interactions occur within ecosystems when neighbors modify abiotic and/or biotic conditions, resulting in positive effects such as plant growth and survival (Bertness and Callaway, 1994). One type of positive interaction is facilitation, a process that influences community structure through modulation of environmental stresses and the availability of resources (Callaway, 1995; Butterfield, 2009). Competition among species that may occur in benign environments tends to give way to facilitation in communities that endure high physical stress (Bertness and Callaway, 1994), such as in alpine environments. Facilitation is an important structuring force when considering plant colonization, diversity, and dynamics (Bertness and Callaway, 1994; Callaway, 1998; Bruno et al., 2003; Baumeister and Callaway, 2006). In the stressful environments of the ATE where high winds and cold and dry climates are prevalent, habitat amelioration is important for structuring the ATE landscape. Survival through facilitation is also positively associated with population density (Bruno, et al., 2003); this concept applies to the dense patches of conifer species within tree islands, which have a greater chance of survival then if growing individually in the ATE.

Direct positive plant interactions (Bertness and Callaway, 1994) in which neighboring conifers help ameliorate harsh abiotic conditions and result in the establishment of additional trees (Callaway, 1998) are partly responsible for the patchy landscapes of the treeline ecotone. This process creates a positive feedback loop, which results in the formation of tree islands (Alftine and Malanson, 2004; Bekker, 2005). Tree island formation, at least those initiated by the relatively shade-intolerant whitebark pine (Tomback et al., 2001; Weaver, 2001; Resler, 2004), originates from the mutualistic relationship between whitebark pine and Clark's nutcracker (Hutchins and Lanner, 1982; Tomback, 1982). When whitebark pine seedlings survive in the ATE, they facilitate the establishment of conifer species. Particularly in Glacier National Park, whitebark pine's tolerance to sun is a benefit for shade-tolerant and moisture-loving subalpine fir and Engelmann spruce, which often establish behind whitebark pine to form tree islands (Habeck, 1969). These shade-tolerant conifers may replace whitebark pine if conditions become stressful or otherwise inhibit the growth of whitebark pine (Habeck, 1969), such as mortality due to blister rust, a lack of fire disturbance, or other environmental stressors.

As a result of these facilitative effects, whitebark pine may potentially increase the biodiversity of plant species within the ATE. In harsh physical systems such as the ATE and others where trees struggle to exist, foundation species often provide habitat for other species, and in the absence of these foundation species, the overall diversity of facilitated species often decline (e.g., Bruno et al., 2003). These interactions are a result of positive feedbacks, which form the framework of the ATE landscape, and revolve around the importance of foundation species such as whitebark pine.

Negative Feedbacks

Negative feedbacks diminish a response (DeAngelis et al., 1986), and can create a limiting process in natural systems (Wiens and Moss, 2005). Negative interactions within plant communities can interfere with the development of community structure and diversity (Callaway, 1995). Negative feedbacks can result in decreased growth rate when beneficial mutualistic interactions are reduced (e.g., Bever, 2002) and apply to whitebark pine, other treeline conifers, and the development of tree islands. Blister rust-induced mortality of whitebark pines introduces a potentially important negative feedback into treeline systems—decreased growth of whitebark pine may also reduce tree island development. This may potentially reduce biodiversity in the current mosaic landscape of the ATE to a more homogeneous landscape—an ATE in which the boundary becomes more distinct between upright trees of the subalpine forest and alpine tundra. The decline of this important foundation and keystone conifer species may result in the decline of tree island colonization (Tomback and Resler, 2007).

Negative interactions may impact plant-animal relationships in diseased whitebark pine communities. Diffuse coevolution (e.g., Strauss et al., 2005) is occurring with the introduction of blister rust to whitebark pine ecosystems—in which the mutualistic relationship between whitebark pine and Clark's nutcracker is being altered by the occurrence of *Cronartium ribicola*. Blister rust-induced mortality of whitebark pine trees in the subalpine may yield lower cone crops available for avian-assisted seed dispersal from cone-bearing trees in the subalpine to the ATE, decreasing food resources for Clark's nutcracker (McKinney et al., 2009) as well as decreasing the potential for tree island formation. The loss of whitebark pine to blister rust mortality is clearly a complex ecological problem, and raises questions as to whether there will be a change in the mutualism between bird and pine, and how the loss of whitebark pine will effect the tree island formation in the ATE.

PATTERNS AT TREELINE

The theory of metacommunity has helped scientists understand how spatially integrated ecological mechanisms alter community dynamics and patterns of species diversity (Urban and Skelly, 2006; Urban et al., 2012). This study focuses on the function and dynamics of whitebark pine treeline communities, the facilitative processes among treeline species, and the positive and negative interactions acting within the treeline community. In this context, whitebark pine treeline communities (and the formation of tree islands) can be viewed as metacommunities.

Metacommunities consist of a network of local communities composed of multiple interacting species, linked to these local communities through dispersion (Urban et al., 2008). Metacommunities are patches of species populations across a landscape, in which populations exist where habitats are suitable. The landscape between these populations, where habitat is unsustainable, is void of populations. Metacommunities help form patchy distributions of habitats, and one prime example is the formation of tree islands in the ATE.

Whitebark pine seed-dispersal by Clark's nutcracker from the subalpine to the ATE, subsequent establishment and growth, and resulting facilitation of other tree species in some treeline landscapes, contributes to the formation of tree islands—forming a patchy mosaic across the wind-swept ATE landscape. Colonization occurs as new species disperse to new locations and germinate in clusters (Urban and Meester, 2009) forming tree islands. The formation of such patches is very similar to species sorting, in which species inhabit locations suited to their specific traits as a result of colonization (Urban et al., 2008). Patches of mixed species sorted by suitable habitat represent metacommunities, in which each patch is linked through the dispersal activities of multiple interacting species. Factors controlling dispersal affect the colonization rate and size of patches. As these metacommunities evolve, and adaptation, dispersal, and species sorting continue, landscape patterns change (Urban and Meester, 2009). In whitebark pine ecosystems, in which dispersal of this pine to the ATE appears a key factor in tree island development (Tomback and Resler, 2007), the pine's facilitative effects have the potential to harbor a diverse number of conifer species in the ATE.

Dispersal is an important mechanism in patchy, heterogeneous landscapes, and is highly influenced by topography (Pe'er et al., 2006). The Clark's nutcracker almost completely controls seed dispersal of whitebark pine to the ATE due to its preference for seed-caching sites (Tomback, 2001). Nutcrackers often choose cache sites near natural landmarks, such as the base of trees, logs, or rocks, which serve as visual memory cues for a return harvest (Tomback et al., 1990; Tomback et al., 1995). The complex topography and vegetation structure of the ATE has been shaped by periglacial processes such as solifluction, rock shattering, and rock sorting, resulting in patterned ground consisting of terrace risers, treads, and boulders, that act as potential microsites for seedlings to establish (Butler and Malanson, 1989; Butler et al., 2004; Resler et al. 2005). The availability of microsites, and the nutcracker's preference for seed cache sites near natural features, all work in favor of whitebark pine survival at treelines. Many of these microsites provide shelter and ameliorate climate conditions for whitebark pine seedlings (Resler, 2006). Hypothetically speaking, the more variable and heterogeneous the landscape, the more microsites that are available, and it is more likely that seed caching will occur. These conditions contribute to seedling growth and survival in the ATE.

Whitebark pine, as a keystone species, influences the spatial patterns of treeline landscape in the northern Rocky Mountains (Resler and Tomback, 2008), and the numerous ecosystem services it provides in these high elevation forests. The term keystone species originated from Paine's (1966) study of keystone predators, in which he found that starfish predation greatly affected the structure, diversity, and spatial pattern of marine communities. This study gave way to the meaning of keystone species, a species that plays a large role in affecting community structure relative to its abundance, is disproportionate. This idea can be applied to whitebark pine ecosystems (Tomback et al., 2001), where the keystone species whitebark pine has coevolved with its seed predator and disperser, Clark's nutcracker (Tomback, 1982), together modifying the landscape in subalpine and alpine ecosystems of western North America. Holling (1992) states in his extended keystone hypothesis: "…All ecosystems are controlled and organized by a small number of key plant, animal, and abiotic processes that structure the landscape at different scales." He suggests that landscapes are hierarchically structured in nature, and are composed of nested levels formed by differing biotic and abiotic influenced structuring variables that are modified by structural processes (e.g., photosynthesis, tree growth, disturbance, erosion, evolution, and climate).

As whitebark pine plays a major role in forming metacommunities, and the mosaic patterns of patchy landscape across the ATE, one might expect a change in these patterns with the introduction of blister rust disease. Positive feedbacks are important in tree island development because increased facilitation helps increase tree growth and survival in the ATE. Positive feedbacks associated with patch (or tree/tree island) size result in greater survivability among patches with higher population densities of trees. Yet, there is also an associated negative feedback within these patches of trees. Studies have shown a direct correlation between patch size and blister rust infection where whitebark pine grows in tree islands (Resler and Tomback, 2008; Smith et al., 2011). The very mechanism that aids in the survivability of these trees in treeline ecosystems, may in turn act against them in the face of an invasive disease.

CLIMATE CHANGE AND TREELINE DYNAMICS

The Intergovernmental Panel on Climate Change (IPCC) defines climate change as a change in the state of climate over time, usually persisting over an extended period (decades, or longer), whether caused by natural variability or human activity (IPCC, 2007). This definition differs from that of the United Nations Framework Convention on Climate Change (UNFCCC), which attributes the cause of climate change directly or indirectly to human activity altering atmospheric composition at a global scale, in addition to natural climate variability (IPCC, 2007). The IPCC (2007) reports a clear trend of warming temperatures and widespread melting of snow and ice at a global scale. More than 89% of climate studies examining changes in biological and physical systems indicate that these systems are changing as expected in response to climate warming (IPCC, 2007). Researchers anticipate that these trends will continue as the IPCC (2007) projects continued warming over the next two decades at a rate of 0.2ºC per decade.

There has been a remarkable increase in scientific research on the subject of climate change, with publications on the subject increasing exponentially since 1991. Climate change spans spatial and temporal scales, and has many links to geographic themes such as nature-society relationships and environmental dynamics. With such a diverse assemblage of disciplines, the field of geography provides an excellent platform for integrating interdisciplinary research in the face of climate change (Aspinal, 2010).

A major challenge to biogeographers and ecologists is linking vegetative response to future climate change (Rochefort et al, 1994). Treeline conifers are sensitive to temperature variability, and therefore logically, treeline may serve as a bioclimatic indicator of climate change (Schrag et al., 2008). With regard to warming temperatures, the alpine treeline plays a key role for the detection and understanding of climate-dependent ecosystem processes in the context of biodiversity patterns and ecosystem services benefitting human society (Kullman, 2007). Studying abiotically-controlled ecosystems, such as the alpine treeline ecotone, can provide insight into plant sensitivities to climate variation (Lloyd and Graumlich, 1997). The climatically-driven alpine treeline ecotone, in general resulting from environmental gradients, will likely be responsive to climatic changes since many of the species that make up this ecotone are already at the spatial limit of their range (Rochefort et al, 1994).

Paleoecological records show that the climatic response of elevational treeline has fluctuated throughout the Holocene (Rochefort et al., 1994; Lloyd and Graumlich, 1997), and following the end of the Little Ice Age (approximately 250 years ago) treeline appears to be rising altitudinally (Holtmeier, 2009; Smith et al., 2009). Several studies have examined the change in spatial distribution of high elevation conifer forests, specifically tree migration upslope, in response to climate change (e.g. Kullman, 1991; Rochefort et al., 1994; Lloyd and Graumlich, 1997; Körner, 1998; Grace et al., 2002; Dullinger et al., 2004; Körner and Paulsen, 2004; Kullman, 2007). There is agreement among most studies that treelines are currently advancing up slope, with the expanding distributional range largely attributed to a warming climate (Kullman, 1991; Rochefort et al., 1994; Smith et al., 2009). Warming temperatures could significantly alter patterns of high elevation forests and the adjacent alpine treeline ecotone, which may further alter forest ecosystem processes such as those effecting snow accumulation and distribution, and natural regulation of downstream runoff (Smith et al., 2009). Additionally, high altitudes experience the coldest air temperatures and lowest CO_2 partial pressures, which may cause increased forest sensitivity and response to increased atmospheric CO_2 – the most widely measured global change parameter (Smith et al., 2009).

When considering the relationship between tree cover and changing climate, abiotic and biotic factors that govern controls on treeline dynamics are key variables when predicting future climate change (Sveinbjörnsson, 2000). Kullman (2007) determined that positive feedback processes along with soil and atmospheric temperatures during the winter and summer were important explanatory factors to treeline change in *Pinus sylvestris* communities of the Swedish Scandes. Lloyd and Graumlich's (1997) treeline study in the Sierra Nevadas showed that changes in treeline position are associated with the interacting effects of warming temperatures and increased precipitation; their study found a correlation between drought severity and treeline decline. These studies provide insights that additional factors aside from climate change need consideration when assessing treeline dynamics. Findings from paleoecological records reveal that future warming alone will not drive treelines geographically upslope, unless it is coupled with adequate precipitation (Lloyd and Graumlich, 1997). With increasing temperatures, some mountain forests may advance upslope, however in other mountain communities these warming temperatures may induce drought conditions and actually trigger a decline in treeline position.

Many studies have examined the effects of forest pathogens on forested ecosystems as a result of climate change (Manter et al., 2005; Stone et al., 2008; Kliejunas et al., 2009; Woods et al., 2010). Additional factors such as, influences on seed-dispersal of tree species, competition among trees, and movement of forest pathogens, deserve consideration when assessing treeline shift in the face of a warming climate. In whitebark pine treelines, the high mortality among whitebark pine populations caused by the invasive blister rust disease (particularly in the northern Rocky Mountains of Montana) (Kendall and Arno, 1990), is likely to skew interpretations of treeline response to climate change (Tomback and Resler, 2007). In order to understand the vulnerabilities of forested ecosystems to warming climates, one approach is through modeling species response to environmental changes within an ecosystem (Dullinger et al., 2004; Nitschke and Innes, 2008).

INTERACTION OF TREELINE PATTERNS AND PROCESSES: CELLULAR AUTOMATA MODELING

The ecological literature is rich in studies that examine forest ecosystem response due to changes in environmental conditions. Studies include those resulting from disturbance-induced fragmentation (Dunn and Majer, 2007; Roland and Matter, 2007; Gastner et al., 2009), climate change (Nitschke and Innes, 2008), and the combination of climate change and disturbances to ecosystem processes (He et al., 2005; Wallentin et al., 2008). Many of these studies involve landscape-scale analyses of patch dynamics, in which the landscape is composed of patches defined by discrete boundaries or environmental gradients (Malanson et al., 2006; Dunn and Majer, 2007; Gastner et al., 2009). Anthropogenic, climatic, or ecological factors may form discrete boundaries. Due to the differing scales of processes that form landscape patches in the ATE, the hierarchical patch dynamics theory, which states that patches representing a large landscape area are comprised of smaller patches, is quite applicable (Dunn and Majer, 2007). Examining the components of a landscape in terms of spatial patches (and/or cells that represent trees/tree islands, or other natural features), is an excellent way to explore the interconnectedness between vegetation patches within the ATE.

Computer simulation models are a powerful method for examining the dynamics of patchy vegetation systems (Cairns, 2005). Cellular automata (CA) are a class of computer simulation model that uses local neighborhood associations in calculating dynamic response within a system (Malanson, 1999; Fonstad, 2006). Cellular automata was introduced by John von Neumann and Stanislaw Ulam in the 1950s, and since then has been used as a simulated world-view, incorporating mathematical and geographical concepts, using sets of transition rules based on local associations within a cellular neighborhood (Fonstad, 2006). The cellular neighborhood defines the geographic domain and the cells that influence the cell of interest (Tobler, 1979) or ‘target cell’. One of the first popularized applications of cellular automata was mathematics professor John Conway’s “Game of Life” developed in 1970. This CA game, based on a raster geographic domain, involves transition rules regarding the live or dead state of a cell within the cellular neighborhood of a raster. Similar to the “Game of Life”, the dynamics of a system are observable through a series of rules applied to each cell in a neighborhood. Tobler (1979) demonstrated the concepts of cellular geography using examples of urban growth and land use change. The use of local effects rules in cellular neighborhoods through CA modeling is an effective way to study the patterns and processes occurring in the ATE.

Complex ecosystems are inherent in biogeographical studies, and the complicated patterns and processes occurring in ecotones are no exception (Malanson, 1999). Cellular automata is an appropriate type of modeling for studying the ATE because of the models flexibility in incorporating multiple complex interacting factors in the model design, its ability to represent spatial patterns and processes, and its capability of modeling landscapes based on a raster framework. Other studies that have examined the dynamics of spatial patterns occurring in transition zones, use cellular automata to incorporate biotic/abiotic factors and set rules based on feedback patterns prominent in alpine systems (Malanson et al., 2001; Alftine and Malanson, 2004; Zeng and Malanson, 2006). Zhang et al. (2008) used a combination of GIS analyses involving multi-criteria evaluation and raster calculations using Idrisi, and cellular automata to build a model that simulates the response of alpine tundra vegetation to climate change in China.

Similar analyses incorporating GIS and CA modeling tools will be useful in examining pattern and process of treeline dynamics in this study.

INTERACTION OF TREELINE PATTERNS AND PROCESSES: AGENT-BASED MODELING

Agent-based models are suitable for modeling complex systems where there are many interacting factors (Grimm et al., 2005; Robertson, 2005), and are particularly useful for the research community when exploring theoretical aspects of systems (Matthews et al., 2007). Primarily, two components make up agent-based simulations: the environment, and "agents" (Grimm and Railsback, 2005; Lauberte, 2005). Typically, a cellular automata framework represents the environment, governed by rules assigned to each of the neighboring cells in the cellular neighborhood. Within the CA framework agents, influenced by their surrounding environment, interact with one another, and the agent's behavior may influence the environment. The architecture of agent-based simulation models are the result of a simple cellular automata framework, coupled with the dynamics of agents in order to model complex systems (Janssen, 2005).

Simulating natural systems within a cellular automata framework, allows the modeler to ask "what if" questions about natural system processes, and to observe and predict possible outcomes over different spatial and temporal scales (Fonstad, 2006). Simulation has become a popular approach to ecological modeling, especially in landscape dynamics (such as competition and colonization dynamics) (Malanson et. al, 2007). Research in landscape ecology has emphasized the usefulness of agent-based modeling for analysis in landuse studies ranging from landscape dynamics in response to human disturbances and climate change, to landuse planning and management issues (Veldkamp and Verburg, 2004; Mathews et al., 2007; Houet et al., 2010). These models simulate the actions and interactions of players or agents in a simulated world (Matthews et. al, 2007).

Acting on the basis of cellular neighborhoods in which the fate of each cell is dependent on its placement configuration within a cell neighborhood, agents within the ATE landscape for example, can be represented by any ecological phenomena (i.e., abiotic/biotic factors, patches of trees or tree islands, rock shelters). The agents may respond to other agents and their surrounding environment, and can be controlled based on information learned from the real world. Since agent-based models are useful in building complex ecosystems for the purpose of understanding complicated patterns and process (Grimm et al., 2005), agent-based models are a potentially valuable learning tool for studying the ATE. Whitebark pine treeline communities in particular involve multiple interacting factors among species in terms of avian assisted seed-dispersal from subalpine to ATE, whitebark pine's facilitative role in tree island development, the introduction of blister rust, and the implications of disease and climate change to treeline dynamics (e.g., Tomback, 2001; Tomback and Resler, 2007; Resler and Tomback, 2008). Therefore, whitebark pine treeline communities provide an interesting platform for building an agent-based model. Observing the pattern and process of interacting treeline agents, and the combined effects of invasive disease and changing climate on agents, provides a unique agent-based model for studying the spatially and ecologically complex processes of a whitebark pine treeline community.

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Chapter 3: Topographic Influences on the Distribution of White Pine Blister Rust in *Pinus albicaulis* Treeline Communities

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Accepted for publication in *Écoscience* (2013), vol. 20 (3): (forthcoming)

Abstract

The exotic disease white pine blister rust (caused by *Cronartium ribicola*) damages and kills whitebark pine (*Pinus albicaulis*), even in the extreme environments of alpine treeline communities. We surveyed *P. albicaulis* trees and tree islands for blister rust in two distinct alpine treeline communities in Montana, USA, and examined meso- and micro-topographic factors potentially related to the climatic requirements for blister rust infection. For each of 60 sampling plots, we created high resolution digital elevation models, derived microtopography variables, and compared these and distance to water feature variables with blister rust occurrence and intensity (number of cankers per infected tree) for every sampled *P. albicaulis* tree. Infection rates were 19% (of 328 sampled trees) and 24% (of 585 sampled trees) at the two sites. Tree island *P. albicaulis* had higher infection percentages than solitary trees. Using Bayesian analysis and a zero-inflated Poisson regression model, we determined that solar radiation and moisture-related variables correlated with both presence and number of blister rust cankers on *P. albicaulis*. Site factors that influence moisture, such as local topography, hydrology, and climate, differed between the two treeline study areas, which may account for the model variability.

Keywords:
Whitebark pine, treeline, *Cronartium ribicola*, Rocky Mountains, Digital Elevation Models (DEM), Zero-inflated Poisson regression

Introduction

Landscape pathology integrates concepts from disease ecology and landscape ecology, and emphasizes pattern-process relationships between vegetation and disease manifestation at a landscape scale (e.g., Jules *et al*., 2002; Holdenrieder *et al*., 2004; Condeso & Meentemeyer, 2007; Meentemeyer *et al*., 2011). Variation in meso- (e.g., spanning across watersheds) and micro- (e.g., local, small depressions) topographic landscape features may influence the spatial distribution of host and disease reservoir species, pathogen spread, and disease manifestation (e.g., Rizzo *et al*., 2002; White, Brown & Host, 2002; Wilson, Lewis & Aberton, 2003; Holdenrieder *et al*., 2004; Kearns & Jacobi, 2007; Smith *et al*., 2011; Larson, 2011). Since specific abiotic conditions resulting from topographic heterogeneity can affect disease incidence (e.g., Smith & Hoffman, 2001; White, Brown & Host, 2002; Kearns & Jacobi, 2007; Smith *et al.,* 2011), a landscape pathology approach for pathogens with complex life cycles may relate to how disease manifestation and affected vegetation dynamics are expressed in mountainous regions, especially under scenarios of global environmental change (e.g., Shafer *et al.,* 2005).

The introduced fungal pathogen *Cronartium ribicola,* which causes white pine blister rust (here referred to as blister rust) in five-needle white pines (Genus *Pinus*, Subgenus *Strobus*) is a problematic plant pathogen with a wide distribution and complex life cycle (Hoff, Bingham & McDonald, 1980). The life cycle comprises five stages of spore production and windborne transmission between the white pine host and alternate host—typically *Ribes* spp. but also *Pedicularis racemosa* and *Castilleja miniata* (Spaulding & Gravatt, 1917; McDonald *et al*., 2006). Spore production and transmission between hosts require environments with moderate temperatures, humidity, and wind conditions (McDonald & Hoff, 2001). In the extreme environments of the alpine treeline ecotone (ATE), a transition zone between closed contiguous upright trees and treeless tundra (Holtmeier, 2009), blister rust now occurs in *Pinus albicaulis* (whitebark pine) treeline communities in the northern Rocky Mountains east of the Continental Divide (Resler & Tomback, 2008; Smith *et al.*, 2008; Smith *et al.*, 2011). These environments are exposed to conditions previously thought too dry and cold for blister rust spore production (e.g., Van Arsdel, Riker & Patton, 1956; Campbell & Antos, 2000).

Inadvertently introduced to western North America in the early 1900's, *Cronartium ribicola* now occurs nearly range-wide in *P. albicaulis*, a highly susceptible species, and has been responsible for precipitous population declines in the northern Rocky Mountains (Hoff, Bingham & McDonald, 1980; Tomback & Achuff, 2010). Blister rust cankers girdle branches, ending seed production and reducing photosynthetic biomass; cankers in main stems kill trees (McDonald & Hoff, 2001; Geils, Hummer & Hunt, 2010). *P. albicaulis* functions as a foundation and keystone species by fostering community development and biodiversity across its range in the US and Canada (e.g., Tomback, Arno & Keane, 2001; Ellison *et al*., 2005); and *P. albicaulis* depends primarily on the Clark's nutcracker (*Nucifraga columbiana*) for dispersal of its large, wingless seeds (e.g., Tomback, 1978, 1982; Tomback, 2001). Loss of seed production has resulted in the decline of *P. albicaulis* seed dispersal by nutcrackers as well as a decline in *P. albicaulis* regeneration in the northern U.S. Rocky Mountains (McKinney, Fiedler & Tomback, 2009, Barringer *et al*., 2012).

Blister rust spore production, transmission to alternate hosts, and infection of *P. albicaulis* require specific temperature, humidity, and wind conditions (Mielke, 1943; Van Arsdel, Riker & Patton, 1956; Smith & Hoffman, 2000, 2001; McDonald & Hoff, 2001; Frank *et al*., 2008; Rochefort, 2008). Studies of *Ribes* and white pine hosts show the optimal conditions required for each spore development stage vary in temperature (ranging 13°C to 20°C), moisture, transport distances (both local- and long-distance), and length of time (hours, days, or weeks) to complete the blister rust life cycle (Hirt, 1942; Van Arsdel, Riker & Patton, 1956; McDonald & Andrews, 1980). For example, the final stage and development of fragile basidiospores, that infect white pine hosts, requires cool temperatures (less than 20°C), 48 hours of near 100% relative humidity (Van Arsdel, Riker & Patton, 1956), limited sun and frost exposure, and wind to transport basidiospores from *Ribes* spp. over short distances (less than 300 m) (McDonald & Hoff, 2001).

Topography influences a hierarchy of abiotic conditions by moderating meso- and microclimates over a range of spatial scales, especially at alpine treelines where tree physiology is limited by adverse climatic conditions (e.g. Holtmeier, 2009). In mountain environments, topography affects environmental controls at local to regional spatial scales, including (but not limited to) local soil structure and moisture, freeze-thaw processes, snow accumulation, and local climate in sheltered versus exposed sites (Johnson & Billings, 1962; Oke, 1978). Alpine microtopography has been linked to species richness, microclimate conditions, and microsite variation, which can determine the survival or demise of seedlings (e.g., Germino, Smith & Resor, 2002; Butler *et al*., 2007; Rose & Malanson, 2012). Microtopography such as depressions and boulders, can shelter and promote growth of conifer seedlings (Resler, 2004), by reducing wind exposure and snow abrasion in severe ATE environments (Holtmeier, 2009). Concurrently, these sheltered areas may also provide higher humidities that favor fungal disease (Oke, 1978) such as blister rust.

Abiotic conditions can be derived from topography through the use of digital elevation models (DEMs), which is effective for deriving surrogates of field-collected environmental variables such as slope and moisture (Brown, 1994), and solar radiation (Guisan, Theurillat &

Kienast, 1998) in models of mountain landscapes (Del Barrio *et al*., 1997; Bader & Ruijten, 2008). Environmental gradients resulting from complex topography have been associated with varying levels of blister rust infection severity (e.g., White, Brown & Host, 2002; Kearns & Jacobi, 2007; Smith *et al*., 2011), the distribution of *Ribes* spp. (that vary in their susceptibility to *Cronartium ribicola* infection [Newcomb, 2003; Newcomb, Upper & Rouse, 2010]), and ability of *Ribes* spp. to support production of pine-infecting basidiospores (Childs & Kimmey, 1938; Kearns *et al*., 2008). For example, higher incidence of blister rust-infected *Pinus flexilis* (limber pine) and *P. albicaulis* have been associated with topographic depressions (Kearns & Jacobi, 2007; Smith *et al*., 2011) and proximity to perennial streams, which may increase humidity and the occurrence of some riparian species of *Ribes* (Newcomb, 2003).

The decline of *P. albicaulis* from blister rust may alter treeline community structure by disrupting the dynamics of tree island development at some Rocky Mountain treelines. In *P. albicaulis* treeline communities, krummholz (environmentally stunted) forms of *P. albicaulis* typically shelter conifers less tolerant of cold and windy conditions, resulting in the formation of tree island colonies—a notable treeline pattern (e.g., Habeck, 1969; Resler, 2004; Resler & Tomback, 2008; Resler & Fonstad, 2009). For example, near Logan Pass in Glacier National Park, Habeck (1969) predicted that high blister rust infection levels could alter the dynamics of meadow invasion by trees, given the facilitative relationship between *P. albicaulis* and *Abies lasiocarpa* (subalpine fir) in that area. Resler and Tomback (2008) noted that blister rust is killing established *P. albicaulis* trees in the ATE before they facilitate the recruitment of other conifers, hastening the decline of *P. albicaulis* and the facilitation of tree islands, as well as killing *P. albicaulis* established within tree islands. Furthermore, subalpine *P. albicaulis* seed sources are diminished, resulting in fewer seeds available for dispersal by nutcrackers to the

ATE (McKinney & Tomback, 2007; McKinney & Fiedler, 2010). The loss of *P. albicaulis* to blister rust at alpine treeline is likely to slow and/or diminish the predicted upslope advance of treeline as climate warms (Tomback & Resler, 2007). Treeline position in some regions may serve as a bioclimatic indicator of climate change (Körner & Paulsen, 2004), but interpretations of treeline position may be confounded in treeline ecosystems where *P. albicaulis* is the predominant conifer species, because blister rust-induced mortality of *P. albicaulis* may impact treelines that must respond to both a warming climate and a disease-altered ecosystem (Smith-McKenna *et al.*, manuscript in prep).

The presence of blister rust in the dry and cold climates of *P. albicaulis* treelines in the northern Rocky Mountains east of the Continental Divide (Resler & Tomback, 2008; Smith *et al.*, 2008; Smith *et al.*, 2011) is perplexing since controlled experiments suggest that blister rust spore production requires moist and moderately cool environments to thrive (Van Arsdel, Riker & Patton, 1956). Previous research indicates that vegetation pattern and structure, and topography influence the rate of blister rust infection in *P. albicaulis* treeline communities (Resler & Tomback, 2008; Smith *et al.*, 2011). These studies have been exploratory in nature, and have primarily focused on characterizing general relationships between fine-scale topographic and environmental variables, and blister rust infection rates, aggregated at the sampling plot level (e.g., Smith *et al*. 2011). However, it is unknown how infection presence and intensity varies spatially from one *P. albicaulis* tree to another, and how this spatial variation is influenced by the underlying and surrounding topography of the tree. Given the topographic influences on abiotic conditions over a range of spatial scales at alpine treelines (Malanson *et al*., 2007; Holtmeier, 2009), there is merit in investigating the link between topography and blister rust infection through a multiscale analysis that considers the impact at the tree level, in addition to broader spatial scales of influence. Here, we investigate topographic factors (both meso- and micro-) that are potentially related to blister rust infection of *P. albicaulis* trees.

The purpose of this study is to examine the relationships between blister rust infection and ecologically significant topographic variables at the tree-level, for two alpine treeline study locations in the US Rocky Mountains. Our objectives were to 1) survey the presence and intensity of blister rust infection (if any) in two geographically different *P. albicaulis* treeline communities in Montana, USA, one in northern Montana—near the pine's mid-latitudinal distribution, and the second in the Beartooth Plateau—near the southernmost region of the pine's Rocky Mountain range, 2) determine which meso- and micro- topographic factors (that affect moisture and exposure conditions at a tree's site) correlate with the presence and intensity of blister rust infection among the sampled *P. albicaulis* trees, and to 3) assess any geographic differences in blister rust infection and potential influential factors between the two treelines.

Methods

STUDY AREAS

Working at treeline in the Northern Divide Ecosystem, specifically in Glacier National Park, we previously found that *P. albicaulis* was an important facilitator of tree island development (Resler & Tomback, 2008). Additional work in this region in 2008 determined significant relationships between topography and areas of blister rust infection at treeline, at the plot level (Smith *et al*., 2011). In 2010 we extended our work by increasing sampling intensity and geographic coverage, and sampled in two treeline study areas along the Rocky Mountain Front of Montana. Each treeline study area shares the following characteristics: *P. albicaulis* is a major treeline component, they differ in surrounding topography but have similar microtopography, and their separation by three degrees of latitude and 500 km distance collectively allowed us to sample from *P. albicaulis* communities across a range of environmental conditions (Figure 1). We collected data from these two climatic treelines near the mid- and southern- Rocky Mountain range of *P. albicaulis* east of the Continental Divide in the Rocky Mountains of Montana, USA, dominated by dry, continental climate regimes (Johnson & Billings, 1962; Finklin, 1986).

Our northern study area, Divide Mountain (~48.6°N, 113.4°W), crosses the eastern boundary of Glacier National Park (GNP) and western boundary of the Blackfeet Indian Reservation along the eastern Rocky Mountain Front, within the Northern Divide Ecosystem. Here, *P. albicaulis* is a major component of krummholz forest communities, where we sampled at elevations ranging from 2097 to 2261 m, on the slopes of Divide and White Calf Mountains (Figure 1). To characterize summer climate conditions during the sampling season, we measured temperatures at the Divide Mountain study area using two Hobo® weather stations (~2 m tall) from July through September 2010. Summer temperatures in 2010 averaged 9.6°C (T_{min} = -1.4°C, T_{max} = 22.2°C).

The southern study area lies just north of the Wyoming border on the northeastern edge of the Beartooth Plateau (part of the Greater Yellowstone Ecosystem (GYE)), in the Line Creek Research Natural Area (RNA), Custer National Forest (~45.0°N, 109.4°W) (Figure 1). Mellmann-Brown (2005) found *P. albicaulis* to be a predominant conifer species in treeline communities within the Line Creek RNA. Here, we sampled treeline communities on a narrow, exposed, and wind-swept ridge bounded by steep slopes above Wyoming Creek, at elevations ranging 2960 to 3029 m. Temperatures measured at the Line Creek RNA (July-September 2010) averaged 8.9°C (T_{min} = -8.6°C, T_{max} = 22.1°C).

At both study areas, surface microtopography, including topographic depressions, turf-banked terraces, patterned ground, and surface boulders transported from cliff bases through active solifluction processes, occur throughout the landscape. Ongoing periglacial processes such as solifluction, needle ice activity, and rock sorting (Johnson & Billings, 1962; Butler & Malanson, 1989) have shaped the microtopography. Uneven microtopographic surfaces can facilitate conifer establishment and growth (Butler, Malanson & Resler, 2004; Resler, Butler & Malanson, 2005) through climatic amelioration. Furthermore, microtopographic features may serve as landmarks for the placement of *P. albicaulis* seed caches by Clark's nutcracker (Tomback, 1978). Each treeline community contained tree island colonies, groupings of sheltered conifers that established in the lee of more tolerant trees (such as *P. albicaulis*) or topographic features. Sampled tree species within each treeline community, which coexist in tree islands or grow solitarily in both study areas, include *P. albicaulis*, *A. lasiocarpa*, *Picea engelmanii* (Engelmann spruce), *Pinus contorta* (lodgepole pine), and *Pseudotsuga menziesii* (Douglas-fir).

Alternate host species for *Cronartium ribicola* (*Ribes* spp., *C. miniata, P. racemosa*) (McDonald & Hoff, 2001; McDonald *et al*., 2006) are prevalent within both study areas. In particular, *Ribes* spp. plants were observed growing in and around our sampling plots, as well as within tree island patches (Smith-McKenna, personal observation). Undoubtedly, the spatial configuration of alternate host species in relation to disease manifestation in host trees is important; however it is also complex and not fully understood at alpine treelines, and an exhaustive survey of alternate host species was precluded in this study due to the level of sampling intensity, time, financial, and personnel limitations. Since Smith *et al*. (2011) previously found proximity to Ribes to be of lesser importance than topographic variables (e.g., such as surface curvature, aspect, and flow accumulation) in predicting disease canker intensity at the sampling plot level, we therefore focus here specifically on abiotic controlling factors at the tree level.

SAMPLING CONFIGURATION

In July 2010, we sampled from thirty 15 m x 15 m plots (following methods from Smith *et al*., 2011) within the elevational limits of the ATE at each study area, for a total of 60 plots. The 225 m^2 plots captured a range of tree/tree island sizes and topographic variation within each treeline study area, and maintained within-plot homogeneity in obvious environmental variation. Because slope orientation (e.g., aspect) has been linked to blister rust infection (Smith *et al*., 2011), we stratified the sampling plots proportional to each treeline sampling area in four quadrants (northeast [0-90°], southeast [90-180°], southwest [180-270°], northwest [270-360°]). Using terrain and aerial imagery in a geographic information system (GIS), we delineated potential sampling boundaries at each treeline and calculated the areal proportion within each aspect quadrant. For example, plots were randomly dispersed across the Divide Mountain treeline study area on slopes facing NE (40%, 12 plots), SE (34%, 10 plots), SW (13%, 4 plots), and NW (13%, 4 plots). Within each treeline study area we navigated with a topographic map and compass to determine aspect, and used blind and random pin tosses (toss distances > 20 m) to designate sampling plot centers. We chose specific sample locations based on conifer presence, hiking accessibility, and safety (see Figure 1). Within each sampling plot, we 1) recorded *P. albicaulis* tree/tree island geospatial positions, 2) classified and quantified blister rust presence and canker intensity, and 3) characterized the microtopography by creating high resolution digital elevation models, as detailed below.

PINUS ALBICAULIS AND BLISTER RUST CHARACTERIZATION

Within each sampling plot we inventoried all *P. albicaulis*, living and dead, and noted the characteristics of growth, size, and whether they grew solitarily or within tree islands. We inventoried dead trees displaying 100% tree and canopy kill (dead needles), and noted whether blister rust caused the death (showing evidence of cankers) when *P. albicaulis* species identification could be discerned. The majority of sampled *P. albicaulis* were krummholz trees less than 1 m in height, and we included all ages of trees (from seedlings to very old trees) in our inventories. Tree islands were defined as two or more trees growing contiguously, with spatially overlapping foliage. We considered a cluster of *P. albicaulis* stems apparently originating from a single nutcracker cache as a single tree (e.g., Resler & Tomback, 2008). We inspected each *P. albicaulis* tree for evidence of blister rust infection on the stems and branches, and recorded the number and class of cankers, following Hoff (1992). Cankers were distinct from one another if separated by healthy tissue on the stem or branch (see Figure 2). We geolocated each *P. albicaulis* tree in our sampling plots in order to relate tree and disease characteristics (blister rust presence/absence, and number of cankers) to the underlying microtopography surface variables—which were derived geospatially and described in the following section.

Mountain pine beetles do not attack trees as small in stem diameter as krummholz *P. albicaulis* (Gibson *et al*., 2008). However, larger diameter non-krummholz trees within sheltered areas of the lower ATE were, in fact, attacked in our study areas, and particularly in the Line Creek RNA. None of our sampling plots contained these trees, and therefore infestation by mountain pine beetle was not a confounding factor in this study.

SPATIAL CHARACTERIZATION OF TOPOGRAPHIC VARIABLES

We characterized the microtopography of each sampling plot by recording elevation points across the plot's surface with a handheld Trimble GeoXT global positioning system (GPS) unit, in order to represent the varying surface gradients and topographic depressions. We differentially corrected all GPS points to submeter accuracy. Terrain complexity varied within each plot, as did the number of representative elevation points (on average, 600 points per plot) with which we created fine resolution (on average, 0.08 m) digital elevation models (DEMs) following methods from Smith (2009) and Smith *et al*. (2011).

Submeter resolution DEMs provide more detail in our 15 m sampling plots than the currently available USGS 10 m DEM, an important consideration since our scale of analysis is at the tree-level, and many of our sampled trees are less than 1 meter apart. Additionally, periglacial surface features are quite variable in the ATE (e.g., Butler & Malanson, 1989, 1999), and fine scale DEMs are important for characterizing the microtopographic variability (Allen & Walsh, 1996; Walsh *et al*., 2003). For example, the size and type of fine-scale patterned ground topographic features characteristic of our sampling plots included ~14-18 cm turf-banked terrace risers (near Divide Mountain, e.g., Butler, Malanson & Resler, 2004; Resler, 2004), ~17-35 cm frost hummocks, 1-3 m high solifluction terraces (near Line Creek RNA, e.g., Johnson & Billings, 1962), and rock clasts ranging 10 cm to very large boulders (Resler, 2004). In the severe ATE environment, this topographic variability creates microhabitats that ameliorate exposure to abiotic conditions, and influence seedling survival, patchy vegetation, and snow retention patterns across the treeline landscape (Johnson & Billings, 1962; Oke, 1978; Holtmeier & Broll, 1992).

We derived all topographic variables using ArcGIS (v.9.3.1, ESRI, Redlands, CA) Spatial Analyst tools. From each of the 60 submeter DEMs, we calculated four submeter microtopographic raster surface variables influential to moisture and humidity conditions (slope, curvature, flow accumulation, and solar radiation) (ESRI, 2009). Topographic features that control water runoff and flow rate (e.g. slope), cool air drainage, and soil moisture conditions, are potentially influential for spore production and blister rust infection. Surface curvature indicates the reflection (convex, positive curvature), or retention (concave, negative curvature) of water. High flow accumulations indicate concentrated areas of drainage, particularly where water pools in depressions (Florinsky & Kuryakova, 2000). Solar radiation affects soil moisture conditions, and surfaces with more sun exposure tend to have drier soils (which may be less favorable for blister rust).

The proximity of white pine trees to water features has been linked to blister rust infection (Van Arsdel, 1965; White, Brown & Host, 2002; Smith *et al*., 2011). Since alpine glaciers and snowmasses are present at the highest elevations within and surrounding both treeline study areas, and may provide moisture, we considered the distance to ice a potential blister rust correlate. Furthermore, we determined proximity distances from each *P. albicaulis* tree to the surrounding streams, lakes, and marsh and included these mesotopographic variables in our analysis. We derived these variables from high-resolution National Hydrography Dataset GIS layers, which are based on 1:24,000 USGS 7.5' Quad maps (Simley & Carswell, 2009). Using the ArcGIS Spatial Analyst distance tool, we incorporated the terrain of a USGS 10 m DEM in the distance calculations to include the mountainous topography (mountains may influence wind-driven spores). We generated GIS raster map layers for the four mesotopographic distance variables (distance to streams, lakes, marsh, and ice).

Using a GIS raster-extraction tool, we extracted the eight topographic values (four micro- and four meso- topographic variables) for each geolocated *P. albicaulis* tree within each sampling plot, in order to examine relationships between disease infection of trees and their corresponding topographic site characteristics. We used eight independent topographic variables for the candidate model selection process: slope, curvature, flow accumulation, solar radiation, and distances to streams, marsh, lakes, and ice. Figure 3 shows an example of a sampling plot's variation in terrain and drainage relative to GPS locations of sampled *P. albicaulis* trees and their disease characteristics, and the detailed DEM microtopography variables used to extract values for each tree. Predictors for the dependent variables—blister rust presence (presence of cankers) and intensity (total number of cankers per infected tree)—were determined from the statistical analyses.

STATISTICAL ANALYSIS

We modeled blister rust presence and intensity as a function of topographic and environmental spatial variables for each sampled tree, within each sampling plot, for each study area. We used a zero-inflated Poisson (ZIP) regression multilevel model with random effects similar in model structure described by Hall (2000), and parameters estimated by Bayesian methodology. To run the statistical analyses, we coded a model simulation procedure similar in structure to that of Hadfield (2010) that uses Markov Chain Monte Carlo (MCMC) methods and incorporated random effects, but implemented in MATLAB (version 7.9.0529 R2009b, The MathWorks Inc., Natick, MA, USA). It was necessary to apply ZIP regression methods since the dependent variable (number of cankers per tree) consisted of count data with many zeros (Lambert, 1992). The addition of a random-effects term accounted for correlated responses and sources of dependency within and among the 30 sampling plots in each study area, which can be problematic with multiple sources of variance (Hall, 2000). By including random effects in our multilevel ZIP models, we can account for dependence of observations (blister rust cankers on each tree) within clusters (sampling plots). Multilevel random effects models can solve potential response dependency and multicollinearity simultaneously (Shieh & Fouladi, 2003).

Potential predictor variables were determined through stepwise selection procedures of two regression analyses 1) a logistic regression with the presence vs. absence of cankers as the dependent variable, and 2) a linear regression with the number of cankers as the dependent variable using SAS® software (version 9.2, SAS Institute Inc., Cary, NC, USA). We screened the initial eight variables for low Mallow's Cp, model fit statistics (AIC, SC, -2LogL), and multicollinearity (risk of multicollinearity was small, most variables displayed $r < 0.2$). Based on these statistical methods (Miller, 2002; Shieh & Fouladi, 2003; Muller & Fetterman, 2003), we selected six variables to include in the ZIP models: curvature, solar radiation, distance to streams, distance to lakes, distance to marsh, and distance to ice (see Table I for variable ranges).

For each study area we generated a ZIP model that uses two link functions, a logit (logistical) link function and a log (Poisson) link function, in order to model two processes at the same time. The models test 1) which variables are associated with the presence vs. absence of blister rust (logistic or zero state), and 2) if blister rust is present, which variables predict blister rust intensity (Poisson state). The resulting ZIP regression model with random effects for the prediction of canker presence (p_{ij}) and mean intensity (λ_{ij}) is expressed as follows (Equations 1-3; for plot $i = 1, \ldots, 30$; and for tree $j = 0, \ldots, n_i$):

$$Y_{ij} \sim \begin{cases} 0, & \text{with probability } (1 - p_{ij}) \\ \text{Poisson } (\lambda_{ij}), & \text{with probability } p_{ij} \end{cases} \qquad [1]$$

$$\log (\lambda_{ij}) = x'_{ij}\boldsymbol{\beta} + \mathrm{w}_i \qquad [2]$$

$$logit\,(1 - p_{ij}) = z'_{ij}\boldsymbol{\gamma} + \mathrm{u}_i\,. \qquad [3]$$

Equation 1 defines Y_{ij}, which represents the number of blister rust cankers on the specific tree j within the specific sampling plot i. Within the log-linear (Equation 2) and logistic (Equation 3) regression equations, x'_{ij} and z'_{ij} represent the covariate vectors of the j^{th} tree within the i^{th} plot ($i = 1, 2, \ldots, 30$; $j = 0, 1, \ldots, \mathrm{n}_i$). We estimated two separate covariance structures for canker intensity and presence in Equation [2] and [3], respectively. Parameters $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ are the corresponding fixed-effects regression parameters. The vectors w_i and u_i are the subject random effects or random intercepts in two equations that are assumed to be independently and normally distributed since there is no spatial dependency between infected and uninfected trees (blister rust disease cannot spread from pine to pine [Mielke, 1943]). These equations are modified from Hall's (2000) ZIP random effects model, which incorporates random effects (a random intercept) only in the log (Poisson) link function.

To determine final models for each treeline study area we implemented Bayesian procedures to produce model runs with credible interval ranges for each variable, assessed whether each interval range did not overlap with zero, and used noninformative priors (e.g., Daniels & Kass, 1999; Barnard, McCulloch & Meng, 2000). Model simulations consisted of 5000 iterations with a burn-in period of 1000 (eliminating the first 1000 iterations) in order to reach model convergence. Bayesian Information Criterion (BIC) values indicate the strength of each variable's contribution to the model. We analyzed a series of candidate models for each study area by running one-variable ZIP models (Table II), and assessing BIC ranking in order to assist with the final model selection. One-variable ZIP models and BIC ranking are useful for providing descriptive analyses for exploratory purposes (e.g., Smith *et al.*, 2011).

The final ZIP regression random effects models define which topographic variables best explain the presence and intensity of blister rust infection at each treeline study area. The final models account for 1) a large number of zero values in the dependent variable, 2) any clustering between sampling plots, and 3) the number of *P. albicaulis* trees per sampling plot.

Finally, previous research has shown important differences in infection rates between solitary *P. albicaulis* and those growing within tree islands (Resler & Tomback, 2008). Therefore, we conducted a G-test of independence (Sokal & Rohlf, 1995) to compare infection rates against growth characteristics (solitary or tree island) at both Divide Mountain and Line Creek RNA.

Results

PINUS ALBICAULIS AND BLISTER RUST SAMPLING RESULTS

We sampled a total of 913 *P. albicaulis* trees among the 60 plots (Table III). Divide Mountain had nearly double the number of sampled *P. albicaulis* trees (maximum per plot, 79) than Line Creek RNA (maximum per plot, 34), and more than double the number of infected trees. Divide Mountain showed a slightly higher percentage of blister rust infected trees (23.6%) and lower canker intensity (maximum cankers per tree, 20) compared with Line Creek RNA (19.2%) (maximum cankers per tree, 62) (Table III). More *P. albicaulis* trees grew in tree islands than solitarily at Divide Mountain; the reverse was true for Line Creek RNA. The G-test of independence indicated that at both sites, *P. albicaulis* growing in tree islands had greater canker intensity and likelihood of blister rust infection than solitary *P. albicaulis* (Table III). Infection rate was highest on SE and SW aspects at Divide Mountain and Line Creek RNA, respectively (Table III).

SPATIAL CORRELATES OF BLISTER RUST PRESENCE AND INTENSITY

The final models showed significant results for both study areas (Table IV). Final model parameters are considered significant when the credible interval ranges (between lower to upper bounds) do not overlap zero. Solar radiation and distance to lakes were statistically significant in explaining some of the variance in blister rust canker intensity at both study areas. Proximal distance to ice was an additional significant variable at Divide Mountain; at Line Creek RNA concave curvature and proximal distance to streams also explained variance in blister rust canker intensity (***β*,** Poisson component, Table IV). At Line Creek RNA, far distances to ice explained a portion of variance in blister rust presence (**γ,** logistic component) on *P. albicaulis* trees. Estimated parameter values for distance to lakes at Divide Mountain and curvature at Line Creek RNA (Table IV) indicated that these variables were linked to the presence of blister rust cankers. However, results in the one variable zero-inflated Poisson ZIP models were not significant for either variable (Table II). Therefore, we considered the relationships to be weak and likely due to the interaction with other variables (e.g., Lambert, 1992).

Discussion

Topography is important at alpine treelines in creating varied microclimates crucial for conifer establishment, survival, and colonization (e.g., Butler, Malanson & Resler, 2004; Resler, Butler & Malanson, 2005), and there appears to be a link between fungal infection and topographic features that ameliorate the harsh conditions in the ATE. These conditions may potentially influence (by inhibiting and/or promoting) the distribution and structure of some Rocky Mountain treeline *P. albicaulis* communities (e.g., Resler & Tomback, 2008; Smith *et al*., 2011). Comparing our two *P. albicaulis* treeline study areas, we found that the percentage of blister rust infected *P. albicaulis* varies slightly, but canker intensity differed considerably. Furthermore, between Divide Mountain and Line Creek RNA, there are both geographic differences and similarities in topographic variables that influence blister rust infection.

GEOGRAPHIC VARIATION OF BLISTER RUST IN TREELINE *P. ALBICAULIS*

Our results are consistent with findings from other studies that have examined the influence of landscape factors on blister rust infection in white pine species in locations with comparatively cold and dry climates (e.g., White, Brown & Host, 2002; Smith *et al.*, 2011). We found that SE aspects at Divide Mountain and SW aspects at Line Creek RNA showed the highest blister rust infection levels at alpine treeline. Though Larson (2011) found the highest blister rust infection levels in subalpine *P.albicaulis* stands on north-trending slopes, he sampled west of the Continental Divide where climates are generally wetter and milder than east of the Divide (Finklin, 1986). Blister rust incidence could also be inhibited by cold conditions at key times of development or spore dispersal (i.e. shorter growing seasons and fewer frost-free days (e.g. Campbell & Antos, 2000) on northern slopes (White, Brown & Host, 2002)—a relationship that could hold true in extremely cold and dry, high elevation environments, east of the Continental Divide (Finklin, 1986; Walsh, Malanson & Butler, 1992) and in our treeline study areas. These findings illustrate the importance of geography in blister rust dynamics.

The spread of blister rust to cold, dry treeline communities, was originally considered unlikely (e.g., Campbell & Antos, 2000) because certain stages of the blister rust life cycle require both moderate temperatures and high humidity (e.g., McDonald & Hoff, 2001; Geils, Hummer & Hunt, 2010). However, in this study nearly one-fourth of *P. albicaulis* showed signs of blister rust infection. Infection rates at Divide Mountain were slightly higher than those at Line Creek RNA, which may be explained by variation in treeline-specific factors, such as microclimate and tree island density, which may relate to microtopography. For example, weather stations placed at our treeline study areas (July-September 2010) recorded more frequent readings and longer durations of high relative humidity (> 90%) at Divide Mountain compared to Line Creek RNA (Franklin, 2011). Average and maximum wind speeds and gusts measured at unprotected microsites at Divide Mountain during summers of 2011 and 2012, exceeded measurements at Line Creek RNA (Pyatt, unpubl. data). Furthermore, monthly summer climate averages for the last 30 years (June-September, 1980-2010) showed wetter conditions and milder temperatures at Divide Mountain (76.3 mm precipitation, 11.2ºC T_{mean}, 0.02ºC $T_{dewpoint}$) than Line Creek RNA (44.5 mm precipitation, 9.6ºC T_{mean} , -3.2ºC $T_{dewpoint}$) (PRISM, 2011). Additionally, tree island density (including conifer species other than *P. albicaulis*), and *P. albicaulis* density for the same plots as measured in this study, were consistently higher at Divide Mountain than Line Creek RNA (Franklin, 2011).

However, when comparing our results for Divide Mountain to other reported infection rates solely within the Northern Divide Ecosystem, infection is comparably low—for both regional treeline and subalpine stands. For example, here, we found a 24% infection rate for treeline as compared to 73-85% overall for subalpine in the Northern Divide Ecosystem (Kendall & Keane, 2001; Smith *et al*., 2008). Furthermore, Smith *et al*. (2011) found that infection rates in stands near White Calf Mountain (adjacent to Divide Mountain) were the second lowest among six treeline sites they sampled in Glacier National Park. The comparably low treeline infection rates at Divide Mountain is interesting considering that subalpine *P. albicaulis* communities of the Northern Divide Ecosystem consistently have the highest rate of blister rust infection yet found across the range of *P. albicaulis.* Further research is warranted to investigate why Divide Mountain has relatively low infection levels within a region with very high spore loads, but local factors such as wind direction and complex wind patterns (in addition to wind speed), and geographic variation in genetically resistant trees, may contribute.

Blister rust arrived somewhat later (in 1944 [Kendall & Asebrook, 1998]) in the GYE as compared to the Northern Divide Ecosystem (in 1938), as reported by Mielke (1943). Infection levels in the GYE remained low (0-1%) (Carlson, 1978) until the mid-90s when infection levels began to rapidly increase (Jean *et al*., 2011; Bockino & Tinker, 2012). Evidence exists for rapid intensification of blister rust infection in the GYE in the last twenty years, with 2-13% infection rates reported in the mid-90s (Kendall & Keane, 2001) and an overall 20% infection rate reported by 2007 (Jean *et al*., 2011).

Our overall blister rust infection rates for treeline in the Line Creek RNA (19.2%) compare well with the overall current infection rate for the GYE region (~20%). One possible explanation for the increase in current infection rates may be attributed to increased efforts in blister rust surveys, including surveys within GYE forests that had remained inaccessible in years past (e.g., Hatala *et al.*, 2011). The increase in blister rust in the GYE might also be attributed, at least in part, to climatic warming trends reported for western Montana (Pederson *et al*., 2010). Topography that creates conditions amenable to blister rust infection, combined with continued warming trends, could create favorable conditions for blister rust spore production and transmission, even at treeline.

We found that infection intensity is higher in tree island *P. albicaulis* than solitary *P. albicaulis* (Table III), which is a similar finding to our previous research studies (e.g., Resler & Tomback, 2008; Smith *et al*., 2011). Microclimates within tree islands (e.g., higher humidity) may favor blister rust spore development and infection. Van Arsdel (1965, 1972) noted higher blister rust infection of *P. strobus* trees within forest stand interiors, as opposed to edges—attributing higher blister rust spore development and infection transmission to cool and moist air currents within the stand. At treeline, the spatial clustering of trees within tree islands could similarly facilitate blister rust infection by increasing humidity, reducing ultraviolet light and wind exposure, sheltering alternate host plants, or creating local eddies which could circulate spores for infection transmission. Larger patch size (dimensions) of *P. albicaulis* tree islands have also been correlated with higher blister rust infection (Resler & Tomback, 2008; Franklin, 2011; Smith *et al*., 2011), and tree islands might provide a larger surface area for intercepting wind-borne *Cronartium ribicola* spores. These conditions and characteristics are also a function of the microtopography underlying these treeline communities, in terms of modifying abiotic conditions for growth, and influencing tree island spatial pattern and structure. In our study areas it appears that these conditions, characteristics, and the coexistence of host and alternate hosts, act in synergy to support blister rust disease in an otherwise harsh environment.

INFLUENTIAL TOPOGRAPHIC FACTORS

The topographic factors influencing blister rust presence and intensity on *P. albicaulis* differed between the treeline study areas (see final ZIP models, Table IV), which highlights the importance of meso- and micro- topography factors, in conjunction with climate, in determining blister rust infection. The Divide Mountain model suggests that if blister rust is present, *P. albicaulis* trees growing on surfaces with higher solar radiation exposure, that are farther from lakes, but proximal to ice, are likely to be infected with more cankers per tree than in areas without these characteristics. Solar radiation aids the development of blister rust in the cold climate of our treeline study areas. Though glaciers are quite far from our Divide Mountain plots (Table I), and lakes are closer, the sign of their influence is opposite (although both are hypothesized sources for moist air). These variables are probably surrogates for the broader influence of topography (and glaciers and lakes themselves) on wind. Wind is a major factor affecting both snow and tree distribution on exposed slopes in the ATE (Arno & Hammerly, 1984; Malanson *et al*., 2009), as well as the transportation of blister rust spores (Frank *et al*., 2008). Van Arsdel (1965) attributed higher blister rust intensity in *P. strobus* (eastern white pines) trees located on high ridges further from lakes to the role of wind for spore dispersal, which could also be true at Divide Mountain. In fact, the Divide Mountain plots are located ~7 km distance from and at an elevation ~900 m higher than the very large Saint Mary Lake (15.9 km^2 in area)—emphasizing the importance of topographic position, potentially for the interception of wind-dispersed blister rust spores.

The final model for Line Creek RNA uncovered more significant relationships between blister rust presence and intensity and topographic variables than did the Divide Mountain model. The model suggests that trees farther from glaciers are more likely to be infected with blister rust, and that infected *P. albicaulis* trees tend to have more cankers in areas closer to streams and lakes, with higher solar radiation, and concave surface curvature. Though glaciers and ice masses are closer to *P. albicaulis* trees at Line Creek RNA (Table I) compared with Divide Mountain, their influence probably has a similar surrogate explanation to that of the Divide Mountain model. The high and exposed topographic position of the Line Creek RNA treeline community may compensate for the far distances to moisture sources, a position potentially favorable for the interception of wind-dispersed blister rust spores. The relationship between canker intensity, and the variables concavity, and proximity to streams and lakes may indicate the combined importance of microtopography and surrounding moisture sources. Together, these features potentially provide the humidity and alternate host plant habitat necessary for blister rust transmission and infection in the Line Creek RNA study area, an area with more arid summers than Divide Mountain (PRISM, 2011).

Other researchers have found similar trends between fungal infection and moisture-associated topographic variables at varying scales. For example, Kearns and Jacobi (2007) examined stand-level relationships between blister rust and *P. flexilis* and found that plots located in concave areas where moisture or cold air collects (i.e., valley bottoms and foot slope positions) had higher infection rates than other topographic positions. Similar to our model findings, Wilds (1997) found that fine-scale concave topography and proximity to streams were significant moisture characteristics related to the severity of dogwood anthracnose fungal disease (caused by the fungus *Discula destructiva)*. In addition to moist conditions, concave microtopography potentially provides protective seedling microsites for *P. albicaulis* regeneration in the ATE. At a finer scale, the tendency of *P. albicaulis* to grow in protected microsites such as topographic depressions or leeward of rocks (Resler, Butler & Malanson, 2005) may also increase susceptibility to blister rust infection. Such microsites favoring seedling regeneration may also hinder *P. albicaulis* by providing moist conditions that increase the risk of fungal infections (Mellmann-Brown, 2005), such as blister rust, because depressions may also harbor abiotic conditions ideal for blister rust spore development. These combined conditions and processes may create “the perfect storm” for supporting the disease at treeline.

Conclusion

One major challenge for environmental change research is to understand how future vegetation changes will evolve in mountain ecosystems, where physiographic complexity creates highly variable environmental conditions over fine spatial scales (Shafer *et al*., 2005). The dynamics of pathogens, coupled with climate change, is likely to further complicate understandings of such vegetation change, particularly where keystone species are affected (Tomback & Resler, 2007). Our model results provide some insight (at a fine scale) as to where treeline patterns may be disrupted first by blister rust, in addition to climate change impacts. Between our two study areas, we found both differences and similarities in topographic and moisture-associated factors that influence blister rust infection of *P. albicaulis* trees, and so a landscape approach to uncover factors affecting forest disease (e.g., Holdenrieder *et al*., 2004) set in a geographic context with multiscale analyses is appropriate. The establishment of permanent plots at alpine treelines would facilitate understanding of the long-term consequences of blister rust on tree island development, in the context of treeline dynamics, particularly if combined with remote sensing and climate models in mountain areas. Identifying treelines with potential blister rust severity could aid restorative management applications (some of which are ongoing, e.g., Keane *et al.*, 2012), and might also aid proposed assisted migration (e.g., McLane & Aitken, 2012). For example, blister rust-resistant *P. albicaulis* seedlings could be planted to restore treeline ecosystems, as they are being used at subalpine elevations (e.g., Tomback & Achuff, 2010). Targeted efforts could mitigate the potential combined impact of blister rust and climate change on the treeline ecotone.

Acknowledgements

This study is based upon work supported by the National Science Foundation Geography and Spatial Sciences Program, Grant 808548. We thank Tara Carolin and the Crown of the Continent Research Learning Center of Glacier National Park, and Mark Magee and the Land Department of the Blackfeet Nation for working with us to obtain research permits for the Divide Mountain study area; Kent Houston, Shoshone National Forest and the Rocky Mountain Research Station for coordinating research permits for the Line Creek Research Natural Area; Lauren Franklin, Kathryn Prociv, Virginia Tech; Jill Pyatt and Sarah Blakeslee, University Colorado Denver for assistance in field and weather station logistics. We also thank the Laboratory for Interdisciplinary Statistical Analysis at Virginia Tech, as well as two anonymous reviewers, an Associate Editor, and a co-editor in Chief for their suggestions on this manuscript.

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TABLE I. Descriptive statistics for six potential variables input to each treeline model.

Divide Mountain (GNP)

Variable	Range	Mean ± *SD*[*]
Curvature (1·100 m^{-2})	-698.72 – 1295.78	0.85 ± 161.99
Solar Radiation (watt hours·m^{-2})	454 780 – 1 533 950	1 140 277 ± 221 029
Distance to Streams (m)	56 – 688	311 ± 166
Distance to Ice (m)	8898 – 12 534	11 422 ± 801
Distance to Lakes (m)	1853 – 2781	2209 ± 259
Distance to Marsh (m)	2469 – 4673	3532 ± 559

Line Creek RNA (Beartooth Plateau)

Variable	Range	Mean ± *SD*[*]
Curvature (1·100 m^{-2})	-1337.65 – 622.57	-4.91 ± 165.79
Solar Radiation (watt hours·m^{-2})	336 234 – 1 785 500	1 358 323 ± 271 740
Distance to Streams (m)	123 – 702	545 ± 128
Distance to Ice (m)	974 – 3077	1970 ± 530
Distance to Lakes (m)	1792 – 2887	2430 ± 326
Distance to Marsh (m)	3007 – 5107	4001 ± 528

[*] *SD*, one standard deviation

TABLE II. Bayesian Information Criterion ranking for zero-inflated Poisson regression model prediction variables.

Divide Mountain (GNP) treeline study area

Independent Variables	β[*]	γ[*]	BIC[†] criteria ranking (ranked lowest to highest)
Solar Radiation	0.3165[**]	-0.0040	1237.1
Distance to Lakes	0.1557[**]	-0.1881	1258.5
Distance to Ice	-0.0925[**]	-0.1442	1260.5
Distance to Streams	0.0607	0.1572	1265.4
Curvature	0.0912	-0.0941	1265.9
Distance to Marsh	0.0373	-0.0433	1268.9

Line Creek RNA (Beartooth Plateau) treeline study area

Independent Variables	β	γ	BIC criteria ranking (ranked lowest to highest)
Distance to Streams	-0.5162[**]	-0.4683[**]	957.9
Distance to Ice	0.4556[**]	0.4128[**]	1017.4
Distance to Marsh	0.4492[**]	0.4200[**]	1017.9
Distance to Lakes	-0.4537[**]	-0.3900[**]	1019.3
Solar Radiation	0.3644[**]	0.3951[**]	1061.4
Curvature	-0.1747[**]	0.2887	1085.6

[*] β, Poisson component parameter (test for canker intensity); γ, logistic component parameter (test for canker presence).

[†] Bayesian Information Criterion (BIC). Variables ranked in order of importance, based on BIC. Model parameters with low BIC values are better predictors than parameters with high BIC values.

[**] The parameter is significant at the 95% significant level. Parameters shown for the Poisson (β) and logistic (γ) components reflect the median values of the credible interval.

TABLE III. Tree and disease statistics for two treeline study areas, summarized by aspect category.

Divide Mountain (GNP)

Aspect:	**NE**	**SE**	**SW**	**NW**	***Totals***
Number of sampling plots	12	10	4	4	*30*
Number of sampled PIAL[*] (N)	*293*	*111*	*49*	*132*	*585*
Number of ***solitary*** *PIAL*	*157*	*55*	*15*	*42*	*269*
Number of ***tree island*** *PIAL*	*136*	*56*	*34*	*90*	*316*
% **Solitary** *PIAL*	53.6%	49.5%	30.6%	31.8%	*46.0%*
% **Tree island** *PIAL*	46.4%	50.5%	69.4%	68.2%	*54.0%*
Number of blister rust cankers found	256	160	26	63	*505*
Number of Infected *PIAL*	64	38	9	27	*138*
% Infected *PIAL*	21.8%	34.2%	18.4%	20.5%	*23.6%*
% Infected **solitary** *PIAL*	17.2%	21.8%	13.3%	11.9%	*17.1%*
% Infected **tree island** *PIAL*[†]	27.2%	46.4%	20.6%	24.4%	*29.1%*
Canker intensity (cankers per infected tree)	4.0	4.2	2.9	2.3	*3.7*
Canker intensity on **solitary** *PIAL*	2.0	2.6	1.0	1.8	*2.1*
Canker intensity on **tree island** *PIAL*	5.4	5.0	3.4	2.5	*4.4*

Line Creek RNA (Beartooth Plateau)

Aspect:	**NE**	**SE**	**SW**	**NW**	***Totals***
Number of sampling plots	14	8	4	4	*30*
Number of sampled *PIAL*[*] (N)	195	84	40	9	*328*
Number of **solitary** *PIAL*	103	63	18	7	*191*
Number of **tree island** *PIAL*	92	21	22	2	*137*
% **Solitary** *PIAL*	52.8%	75.0%	45.0%	77.8%	*58.2%*
% **Tree island** *PIAL*	47.2%	25.0%	55.0%	22.2%	*41.8%*
Number of blister rust cankers found	152	40	245	0	*437*
Number of Infected *PIAL*	31	14	18	0	*63*
% Infected *PIAL*	15.9%	16.7%	45.0%	0.0%	*19.2%*
% Infected **solitary** *PIAL*	11.7%	9.5%	44.4%	0.0%	*13.6%*
% Infected **tree island** *PIAL*[†]	20.7%	38.1%	45.5%	0.0%	*27.0%*
Canker intensity (cankers per infected tree)	4.9	2.9	13.6	0	*6.9*
Canker intensity on **solitary** *PIAL*	5.8	2.2	4.3	0	*4.5*
Canker intensity on **tree island** *PIAL*	4.4	3.4	21.1	0	*8.7*

[*] *PIAL: Pinus albicaulis*

[†] G-test of independence (Sokal and Rohlf, 1995) shows blister rust infection is significantly higher for *P. albicaulis* growing in tree islands as opposed to solitarily: Divide Mountain ($G = 11.85$, $df = 1$, $p < 0.001$; Line Creek RNA ($G = 9.11$, $df = 1$, $p < 0.01$).

TABLE IV. Results of final zero-inflated Poisson random effects models for Divide Mountain and Line Creek RNA treeline study areas. Significant parameter values are shown.

Divide Mountain Model	**β[*]**			**γ[*]**			
Variable	**Lower[†] (2.5%)**	**Median (50%)**	**Upper (97.5%)**	**Lower[†] (2.5%)**	**Median (50%)**	**Upper (97.5%)**	**BIC[‡] rank**
Intercept	1.0154	1.1313	1.2440	-1.3411	-1.1284	-0.9226	Most important
Solar Radiation	0.1870	0.3002	0.4087	-	-	-	
Distance to Lakes	0.1921	0.3218	0.4356	-0.4367	-0.2178	-0.0148	
Distance to Ice	-0.2435	-0.1632	-0.0782	-	-	-	
Distance to Streams	-	-	-	-	-	-	
Curvature	-	-	-	-	-	-	
Distance to Marsh	-	-	-	-	-	-	Least important

Line Creek RNA Model	**β**			**γ**			
Variable	**Lower (2.5%)**	**Median (50%)**	**Upper (97.5%)**	**Lower (2.5%)**	**Median (50%)**	**Upper (97.5%)**	**BIC rank**
Intercept	1.0273	1.2198	1.3855	-1.7145	-1.3750	-1.0623	Most important
Distance to Streams	-0.5016	-0.3966	-0.3024	-	-	-	
Distance to Ice	-	-	-	0.1373	0.4305	0.7390	
Distance to Marsh	-	-	-	-	-	-	
Distance to Lakes	-0.6800	-0.5162	-0.3587	-	-	-	
Solar Radiation	0.1256	0.2439	0.3727	-	-	-	
Curvature	-0.9244	-0.7103	-0.4938	0.2459	0.6931	1.2101	Least important

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[*] β, Poisson component parameter (test for canker intensity); γ, logistic component parameter (test for canker presence).

[†] Credible interval (2.5% - 97.5%) for β and γ. Significant parameter values are shown for credible interval ranges that do not overlap zero.

[‡] Best BIC results determined the final treeline models, variables are ranked in order of importance. Divide Mountain final model BIC=1221.8; Line Creek RNA final model BIC=907.1.

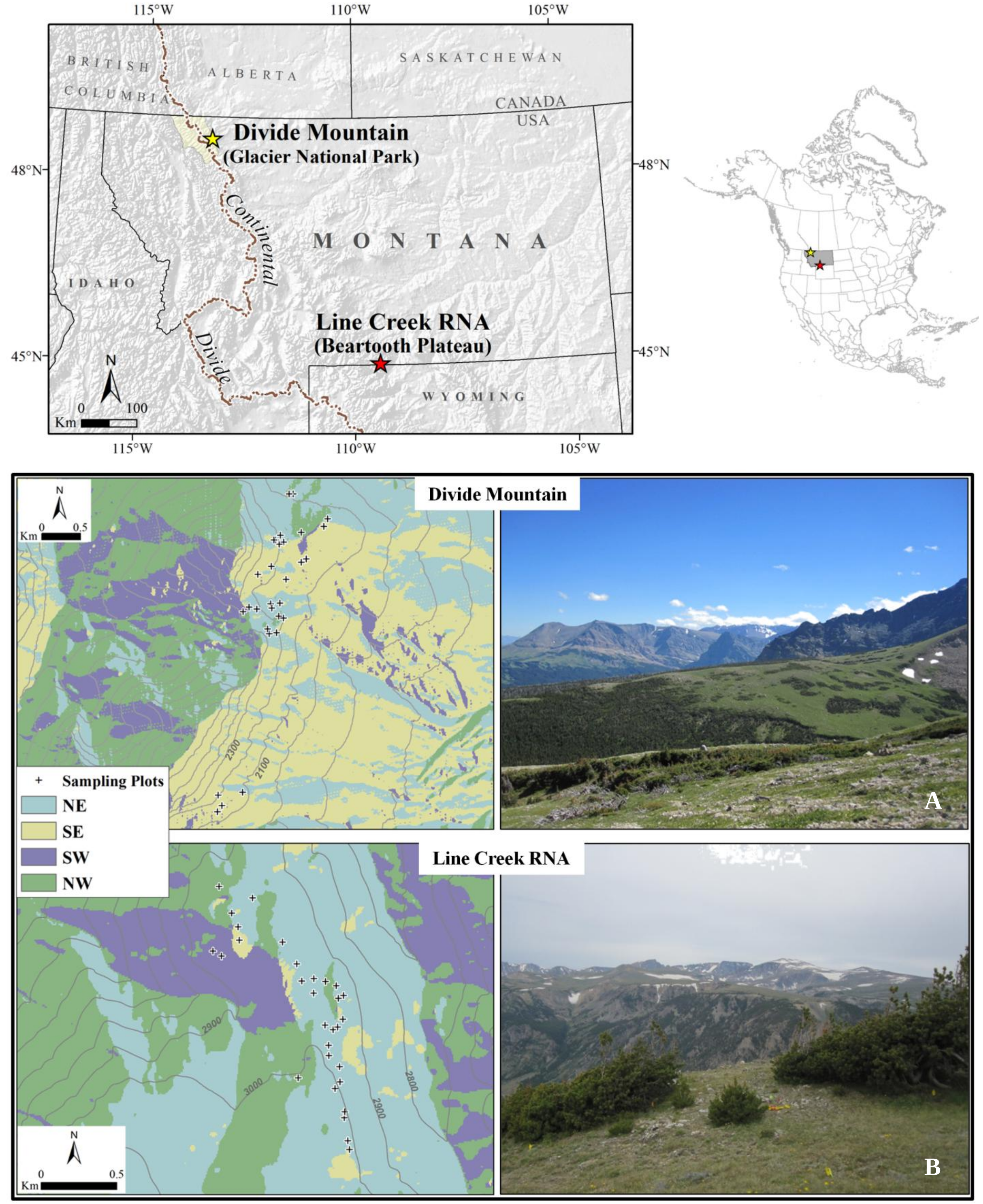

FIGURE 1. Location of two treeline study areas in the central and northern Rocky Mountains of Montana, USA. Detailed areas show sampling plot configuration in reference to the four aspect categories. Treeline photo (A) was taken at the base of Divide Mountain looking south, and treeline photo (B) in Line Creek RNA views north.

FIGURE 2. Example of (A) an inactive blister rust canker (cracked bark on upper stem, indicating past sporulation), and (B) an active canker lower on the stem (aecial sacs have burst, releasing a bright orange dusting of spores). The third canker class, potential (the beginning stage of a canker, exhibited by a swollen stem but no sporulation), is not shown (Hoff 1992).

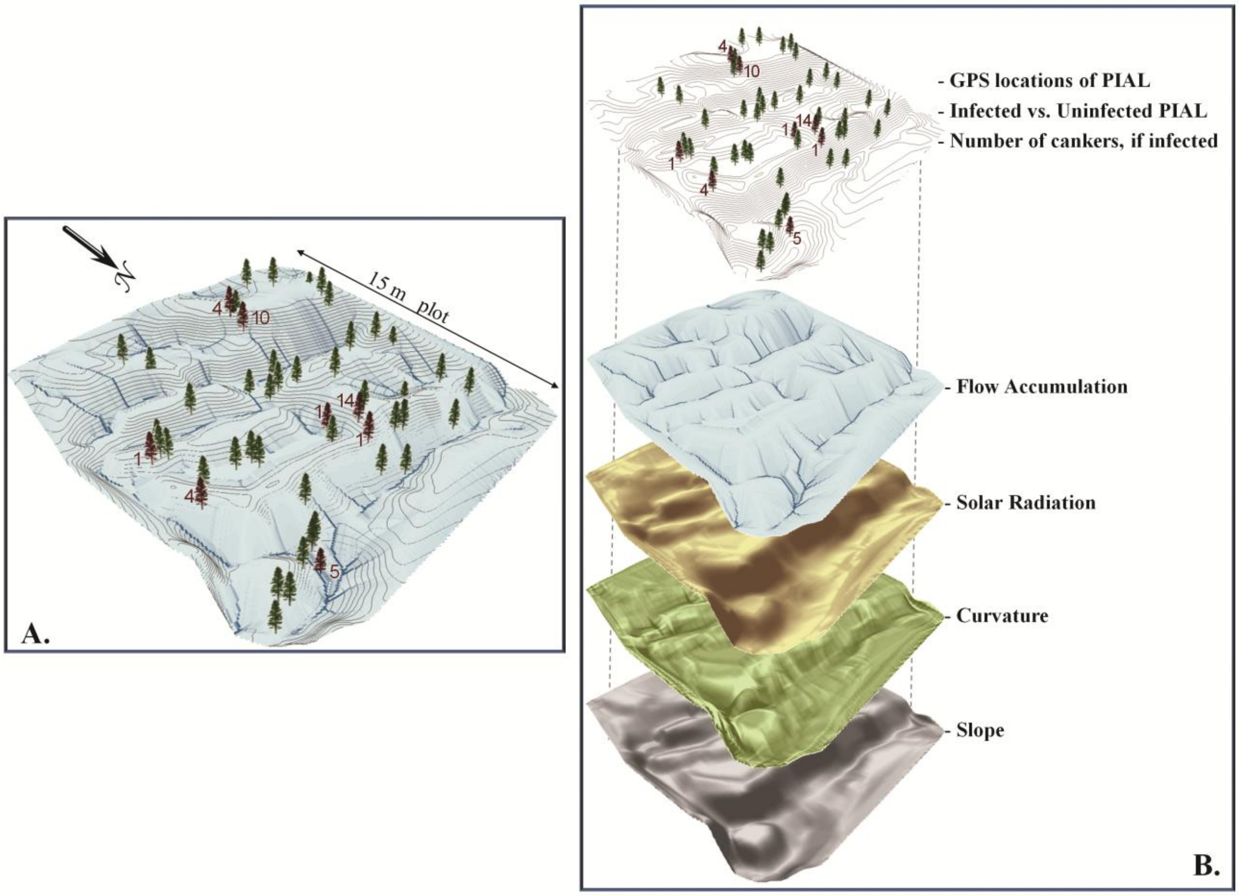

FIGURE 3. Examples of actual DEM microtopography variables and *P. albicaulis* (PIAL) tree spatial positions overlaid in a GIS. Maps are from sampling plot #15 in Glacier National Park. (A) 3D view of the mapped terrain within a 15 m x 15 m sampling plot, showing GPS positions of uninfected (green) and infected (red, noting canker count) trees relative to elevation contours, and flow accumulation (drainage) concentrations on the underlying surface. (B) Topographic raster values were extracted for each corresponding PIAL GPS location, to correlate with blister rust infection presence and intensity (number of cankers) for each tree. Microtopography variables are shown here, mesotopographic variables (distance to water features) extend beyond view, and are therefore not shown in this figure. The 3D maps were generated using ArcScene (v.10.1, ESRI, Redlands, CA, USA).

Chapter 4: Feedbacks, disease, and climate influences on whitebark pine treeline dynamics: An agent-based treeline model.

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In review: *Ecological Modelling*

ABSTRACT

Feedbacks influence the dynamics of high-stress alpine treeline ecosystems, and may have strong influence on treeline communities facing disease and climate change. We developed an agent-based model to examine the combined impacts of blister rust infected whitebark pine and climate change on treeline pattern and process. Model parameters related to biotic and physical processes were determined using a combination of empirical field experiments, data, observations, and literature review. We simulated a present-day-like whitebark pine treeline community in the northern U.S. Rocky Mountains alpine treeline ecotone and compared five hypothetical scenarios demonstrating differing levels of climate change and disease. Model simulations incorporated important feedbacks influencing whitebark pine treeline communities under relatively stable conditions, and under conditions of blister rust disease and climate amelioration. We compared changes in the populations and spatial patterns of species among scenarios. Modeled blister rust-induced pine mortality reduced pine populations despite the beneficial effects of climate amelioration, with little change in spruce/fir populations between the two climate and disease scenarios. Spatially clustered tree patterns may be due to the influence of facilitation processes in these simulated stressful environments in all scenarios except climate change alone. The dispersed patterns in this latter scenario resembled patterns of infilling and spreading of tree neighbors—likely due to the improved site quality conditions that promote tree establishment and growth. Facilitation processes proved important drivers in population dynamics, and our simulated treelines overall showed a negative response to climate amelioration when disease was introduced to the ecosystem. The influence from blister rust disease superseded that of climate, causing the decline of an important facilitator, whitebark pine. Model simulations reveal some key factors instrumental for understanding treeline response to global change.

Keywords:
agent-based model; alpine treeline ecotone; whitebark pine; white pine blister rust; climate change; facilitation.

1. Introduction

Forest ecosystems worldwide are increasingly subject to the interacting effects of multiple disturbance processes, which include climate change and pathogen invasions (Millar et al., 2007). The significant decline of whitebark pine (*Pinus albicaulis*) due to white pine blister rust (*Cronartium ribicola* (Uredinales: Cronartiaceae) (hereafter referred to as blister rust) and its consequences for forest ecosystems provide a compelling illustration of this problem. In forest ecosystems dependent on keystone species, such as whitebark pine treeline communities, there is a pressing need to understand the complex interactions between vegetation, disease, and climate change—because the combined impacts of disturbance and increasing temperatures on these fragile ecosystems are unknown (Tomback and Resler, 2007). Simulation modeling is one approach to understanding the potential impacts of such interactions. Here, we investigate a relatively underexplored area of research, using a simulation model to examine dynamics of whitebark pine treeline communities in response to the combined effects of climate change and blister rust. These communities represent ecosystems driven by complex interactions, and abiotic/biotic disturbances can have measureable consequences, in terms of ecosystem response to change (Hobbs et al., 2009). By examining these dynamics through spatially defined simulations, we thus contribute to much-needed research in spatially and ecologically complex systems (Agrawal et al., 2007). Our simulations demonstrate some key factors instrumental for understanding treeline response to global change.

1.1. Alpine Treeline

The alpine treeline ecotone (ATE) is a transition zone between upper elevation subalpine forest and treeless alpine tundra (Holtmeier, 2009). At the ATE, trees approach their physiological limits in the stressful high elevation environments, where factors such as high evapotranspiration, cold temperatures, and wind abrasion limit their growth (Arno and Hammerly, 1984; Hansen-Bristow et al., 1988; Körner and Paulsen, 2004; Holtmeier, 2009). In mountain environments a shift occurs in the function of neighbors; from competition in lower elevations to more facilitative processes at higher elevations (Callaway et al., 2002). Neighbors ameliorate abiotic stresses rather than compete for resources in alpine plant communities (Callaway et al., 2002; Brooker, 2006) and create positive interactions (Bertness and Callaway, 1994). This relationship holds true for neighboring conifer trees at the ATE—where the amelioration of abiotic stresses facilitates the establishment of additional surrounding trees. These interactions, coupled with the spatial availability of scarce resources necessary for growth (van der Valk and Warner, 2009) and sheltered sites (Resler et al., 2005), can create tree islands, often wind-shaped 'hedges', which result in a patchy vegetation pattern across the ATE landscape (Marr, 1977; Holtmeier, 1982).

1.2. Whitebark Pine and Tree Island Development

Research conducted in whitebark pine treeline communities east of the Rocky Mountain Continental Divide in Montana, USA, suggests whitebark pine plays a key role initiating tree islands because of its frequency in lead, windward positions relative to other species—where it shelters and facilitates conifers such as Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) (Resler and Tomback, 2008). Whitebark pine is both a foundation species in promoting forest structure (Ellison et al., 2005), and a keystone species by providing more ecosystem services than its abundance would suggest (Tomback et al., 2001). Whitebark pine is primarily dependent on Clark's nutcracker (*Nucifraga columbiana*) for seed dispersal and propagation (Tomback, 1982). Nutcrackers transport seeds from the subalpine and cache them near boulders or other natural landmarks (such as the base of trees or logs) in the ATE, enabling whitebark pine regeneration at treeline (Tomback and Linhart, 1990). Upon successful seed germination and seedling establishment, whitebark pine typically provides the foundation for tree island development in multi-species treeline communities (particularly in northern Montana treelines) (Resler and Tomback, 2008).

Widespread mortality of whitebark pine throughout western North American mountains, induced by multiple disturbances, is notably attributed to the invasive blister rust disease (Schwandt et al., 2010). *Cronartium ribicola*, the exotic fungal pathogen causing blister rust, is present in the dry and cold environments of the ATE and causes blister rust in high elevation whitebark pine, particularly east of the U.S. Rocky Mountain Continental Divide (Tomback and Resler, 2007; Resler and Tomback, 2008; Smith et al., 2011). Disease-induced mortality of whitebark pine is a potentially important negative feedback occurring in treeline systems given that the decline of whitebark pine may also reduce tree island initiation in the upper ATE (Tomback and Resler, 2007). From research examining treeline positions as bioclimatic indicators of climate change (Kupfer and Cairns, 1996; Körner and Paulsen, 2004; Smith et al., 2009; Harsch and Bader, 2011), and our current knowledge of whitebark pine's climatic niche in forest communities (Rehfeldt et al., 2006), current climate warming trends should advance whitebark pine above the current ATE. However, in blister rust-impacted treelines, the mortality of whitebark pine may confound interpretations of treeline positions—treelines that are responding to a changing climate and a disease-altered ecosystem (Tomback and Resler, 2007). Simulation models are useful tools for investigating possible alternative outcomes in such a system (e.g., Scuderi et al., 1993; Cairns and Malanson, 1998; Zeng and Malanson, 2006).

1.3. Agent-Based Modeling

Simulation models are often used to understand the response of forest species to climate change (Noble, 1993; Dullinger et al., 2004; Nitschke and Innes, 2008; Wallentin et al., 2008). Agent-based models (ABMs) (or 'individual-based models'), are a class of simulation models that use autonomous entities called 'agents' as the building blocks of complex systems (Bonabeau, 2002; Grimm and Railsback, 2005) and are effective in researching landscape dynamics in the context of ecosystem response to climate change, and human disturbance (Parker et al., 2003; Gibon et al., 2010). ABMs show emergent properties resulting from interactions of entities within a system (Bonabeau, 2002), uncover feedbacks between spatial pattern and process (e.g. Malanson et al., 2006) and reveal general principles underlying the internal organization of complex systems (Grimm et al., 2005).

ABMs are appropriate for studying the ATE system because they can simulate spatial patterns and processes of tree agents on landscapes based on a cellular automata (CA) framework. CA (or cellular models) are computer simulation models that use cell neighborhoods to represent a system's geographic domain (Tobler, 1979), such as a landscape, and apply local neighborhood associations among the cells to calculate dynamic response within the system (Malanson, 1999; Fonstad, 2006). In ABMs, agents can represent many ecological phenomena, and move within their cellular landscape based on neighborhood rules. The agents may interact with each other and their surrounding environment, which influence their dynamics. Modeling agents on a CA framework, where a lattice of cells represent the landscape and define an environmental gradient or discrete boundaries, is useful for analyzing the emerging dynamics at a landscape-scale (Travis et al., 2005; Malanson et al., 2006; Dunn and Majer, 2007). Some studies that have examined dynamics of ATE spatial patterns used cellular models to incorporate neighborhood (cellular) rules based on feedback patterns prominent in alpine systems (Malanson, 1997; Malanson et al., 2001; Alftine and Malanson, 2004; Zeng and Malanson, 2006; Diaz-Varela et al., 2010). Examining ATE landscapes as a grid of cells, on which tree agents establish and tree neighbors may build tree islands, elucidates feedbacks affecting the spatial patterns and processes of treeline populations.

1.4. Whitebark Pine Treeline Model

Our goal was to assess treeline response to potential impacts from climate change and disease, by simulating a whitebark pine treeline community in an ABM—built from our field data and observations in Rocky Mountain treelines (Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013; Smith-McKenna, unpublished data) and other findings from the literature. To examine dynamics of agent populations and patterns resulting from the ABM, and to understand the singular and combined effects of blister rust disease and climate change on whitebark pine treeline community dynamics, we implemented five scenarios in our simulations: 1) 'Untreated' (no disease or climate amelioration), 2) 'Disease', 3) 'Climate', 4) 'Climate and Disease', and 5) 'Accelerated Climate and Disease' (a worst-case scenario). From these scenarios, we observed the impacts of disease on conifer agent populations and clustering patterns (the formation of tree islands). We examined the change in treeline dynamics due to the combined influences of feedbacks, climate amelioration, and disease in a system dependent on a foundation and keystone species.

2. Methods

We developed an ABM to simulate a whitebark pine treeline community in the upper limits of the ATE, using field and literature-based data to inform the model (e.g., Figure 1). We incorporated positive feedbacks through cellular rules that allow neighboring conifers to ameliorate conditions and promote subsequent tree establishment. Our research has shown that in some northern Rocky Mountain treelines, sun and wind-tolerant whitebark pines (Arno and Hoff, 1989) facilitate relatively sun-intolerant subalpine fir and Engelmann spruce, promoting growth and development of tree islands under stressful conditions (Resler and Tomback, 2008). These three species dominated our sampled treeline populations and therefore served as agents in our model. We simulated climate change by ameliorating (improving) growing conditions for trees. We also assessed treeline response to the introduction of blister rust by incorporating negative feedbacks to the model (as cellular rules), based on our research findings that whitebark pine trees have slightly higher likelihoods of blister rust infection depending on proximity to tree islands, tree island size (Resler and Tomback, 2008), and proximity to moisture sources (Smith et al., 2011; Smith-McKenna et al., 2013).

We used Netlogo (v. 4.1.2) software (Wilensky, 1999) to develop a hypothetical landscape of the ATE and to simulate scenarios in an ABM. The description of this ABM follows the Overview, Design concepts, Details (ODD) protocol (Grimm et al., 2006, 2010) where appropriate.

2.1. Purpose

The purpose of this model is to understand the effects of an invasive pathogen on treeline dynamics in whitebark pine treeline communities and the combined effects of climate change.

2.2. Entities, state variables, and scales

Agents/individuals. The modeled treeline ecosystem consists of agents represented by main stems and branches of trees. For simplicity, our treeline agents reflect common associates of tree species found in whitebark pine treeline communities in the U.S. northern Rocky Mountains east of the Continental Divide (e.g., whitebark pine, Engelmann spruce, and subalpine fir). Our primary tree agent of interest is whitebark pine (hereafter referred to as pine), and a single tree agent represents spruce and fir (hereafter referred to as spruce). As trees age, their main stems grow branches, resulting in an expansion of tree agents from the stem into the surrounding cellular neighborhood. Agents include pine stems, pine branches, spruce stems, spruce branches, dead stems, and dead branches.

Patches/Environment. The modeled treeline is a spatially explicit ‘world’, as termed in Netlogo, consisting of 101 x 101 grid cells (X-Y coordinates: left bottom [0, 0], right bottom [100,0], left top [0,100], right top [100,100]). Netlogo uses the term ‘patch’ for each cell, contrary to use in landscape ecology, which defines a patch as a contiguous group of cells of the same state; therefore, we will use the landscape ecology definition and refer to the spatial units in Netlogo as cells. These 101 x 101 cells represent a hypothetical slope within the ATE in which elevation increases as the y-coordinate increases. Along the y-axis (increasing elevation) the quality of the cell decreases. We termed this ‘site quality’ to reflect the potential for tree establishment, which thus becomes more difficult with increasing elevation. The quality of the slope is assigned a non-linear inverse relationship with the cell y-coordinate, so that the site quality of the cell decreases with increasing y-coordinate location (Equation 1).

$$\textit{Cell Site Quality} = \frac{1}{(\textit{Cell y-coordinate}) + 1} \qquad [1]$$

State variables. Tree agents grow and die resulting from rules governed by the following state variables: initial starting population and random placement of pine and spruce, initial microtopography characteristics and random boulder assignments, facilitation strength of surrounding trees that provide shelter (stronger protection from an eastward wind), probability of seed production and seedling establishment, and probability of branch growth and tree mortality. Netlogo sliders on the model's interface control parameter values—which are dimensionless, unitless, and affect a parameter's probability by setting thresholds for randomly generated numbers (Table 1). Parameter settings are held constant throughout the simulations, with the only exception being the climate and disease settings. The disease and climate scenarios implement blister rust infection potential among pine, and an increase in site quality (respectively); details are addressed in the 'Simulation Experiments' section.

Spatial and Temporal scale. A cell can be occupied by only one type of tree agent, regardless of the cell characteristics. We classify cells unoccupied by tree agents as tundra. One time step represents one growing year, and model simulations were run 500 – 800 years from the initial setup. The length of model runs were determined in order to allow time to populate the model similar to a "present-day" treeline community, to implement treatments, and to observe change in the system.

2.3. Process overview and scheduling

Conceptual relations of the following model processes are outlined in Equations 2-6 (note: ***P***=probability*;* ***f***=function). Figure 2 illustrates these conceptual relationships and general flow of the treeline simulation model and treatment scenarios.

Initial Setup. At the initial setup of the model, the microtopographic sheltering potential of every cell is randomly assigned across the ATE slope—cells with highest potential are assigned a virtual boulder. Boulders cover less than 1% of the slope (~60-80 boulders), an approximate frequency from our field observations. Boulders provide shelter to trees (Resler et al., 2005), and therefore we assigned cells adjacent to boulders to be especially favorable for initial pine establishment, because boulders ameliorate site quality conditions—improving microclimates that increase pine establishment potential. This rule mimics the pine seed caching behavior of Clark's nutcracker and its preference for caching near natural landmarks (Tomback, 1982). A stream is assigned to the leftmost column of the ATE landscape solely for the purpose of the disease infection simulations. Initially the landscape is populated by pine and spruce tree agents, the proportions of pine/spruce range from 70/30 to 75/25 percent (comparable to our sampled populations, e.g., Smith-McKenna, unpublished data; Smith-McKenna et al., 2013), with anywhere from 450-500 initial tree agents randomly assigned across the landscape. The initiating tree agents are randomly aged from 50-99 years old, to represent trees with seed-producing potential, and to initiate seed production in the model.

$$\boldsymbol{P}(\textit{Tree initiation}) = \boldsymbol{f}\,(\textit{boulder location, site quality}) \qquad [2]$$

Seed Production and Placement. After the intial setup, and with each discrete time step (representing one year), tree agents potentially produce seed according to approximate ages and seed cone production in the literature (Uchytil, 1991; Lanner, 2000; Fryer, 2002). Though seed production age varies, in subalpine communities the minimum age of whitebark pine seed production is ~20 years old, and spruce older than 20 years produce seed (Lanner, 2000). As elevation increases from subalpine to alpine, the stressful ATE environment likely delays seed production age, therefore we assigned seed-producing potential to tree agents 50 years and older. The probability of seed production increases with site quality, facilitation, and healthy trees. A higher probability for pine seed placement and growth occurs east of boulders (sheltered from an eastward wind), where seeds may germinate and establish. Spruce agents have higher seed producing-potential than pine agents. Though seed placement is random in the model, seeds have higher probabilities of germinating tree agent seedlings if placed on cells with higher site quality and facilitation potential.

$$\boldsymbol{P}(\mathit{Seeding}) = \quad \boldsymbol{f}\,(\mathit{healthy\ tree,\ age} > 50\mathit{,\ site\ quality,\ facilitation}) \qquad [3]$$

Growth. With each timestep, a tree agent ages one year, and after 10 years it potentially grows branches into adjacent unoccupied cells within its 8-cell neighborhood. Tree growth is very slow in the ATE (Arno and Hammerly, 1984), and since seedlings younger than 10 years have very low survivorship (Germino et al., 2002; Maher and Germino, 2006), it seemed logical to allow trees older than 10 years to grow branches. Trees have more potential growth in cells with higher site quality and facilitation. Pine agents grow faster relative to spruce agents, reflecting growth trends in the literature (Uchytil, 1991; Fryer, 2002; Blakeslee, 2012).

$$\begin{aligned} \boldsymbol{P}(\mathit{Growth}) &= \quad \boldsymbol{f}\,(\mathit{site\ quality,\ facilitation}) \\ \boldsymbol{P}(\mathit{Branch}_{\mathit{Growth}}) &= \quad \boldsymbol{f}\,(\mathit{tree\ age} > 10\mathit{,\ site\ quality,\ facilitation}) \end{aligned} \qquad [4]$$

Feedback. Facilitation is implemented through positive feedback procedures, which promote tree agent growth (both stem and branch). A tree agent receives the most positive facilitative effects when other agents occupy half its surrounding 8-cell neighborhood. This rule follows Zeng and Malanson's (2006) probability of establishment formula (Equation 5), which incorporates the sheltering potential and tree-occupied neighborhood density so that competition counteracts facilitation at high density:

$$P_e = \frac{\alpha}{1 + \beta e^{-\gamma(x - x^2)}} \qquad [5]$$

Variables represent: α, facilitative strength; β, 150; γ, 20; and x, proportion of tree-occupied neighbors that reflects tree density. To impart an eastward-moving wind, the probability of establishment on a cell is slightly increased when a tree agent occupies a neighboring cell to the west.

Mortality. Tree agent mortality depends on its age, the host cell conditions, and surrounding agents or boulders that ameliorate microclimates. Seedlings and old trees have the highest mortality rates. Tree seedlings aged <10 have low survival due to the harsh conditions of the ATE (Germino et al., 2002; Maher and Germino, 2006). We defined old trees as those past peak cone production years, ~350 years for pine (e.g., Morgan and Bunting, 1990; Fryer, 2002) and ~200 years for spruce (Uchytil, 1991). Though mortality potential increases, many tree agents live beyond these ages. When stems (trunks or boles) die, their branches also die, but branch death does not affect stems (branches are pruned). Dead trees often provide shelter for young conifer seedlings that can eventually grow and spread over the remains of the dead tree (Smith-McKenna, personal observation). Therefore in the model, once trees and their branches die, they remain briefly on the landscape (~5 years before branches fall off, stems last ~10 years); this provides facilitation effects from neighboring dead trees, and frees up cell space to be occupied by new tree agents. Blister rust-induced mortality of pine agents is another cause of death, and infection procedures and rules are detailed in the simulated experiments section discussing the disease scenarios.

$$\boldsymbol{P}(Mortality) = \boldsymbol{f}\,(age, site\ quality, facilitation, disease) \qquad [6]$$

2.4. Design Concepts

Basic Principles. Positive and negative feedback mechanisms underlie this model's design. For example, positive feedback mechanisms, resulting from neighboring trees and the facilitation benefits they provide, promote tree establishment and branch growth in the harsh ATE climate. Facilitative strength combines with site quality conditions to influence growth. Concurrently, negative feedbacks resulting from a pine agents' proximity to neighboring trees may increase the chance of blister rust infection and death among pine agents (discussed further in the 'Simulation Experiments' section).

Emergence. The resulting model population dynamics emerge from feedback mechanisms between individual tree agents and the influential environmental characteristics of the host cell. The quality of the cell affects a tree agent's probability for establishment, survival, and reproduction. For example, in poor site quality conditions, facilitation influences the spatiotemporal patterns of tree agents by promoting tree establishment and growth, producing clustered patterns. Tree agents that establish near a boulder, or just have high survivability, may shelter other tree agents and form tree islands (a notable emergent property found in the ATE) (Resler and Tomback, 2008). The local feedback creates landscape-level relations of process and pattern (Zeng and Malanson, 2006; Bader et al., 2008).

Stochasticity. All parameters discussed in the ‘State Variables’ section (aside from quality and facilitation) are based on probability and utilize Netlogo’s random-number generator (Table 1).

Observation. We generated dynamic population plots and monitors in the model’s interface to aid with simulation and output. All model parameter values, agent and cell counts, infection rate and pine agent characteristics recorded at each time step, were exported from the model’s interface after each simulation. Population data and agent/cell spatial locations were analyzed using statistical and GIS programs.

2.5. Initialization

Initial values set at time $t = 0$ of the simulation runs are based on parameter values detailed in the ‘State Variables’ section. We parameterized a baseline treeline model by using starting populations and proportions of species and tree cover empirically determined from our research, and detailed in the ‘Initial Setup’ section.

2.6. Submodels

We created a baseline treeline model to represent ‘present-day’ like conditions (in terms of pattern, proportion, and composition of trees), based on our field observations and data (Fig. 1) (Smith et al., 2011; Smith-McKenna et al., 2013). Once present-day like conditions were achieved through parameterization and sensitivity analyses, parameters and conditions were held constant for the baseline simulations. We created 30 replicates of the baseline model, in which each initial setup determined random spatial placements of agents and boulders; these were then run for 500 years. Each of the 30 replicates essentially represents a hypothetical field plot of data, similar to the sampling methodology utilized in our field studies. We used the same 30 baseline replicates at year 500 to start five experimental treatments.

2.7. Simulation Experiments

We ran five treatments to compare whitebark pine, spruce, and tundra populations (agent and cell counts) and their spatial patterns. Treatments represented the following scenarios: 1) Untreated treeline (no disease or climate amelioration); 2) Introduction of disease; 3) Introduction of climate change (climate amelioration); 4) Introduction of both climate change and disease; and 5) Climate change accelerated disease. We initiated each treatment with the baseline replicates, running the model an additional 300 years for a total of 150 simulations.

The ‘Disease’ scenarios incorporate blister rust infection rules by assigning infection probabilities to pine agents with the disease virulence parameter. We implemented these infection rules based on our observed infection rates and spatial correlates to infection (e.g. Smith et al., 2011; Smith-McKenna et al., 2013), and other studies that determined infection severity ratings and timing of death due to both canker numbers and their location on the pine tree (Hunt, 1983; Six and Newcomb, 2005; Hatala et al., 2011). Pine agents can become infected with one canker each year. As cankers infect and accumulate on pine agents over time, chance of death increases. While branch cankers cause dieback (pruned branches), stem cankers result in death. Additionally, whitebark pine trees located near moisture sources such as streams have a higher likelihood of blister rust infection. Therefore, we placed a stream within the model’s leftmost cells, and created a rule that pines within a 10 cell distance from the stream had higher infection potential. We also incorporated our findings of higher blister rust incidence among whitebark pine trees growing in tree islands by implementing a rule that increased a pine agent's infection potential if adjacent to other tree agents within its 8-cell neighborhood.

The 'Climate' scenarios implement climate amelioration by increasing each cell's site quality condition on the modeled treeline slope, with the climate multiplier parameter (Table 1). The increase in site quality promotes tree establishment, growth, and survival. Treelines vary in their response to climate amelioration (depending on their latitude, tree species composition, and mountain range), and may result in an abrupt treeline advance (Elliott, 2012), or the response may be less apparent. We applied a rate of quality amelioration to simulate slight increases of tree infilling (3-4%) over 50 years, rather than an upslope advance of closed forest. We chose this rate of increase based on previous treeline studies that examined rate of change within ATEs using aerial repeat photography and dendrochronology (Butler et al., 1994; Klasner and Fagre, 2002; Alftine et al., 2003). These studies noted that treeline changes resemble increased density of existing patches or patchy advance in tree islands, rather than a broad-scale advance of contiguous forest.

We implemented both 'Disease' and 'Climate' scenarios independently by setting the disease virulence (0.04), and climate multiplier (1.003) parameters constant (Table 1) during simulation runs. The two combined 'Climate and Disease' treatment scenarios varied slightly. The fourth treatment holds disease and climate parameters constant. The fifth treatment holds the climate multiplier constant, but accelerates the disease virulence parameter at the rate site quality increases with each time step. This fifth treatment represents a hypothetical 'worst-case' scenario, in which blister rust infection increases as climate improves for trees.

We compared the final outcome of each model treatment simulation, for each of the 30 replicates, at the end of the 300 year treatment runs (a total of 800 time steps since time $t = 0$).

We analyzed population trends and spatial patterns of agents using JMP® (version 9.2, SAS Institute Inc., Cary, NC, USA), and ArcGIS (v. 9.3.1, ESRI, Redlands, CA, USA), respectively, and compared results among the five treatments. We tested these data for normality and homoscedasticity, and they do not violate assumptions of the analysis of variance (ANOVA).

3. Results

3.1. Population Dynamics of Treeline Model Scenarios

We examined population dynamics of pine and spruce agents in our simulated treelines by comparing results among the four treated scenarios with the 'Untreated' scenario. The 'Untreated' scenario represents a hypothetical treeline ecotone growing under relatively stable conditions (i.e., no disease or climate change) and provides a benchmark for comparison. Table 2 shows basic statistics for the proportion of remaining pine agents during the baseline (year 500) and final simulation year (year 800) for each of the model scenarios. Population values of pine, spruce, and tundra (cells unoccupied by trees) for each of the 30 replicates under the five scenarios at the final simulation year are shown in Figure 3. Figure 4 provides an example of the simulated population trends through time (year 500-800) using model replicate #11, which is most comparable to the means of all scenarios.

Populations of agents and proportions of tree cover versus tundra varied among the scenarios. Tree cover includes cells occupied by tree stems and branches, and empty cells represent tundra. Compared to the 'Untreated' scenario, the 'Disease' scenario resulted in a population decline of pine agents, and an increase in spruce agents. On average the number of pine agents decreased by 80% (Table 2), and though vacated cells (available habitat) boosted spruce populations, the overall amount of tundra increased (Fig. 3). The impact of infected pines on the dynamics of pine and spruce populations is noticeable around simulated year 600 (100 years after infection is introduced), which appears to be the threshold at which spruce outnumber pine (Fig. 4).

In the 'Climate' scenario, both pine and spruce populations increased when site quality conditions improved, and trees advanced to higher elevations (higher y-coordinates) into previous tundra cells (Fig. 3). This scenario's ameliorated conditions boosted pine agent numbers by 28.8% (Table 2), and both tree populations gradually increased as tundra concurrently declined (Fig. 4).

The 'Climate+Disease' scenario reveals that mortality from blister rust reduces pine populations (61.4%) despite improved site quality conditions and both the spruce populations and tundra increase. The threshold of change from dominating pine agents to spruce appears around year 630. The 'Accelerated Climate+Disease' scenario shows similar population trends to that of the fourth scenario, except the decline in pine agents (73.7%) is exacerbated by the increased infection rate—benefitting a growing population of spruce. The threshold of this change in dominance (from pine to spruce) appears sooner than that of the fourth scenario, occurring just after simulation year 600.

3.2. Population Statistics of Treeline Model Scenarios

Two statistical tests revealed differences in the observed number of pine agents and proportions of pine/spruce/tundra (response) within each scenario (factor). A one-way analysis of variance (ANOVA) comparing pine agent populations among the five scenarios (Fig. 5) revealed a statistically significant difference in averages among scenarios ($F(4,145) = 3804.432$, $p < 0.0001$). A two-way ANOVA comparing model results of pine/spruce/tundra proportions (Fig. 6), showed that most treatment/type combinations have statistically significant differences among the means ($F(14,435) = 8204.088$, $p < 0.0001$). The only exceptions are that the percent spruce agents resulting from simulation scenarios 'Climate+Disease' and 'Accelerated Climate+Disease' are not significantly different (Tukey-Kramer test, $p < 0.05$). There were no significant differences between pine agent percentage in the 'Climate+Disease' scenario and percent spruce in the 'Untreated' scenario (Tukey-Kramer test, $p < 0.05$).

3.3. Spatial Pattern of Treeline Model Scenarios

We compared spatial patterns of tree agents, particularly clusters that form tree islands, to determine change in tree island formation among the five scenarios (Figs. 7-8). We selected model replicate #11, which is most comparable to the means of all simulation runs, and used ArcGIS spatial statistics to calculate average nearest neighbor indices and determine clustering trends of all agents for each scenario. All scenarios produced a landscape with closed canopy trees near the bottom of the ATE slope, therefore we examined clustering trends near the upper slope of the simulated ATE by narrowing our analysis to cell y-coordinates greater than 50.

While all scenarios exhibited some form of tree clustering and obvious patterns of tree island formation, all scenarios aside from 'Climate' produced statistically significant clustered patterns. Scenarios 1, 2, 4, and 5 showed less than 1% likelihood that the clustered patterns could be the result of random chance (nearest neighbor ratios ranged 0.82 to 0.9, and Z-scores ranged -4.32 to -5.08, $p < 0.01$). 'Climate' scenario 3 differed from others by showing a spatial pattern trending towards dispersion, with less than 1% likelihood that the dispersed pattern could be the result of random chance (nearest neighbor ratio = 1.06, Z-score = 4, $p < 0.01$). Trees became more dispersed with the introduction of climate amelioration alone, a pattern potentially indicating competition.

4. Discussion

Our results indicate similarities in spruce populations between the two Climate and Disease scenarios, as well as similarities in pine populations between the 'Climate+Disease' scenario and spruce populations in the 'Untreated' scenario. Additionally, we found dispersed spatial patterns of trees under ameliorated conditions in the 'Climate' scenario. The population analyses of all three disease scenarios reveal that the blister rust-induced mortality of pine caused a dynamic wherein pine and spruce populations shifted dominance.

Overall, both tree agent populations increased in the 'Climate' scenario in which site quality conditions favor tree establishment—a logical outcome given the neighborhood rules that implement positive effects from site quality and facilitation from neighboring trees. The population decline of pine agents from disease was another logical outcome, but the effect of this decline on spruce was uncertain. For example, spruce proportions show little change between the 'Climate+Disease' and 'Accelerated Climate+Disease' scenarios, which had more impact on pine populations. This balance, coupled with the fact that pine populations in the 'Climate+Disease' scenario are similar to spruce populations in the 'Untreated' scenario, indicates that blister rust mortality reduces pine populations comparable to that of spruce under relatively stable conditions despite the growth potential under climate amelioration. Pine, which was dominant in the 'Untreated' scenario, declines when improved site quality and disease are introduced simultaneously. Pine's mortality from disease appears to free up cells for occupancy by spruce agents, but only to a point. Although disease reduces competition from pine, the decline in pine agents also reduces its lead role in providing shelter and facilitation for spruce. In terms of the modeled population dynamics, facilitation feedbacks appear more influential in these scenarios than resource availability—a simplistic interpretation perhaps, but still an important notion studied in both real (DeAngelis et al.,1986; Tilman, 1985; Wilson and Agnew, 1992; Bekker, 2005; Brooker, 2006) and simulated systems (Malanson, 1997; Malanson et al., 2001; Alftine and Malanson, 2004; Travis et al., 2005; Bader et al., 2008).

Each model scenario produced some degree of clustering and formation of tree islands with increasing elevation (y-coordinate) during model simulations. These observations align with findings that positive plant interactions and feedbacks drive clustered tree patterns at ATEs (Elliott, 2011), and that facilitation surpasses competition in community development within harsh abiotic conditions (Bertness and Callaway, 1994), such as those at alpine treeline (Bader et al., 2008; Elliott and Kipfmueller, 2010). A similarly focused individual-based model (Travis et al., 2005) showed that positive interactions allow species to coexist in their harsh modeled environment, and their model results support other findings that facilitation extends a species' realized niche (Bruno et al., 2003). These patterns align with the concepts that facilitation increases with stress in the physical environment—and in the case of our model, with increasing elevation and poor site quality conditions in the ATE (Callaway et al., 2002; Maestre et al., 2009). However, the 'Climate' scenario trended towards dispersed tree patterns, and this may be attributed to climate amelioration and its relative effects on neighborhood facilitation versus site quality—when site quality improved tree agents tended to infill and spread out, even to higher elevations of the modeled slope. When we simulate climate amelioration in the model, it appears that areas of highest abiotic stress (in the upper slope) subside, and concurrently, facilitative processes diminish. The resulting dispersion under improved site conditions (less stress) also suggests a switch from facilitation to competition. When climate improves and site quality becomes less stressful, positive feedbacks between neighbors are not as important as they once were—agents may compete for available space that was previously limited to them. This result supports concepts of the stress gradient hypothesis (Maestre et al., 2009), in which neighbor facilitation is inversely related to competition along gradients of physical stress—where the physical environment becomes more benign, positive feedback from neighbors recedes and competitive interactions ensue (Bertness and Callaway, 1994).

Our simulations show how blister rust disease and resulting whitebark pine mortality could affect the population dynamics of whitebark pine treeline communities. Modeled treelines showed an unfavorable response (limited growth) to the simulated climate change when disease was introduced. Rather than one tree species replacing the ranks of the other, all tree populations declined when whitebark pine was infected and killed from blister rust disease. These model results illustrate the potential dynamics of whitebark pine and tree island development, and support the notion that blister rust-induced mortality of pines will likely be detrimental to other treeline conifers. Under these scenarios, whitebark pine-dominated treelines may not advance upslope (or may lag) in response to climate warming, as proposed by Tomback and Resler (2007).

5. Conclusion

The ABM presented here provides a simplistic view of a complex ecosystem. It is a simplified landscape consisting of two tree species, tundra, and a few key environmental factors in the ATE—supporting interactions that produce a complex adaptive system that provides a platform for observing emergent phenomena (Malanson, 1999). Using simple processes to model a complex system such as a whitebark pine treeline ecosystem provides intrinsic value for understanding how the system emerges, and the interconnectedness of its patterns and processes.

Alpine treelines, particularly in the Rocky Mountains, are fragile systems sensitive to climate change—and revered for their scenic and recreational value (Fagre, 2009). Our research suggests that treelines with whitebark pine will likely differ in composition and function in the future, due to pine mortality from blister rust. Conservation managers (e.g., resource managers of National Parks, and National Forests) can utilize this information for research and teaching purposes, to both understand climate change effects, and explain the dynamics and their complications to an interested public. Enhancing public awareness can change attitudes about climate change and its effects. Knowing the potential ecosystem changes (e.g., impacts from climate, disease, and/or insect outbreaks), allows managers to plan for transitions in high-elevation forests (Millar et al., 2007, 2012; Larson, 2011). For example, McLane and Aitken (2012) suggest a more direct response to climate change: they have assessed aspects of assisted migration for whitebark pine in the Rocky Mountains. Our simulations show that vegetation-climate-disease interactions complicate ecosystem processes—posing management concerns for those systems dependent on keystone species, particularly whitebark pine treeline communities. Further development of our model could pinpoint where climate and disease interactions will be most problematic or where assisted migration would be most successful. Conservation and management efforts will need to begin with a simple view of the multidimensional problem while new research shores up the gaps in our knowledge. Simulation models can help in both areas.

Acknowledgements

This material is based upon work supported by the National Science Foundation under Grant No. 808548. We thank the Laboratory for Interdisciplinary Statistical Analysis at Virginia Tech.

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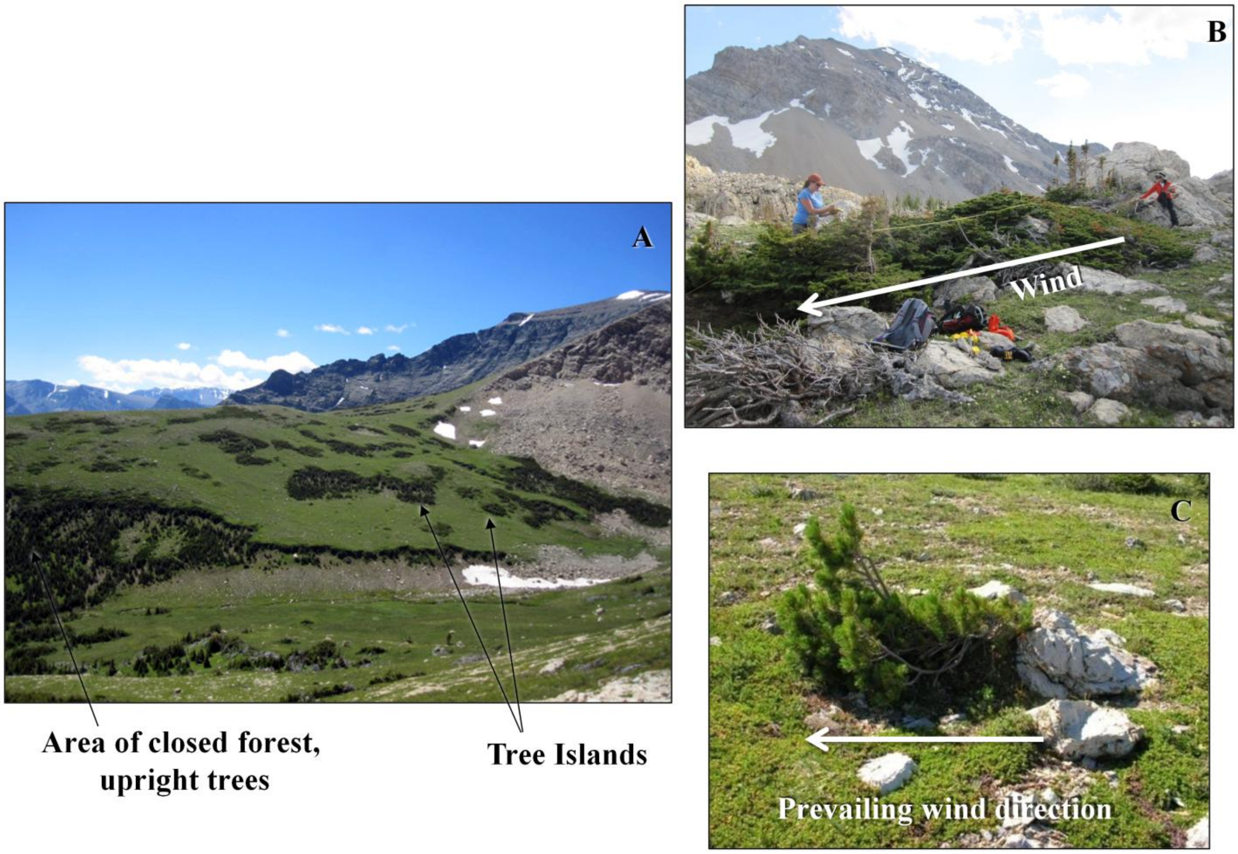


Figure 1. An alpine treeline ecotone in Glacier National Park, Montana, USA. (A) An example of tree islands in a whitebark pine treeline community. (B) Treeline team measuring % tree species coverage in tree island. Neighboring conifer trees help ameliorate conditions in the harsh alpine treeline ecotone, and can form expansive tree islands. (C) A krummholz whitebark pine tree growing in the lee of a boulder, sheltered from the wind.

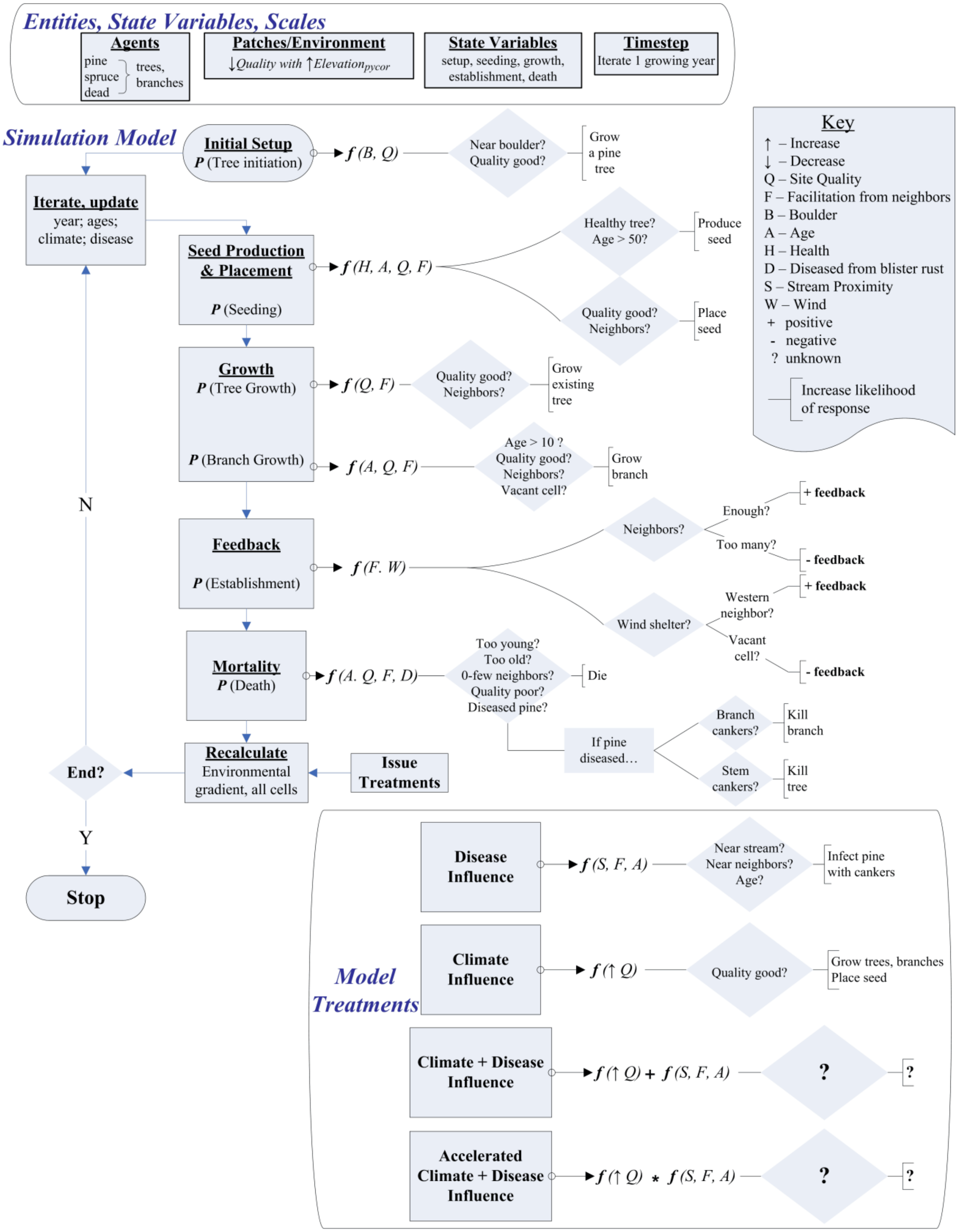


Figure 2. Conceptual flow diagram of the treeline agent-based model to illustrate the general model processes and the treatment scenarios. The probability of an action or response occurring, is a function of key factors (note: ***P***=probability*;* ***f***=function). A 'Yes' outcome to the conceptual

tests results in an increased likelihood of the given response (i.e., growth, death), a ‘No’ outcome does not increase these likelihoods. Note, the conceptual relations of the four treatment scenarios are shown, the untreated scenario follows that of the conceptual flow outlined in the ‘Simulation Model’ and does not include impacts of climate and disease.

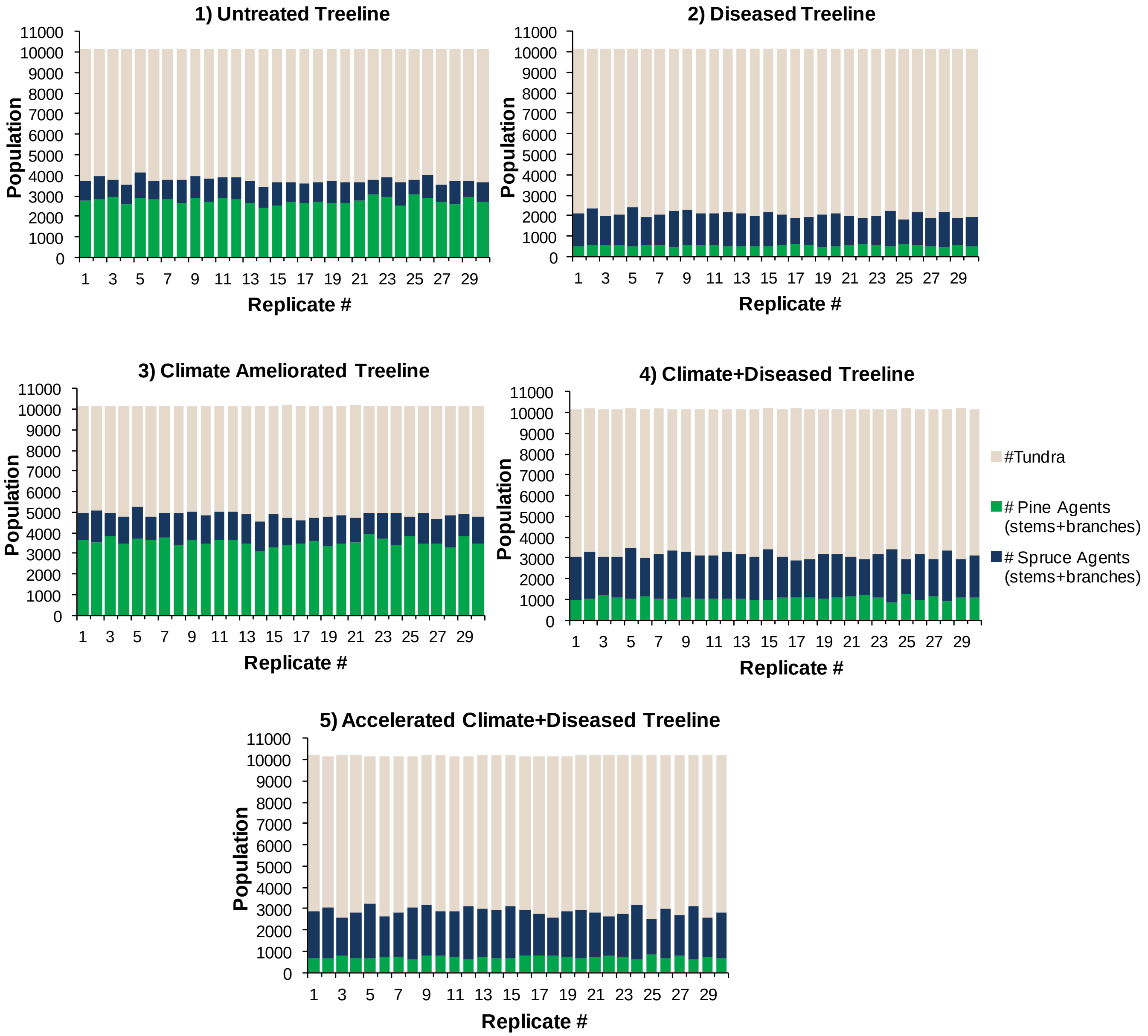


Figure 3. Histograms showing population comparisons among the 30 replicates, for each of the five scenarios. Populations reflect the final simulation year 800.

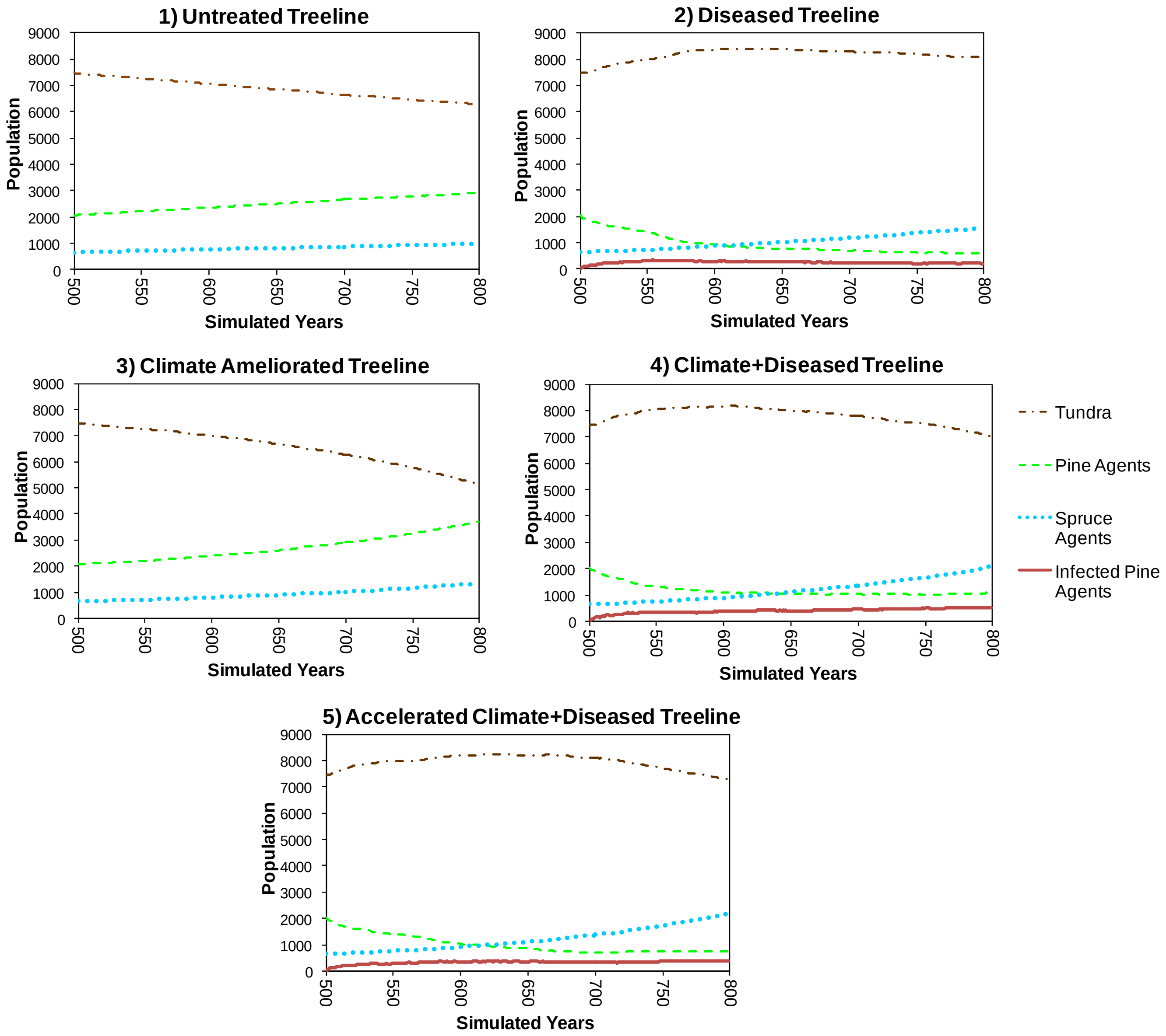
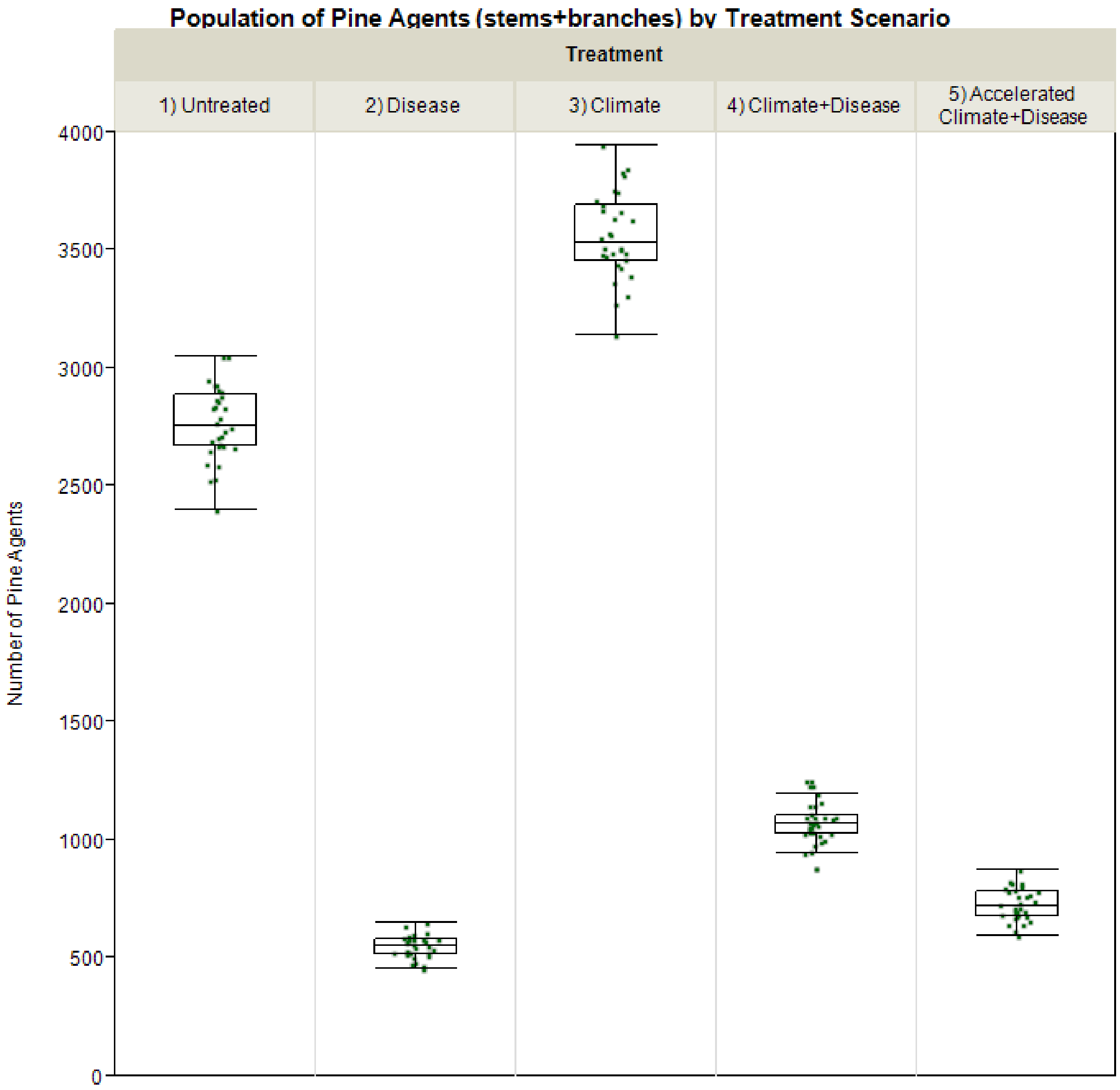


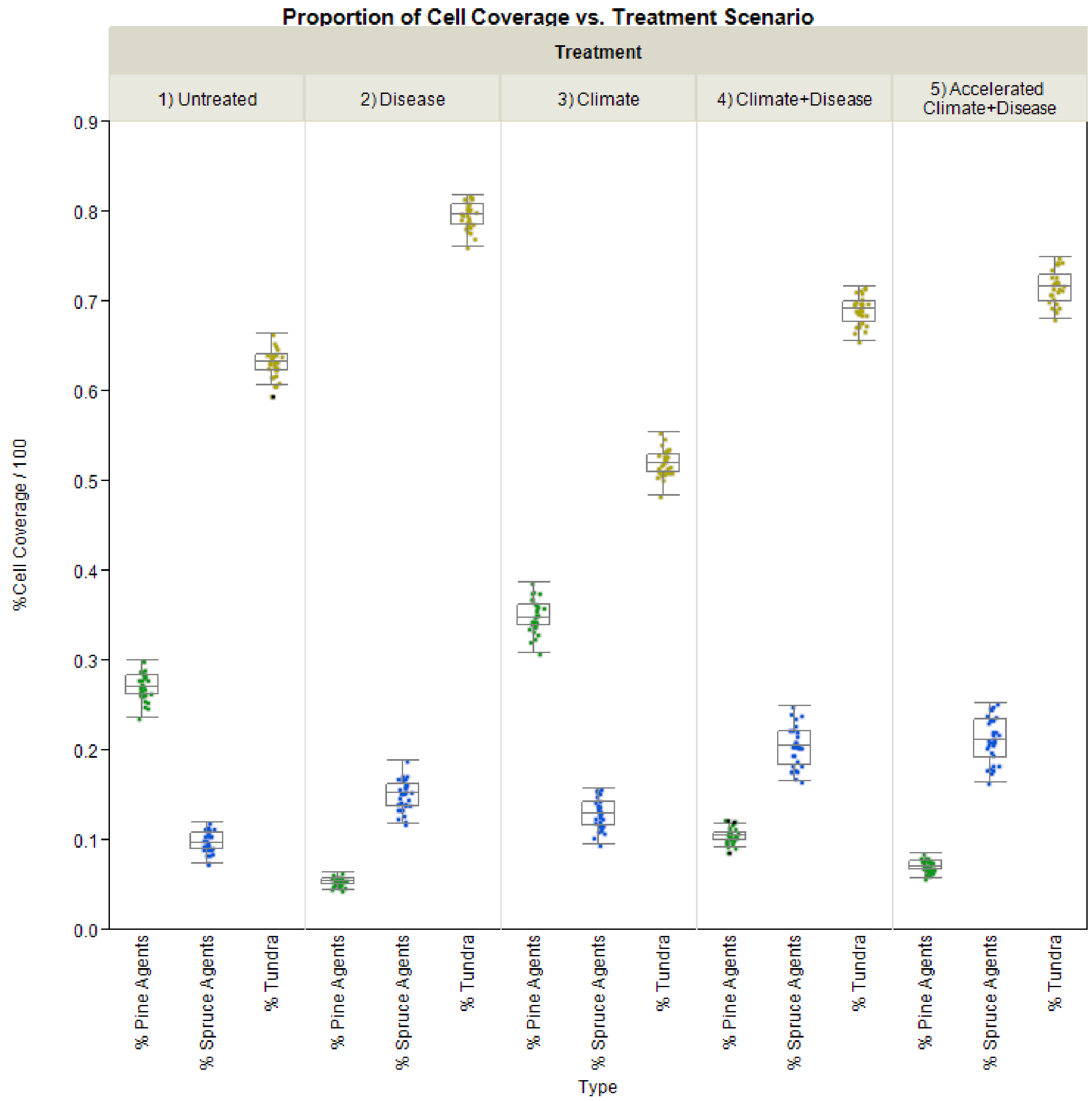
Figure 4. Population trends for each of the five scenarios from simulation year 500-800, using replicate #11 as an example.



Model Scenario	Least Square Mean (Pine Agents)	Tukey-Kramer
1) Untreated	2765.00	B
2) Disease	550.60	E
3) Climate	3563.30	A
4) Climate+Disease	1069.03	C
5) Accelerated Climate+Disease	729.07	D

*Means with the same letter are not significantly different from each other (Tukey–Kramer test, $p<0.05$).

Figure 5. One-way ANOVA and Tukey-Kramer test comparing the number of pine agents for 30 replicates in each scenario, at year 800.



Treatment vs. Proportion of Cells	**Least Square Mean (% Coverage/100)**	**Tukey-Kramer**
2) Disease, % Tundra	0.79576315	A
5) Accelerated Climate+Disease, % Tundra	0.71651168	B
4) Climate+Disease, % Tundra	0.6909641	C
1) Untreated, % Tundra	0.63070216	D
3) Climate, % Tundra	0.52041532	E
3) Climate, % Pine Agents	0.34977703	F
1) Untreated, % Pine Agents	0.27173949	G
5) Accelerated Climate+Disease, % Spruce Agents	0.21197919	H
4) Climate+Disease, % Spruce Agents	0.20414502	H
2) Disease, % Spruce Agents	0.1501883	I
3) Climate, % Spruce Agents	0.12980764	J

4) Climate+Disease, % Pine Agents	0.10489088	K
1) Untreated, % Spruce Agents	0.09755835	K
5) Accelerated Climate+Disease, % Pine Agents	0.07150913	L
2) Disease, % Pine Agents	0.05404855	M

*Means with the same letter are not significantly different from each other (Tukey–Kramer test, $p < 0.05$).

Figure 6. Two-way ANOVA and Tukey-Kramer test comparing the proportion of tree agents and tundra for 30 replicates in each scenario, at year 800.

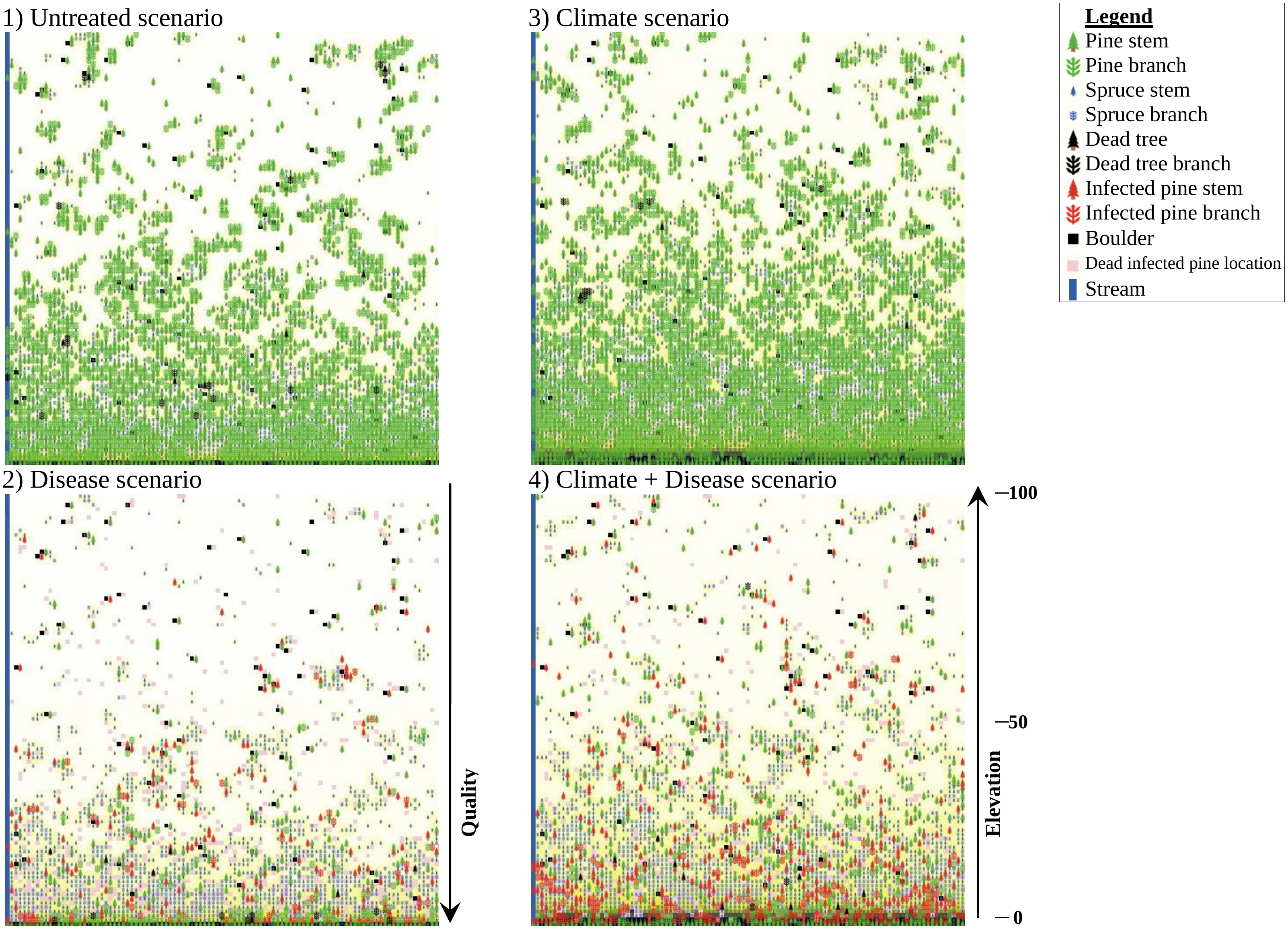
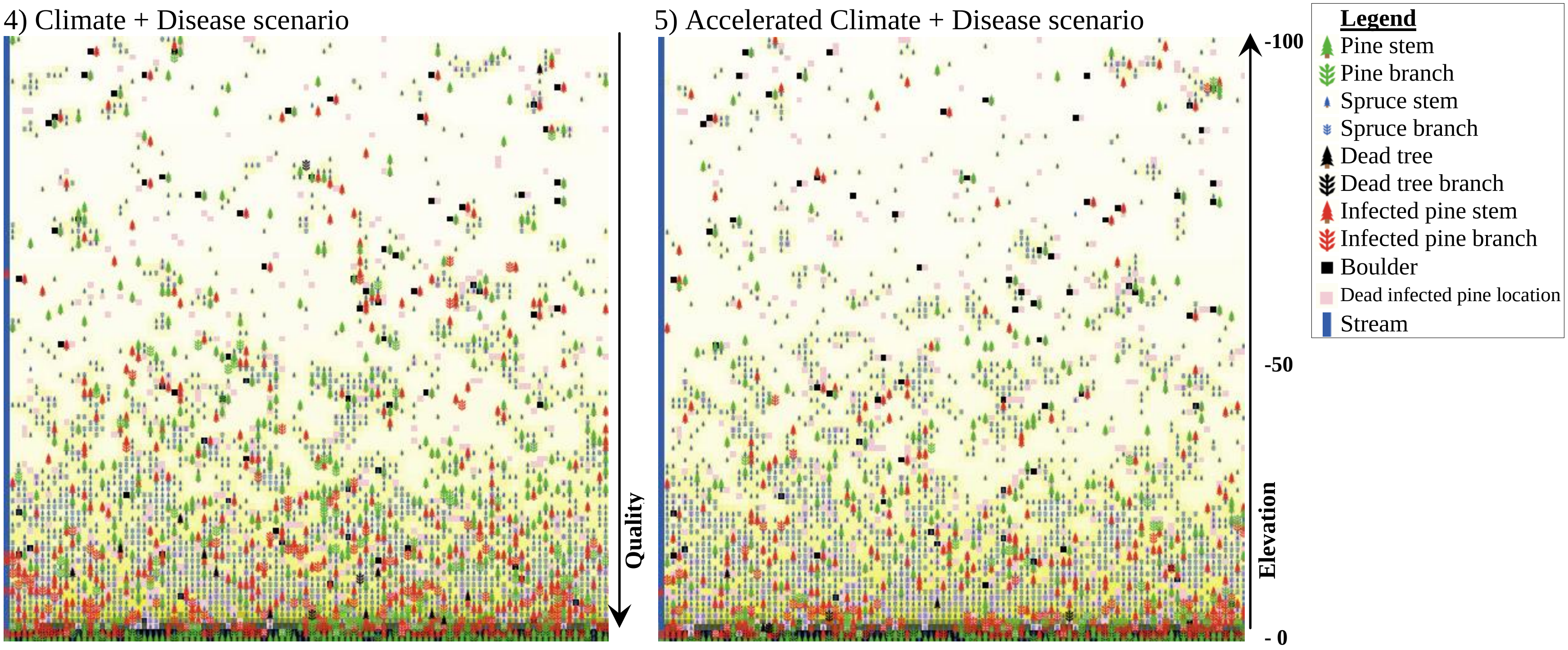


Figure 7. Comparison of four scenarios for replicate #11, at final simulation year 800. Model boundaries range from cell y-coordinates 0-100, site quality decreases with elevation.


4) Climate + Disease scenario

5) Accelerated Climate + Disease scenario

Figure 8. Comparison of two Climate and Disease scenarios for replicate #11, at final simulation year 800.

Table 1. Model parameters used in simulations.

Parameter	**Value**[a]	**Description**
Initiating pine agents	0.701	Starting number of pine agents at initial setup
Initiating spruce agents	0.306	Starting number of spruce agents at initial setup
Microtopography	0.007	Controls the number of boulders at initial setup, and microtopographic potential of cells.
Microtopographic sheltering strength	10	Controls the sheltering strength of the microtopographic shelter (i.e., boulders)
Facilitation strength (α)	0.254	Controls the sheltering strength of neighboring trees
Pine seeder	0.032	Controls amount of pine seed production
Spruce seeder	0.064	Controls amount of spruce seed production
Pine establishment	0.001	Influences the probability of pine establishment
Spruce establishment	0.00078	Influences the probability of spruce establishment
Pine growth	0.012	Controls amount of pine branch growth
Spruce growth	0.009	Controls amount of spruce branch growth
High survivability	0.12	Adjusts high survivability rate
Low survivability	0.04	Adjusts low survivability rate
Killer	0.004	Controls strength of mortality
Climate Multiplier	1 / 1.003 (Off/On)	Climate scenarios only: multiplies factor to site quality
Disease Virulence	0 / 0.04 (Off/On)	Disease scenarios only: controls rate of blister rust infection.

[a]Values effect probability sliders

Table 2. Population statistics of pine agents from 30 model replicates, for each scenario.

Model Scenario	Simulated 500 years	Treatment Scenarios Simulated 300 years from Baseline				
	Baseline	**Untreated**	**Disease**	**Climate**	**Climate+Disease**	**Accelerated Climate+Disease**
	%Cells w/ Pine Agents	**%Cells w/ Pine Agents**	**%Cells w/ Pine Agents**	**%Cells w/ Pine Agents**	**%Cells w/ Pine Agents**	**%Cells w/ Pine Agents**
Min	*17.15%*	*23.56%*	*4.45%*	*30.85%*	*8.63%*	*5.81%*
Max	*21.57%*	*30.01%*	*6.39%*	*38.70%*	*12.26%*	*8.60%*
Mean	*19.73%*	*27.17%*	*5.40%*	*34.98%*	*10.49%*	*7.15%*
SD[a]	*1.08%*	*1.54%*	*0.47%*	*1.80%*	*0.80%*	*0.67%*

	Pine Agents	**Pine Agents**	**Pine Agents**	**Pine Agents**	**Pine Agents**	**Pine Agents**
Min	*1746*	*2397*	*453*	*3141*	*880*	*593*
Max	*2198*	*3052*	*651*	*3942*	*1250*	*877*
Mean	*2011.10*	*2765.00*	*550.60*	*3563.30*	*1069.03*	*729.07*
SD	*109.90*	*156.22*	*47.48*	*183.21*	*81.82*	*68.25*

[a]SD, standard deviation. Thirty baseline replicates were simulated for 500 years and stopped/recorded. Each replicate was then issued a treatment, and ran an additional 300 years.

CHAPTER 5: SPATIAL PATTERNS OF WHITEBARK PINE IN TREELINE COMMUNITIES, AND THE CONNECTION WITH DISEASE

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This chapter is formatted for submission to *Physical Geography*

Abstract

The spread of white pine blister rust disease to cold and dry alpine treeline environments, and the subsequent infection and mortality of the keystone and foundation species whitebark pine, is an environmental and ecological quandary. Tree proximities and their growth and health characteristics may imply spatial patterns of ecological and environmental phenomena within the ecosystem—which may also infer these conditions drive disease infection. I investigate spatial relationships between neighbors and their infection rates, size, and growth habits for multitree and solitary whitebark pine trees from two diseased (Montana, USA) and one undiseased (Canada) treeline communities east of the Rocky Mountain Continental Divide. In the diseased treelines, whitebark pine trees growing near larger sized tree stem diameters and tree islands had more blister rust cankers, particularly those growing within large tree islands. Neighboring trees in diseased treelines revealed clustering patterns of similar characteristics—patterns that indicate spatial autocorrelation. The undiseased treeline exhibited considerably smaller tree island neighbors and stem diameters of multitrees, with random and dispersed patterns. This study explores whitebark pine patterns in the ATE and the notion that in diseased ecosystems, tree patterns may allude to indirect mechanisms promoting disease survival and spread in an otherwise inhospitable landscape.

[Key words: alpine treeline ecotone, whitebark pine, tree islands, krummholz, white pine blister rust disease, spatial autocorrelation, metacommunities]

INTRODUCTION

Spatial Autocorrelation of Disease

Landscape pathology studies typically examine links between vegetation pattern, topography, and climate because they can be integral in influencing disease expression (Real and McElhany, 1996; Holdenrieder, 2004). Living things tend to show spatial structure in nature, and can form patterns along environmental gradients or in patches across the natural landscape (Legendre and Fortin, 1989). The term ‘patch’ used here, refers to discrete areas of suitable habitat surrounded by unsuitable habitat (Hanski, 1997). In plant ecosystems the spatial structure of patches can imply specific environmental conditions (e.g., climate), which is an important consideration when studying patterns of plant disease (Legendre and Fortin, 1989).

The first law of geography, which describes spatial autocorrelation, states that while all things are related, near things tend to be more related than far things (Tobler, 1970). In the context of mixed-species forested ecosystems; in spatially heterogeneous landscapes near neighbors tend to be more similar than far neighbors, and these near neighbors tend to be influenced by similar environmental conditions and ecological phenomenon (Legendre, 1993; Zas et al., 2007). Positive autocorrelation indicates similarity, while negative autocorrelation suggests dissimilarity (Sokal and Oden, 1978). Many studies have examined spatial autocorrelation patterns of tree characteristics and mortality in diseased forested ecosystems (Pielou, 1965; Rosso et al., 1994; Martin et al., 2001; Zas et al., 2007) because spatial autocorrelation analysis is effective for studying the spatial structures of populations (Sokal and Oden, 1978; Legendre and Fortin, 1989). Spatial patterns of plants and forest communities provide a key for understanding the cause and spread of disease dispersal, which are influenced by environmental conditions (Pielou, 1965; Burdon et al., 1989). Forest trees infected with a fungal pathogen for example, can produce a patchy pattern of diseased trees within the stand—areas of infected trees surrounded by disease-free trees (Pielou, 1965). Examining patterns of diseased trees, particularly the pattern of diseased trees relative to healthy trees, may provide insight on how the disease may have spread (Pielou, 1965). For example, Rosso et al. (1994) used spatial autocorrelation analyses to find spatial patterns within diseased cordilleran cypress forests in Argentina, to determine possible causes of cypress tree mortality. Relating nearest neighbor distances among healthy and diseased trees, they concluded the patchy or non-random distribution of diseased trees suggested localized dispersal, attributing the cause of mortality to a root pathogen.

Patterns of Plant-Disease Connections

Disease dispersal among patches of host plant populations determine which patch, if any, becomes infected (Burdon et al., 1989). Depending on the mode of inoculum dispersal (e.g., wind, rain, soil, insect) and disease transmission requirements, the degree of patch connectivity across a landscape (in terms of distance between plant neighbors, patch area, or topographic barriers that separate patches) can influence disease dispersal potential (Ellis et al., 2010; Meentemeyer et al., 2012). In conjunction with dispersal and connectivity, the physical environment, such as climatic and topographic factors, also has a strong influence on the timing and severity of infection—these are all key factors for potential disease spread among host populations (Burdon et al., 1989; Holdenrieder, 2004; Ellis et al., 2010).

In particular, such biotic and abiotic factors are important drivers of forest fungal pathogen transmission and the emerging infectious diseases they cause. For example *Phytophthora ramorum*, which causes ‘sudden oak death’ particularly in oaks and tanoaks of coastal

California, requires a foliar host for spore development and dispersal is driven by rain splash, wind-blown rain, transportation of timber products, or through soil tracked by humans and animals (Rizzo and Garbelotto, 2003; Condeso and Meentemeyer, 2007). *Armillaria ostoyae,* which is a soil-borne fungal pathogen that spreads through underground root systems and causes root rot disease, is a particular problem among *Pinus pinaster* forests in north-west Spain (Zas et al., 2007). *Phytophthora cinnamomi*, which is a water-borne fungal pathogen and attacks major roots of trees, causes eucalyptus or jarrah dieback in Australian forests and is most severe in eucalyptus forests with poorly drained soils, and exacerbated by psyllid insects and Bell Miner birds (Martin et al., 2001). *Cronartium ribicola*, the focus of this study, is a wind-dispersed fungal pathogen requiring two hosts and causes white pine blister rust disease in whitebark pine trees of western North American mountain ranges (Hoff and Hagle, 1990). Examining spatial patterns of fungal disease within forests such as these has provided invaluable information in guiding conservation efforts. For example, in regards to examining distance relationships between healthy and diseased trees, spatial analysis methods have provided novel methods for genetic screening of *Pinus pinaster* trees for fungal resistance (e.g., Zas et al., 2007) and revealed potential warning indicators for fungal-induced dieback of eucalyptus forests (e.g., Martin et al., 2001).

Patterns at Treeline

A forested landscape that provides an interesting and unique platform for analyzing patterns of patch connectivity is that of a whitebark pine treeline community situated in the alpine treeline ecotone (ATE). The ATE is a transition zone between upper elevation closed subalpine forest and treeless tundra (Holtmeier, 2009). In the extreme cold and windy conditions of the ATE trees typically grow stunted and krummholz in form (Holtmeier, 2009), and close to their tree neighbors to form tree islands, because facilitation provides mutualistic survival from the elements of this inhospitable landscape (Arno and Hammerly, 1984). In whitebark pine treeline communities, whitebark pine plays a key role sheltering and harboring the growth of other conifer species from sun and wind exposure, such as Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) (Arno and Hammerly, 1984; Arno and Weaver, 1990). Whitebark pine's facilitative role promotes the growth and development of tree islands (Habeck, 1969; Arno and Weaver, 1990; Resler and Tomback, 2008), patches of dense clusters of trees typically shaped by wind and snow (Marr, 1977; Holtmeier and Broll, 2010).

In the context of island biogeography (MacArthur and Wilson, 1967) and metapopulation (Urban and Skelly, 2006) theories, patches are colonized by a source, and where patch dynamics are controlled by dispersal, metacommunities form on the landscape—where colonization depends on connectivity, proximity, and resource availability (Case, 2000). Similar in framework to these theories—the function and dynamics of whitebark pine treeline communities are primarily driven by Clark's nutcracker seed dispersal of whitebark pine from a subalpine forest seed source to the ATE (Tomback, 2001), and the pine's facilitative role promotes colonization of other treeline conifer species to form tree island patches in the cold and windy landscape above treeline (Habeck, 1969; Resler, 2004; Resler and Tomback, 2008). Patches of multi-species plant populations that are linked through dispersion across a landscape are considered metacommunities (Urban et al., 2008). Discrete population patches form on the landscape where habitats are suitable, and gaps exist between population patches where habitat is unsustainable (Hanski, 1997). This fragmented habitat distribution, and metacommunity formation, is characteristic of whitebark pine tree island communities and the patchy landscapes that may be found in the cold and wind-swept landscapes of the ATE.

Case Study: Spatial Patterns of Whitebark Pine Treelines and Blister Rust Disease

Whitebark pine is a frequent tree island initiator, particularly in the northern Rocky Mountains east of the Continental Divide, and thus influences the spatial patterns of treeline landscape (Resler, 2004; Resler and Tomback, 2008). Populations of whitebark pine are on the decline range-wide due to white pine blister rust (referred hereafter as blister rust) infection, which forms cankers that girdle branches, ceases seed reproduction, and kills whitebark pine trees (McDonald and Hoff, 2001; Tomback and Achuff, 2010). Research has shown that conditions are suitable for blister rust infection and mortality of whitebark pine in subalpine forests (Tomback and Achuff, 2010), and even in the cold and extreme climates in the high elevations of the ATE (Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013).

The spread of blister rust to whitebark pine at treeline is perplexing considering that controlled experiments show blister rust infection requires mild (13°C to 20°C temperatures) and moist (near 100% relative humidity) conditions endured over time (from hours to weeks) to develop certain stages of its five spore life cycle, and wind to transmit spores between alternate host plants (*Ribes* spp., *Pedicularis racemosa,* and *Castilleja miniata* [McDonald *et al*., 2006]) and the host pine (Hirt, 1942; Mielke, 1943; Van Arsdel et al., 1956; McDonald and Andrews, 1980; McDonald and Hoff, 2001). For infection of pine to occur, the final stage of fragile basidiospore development requires cool but moderate temperatures, protection from sun and frost exposure, high humidity, and wind to transport spores short distances (less than 300 m) between

Ribes spp. plants and the white pine host (Van Arsdel et al., 1956; McDonald and Hoff, 2001). These specific environmental conditions suggest that blister rust infection should be limited in cold and dry high elevation environments (Van Arsdel et al., 1956). Nevertheless, treeline whitebark pine is dying from blister rust (Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013), and rust-induced mortality in the subalpine has also caused a reduction in whitebark pine seed source as well as a decrease in the Clark's nutcracker's seed dispersal to the ATE, and an overall reduction in whitebark pine regeneration in high elevation forests in the Rocky Mountains (McKinney et al., 2009; Barringer et al., 2012). Seed source decline leads to a reduction of whitebark pine trees available for recruitment to the ATE, and blister rust is already killing established whitebark pine trees either within tree islands or before they may facilitate other conifer species to form tree islands (e.g., Resler and Tomback, 2008). The loss of whitebark pine due to blister rust may alter treeline community structure, creating an altered landscape pattern that may confound our interpretation of treeline response to a changing climate—an ecological response in which treeline may shift in elevation, and diminish from the expected upslope advance even as climate warms (Tomback and Resler, 2007).

Since whitebark pine plays a major role in the structure of metacommunities in the ATE, and the partially fragmented and connected patches of tree islands across the ATE landscape, one may expect to see a spatial pattern of blister rust-infected whitebark pine trees across a diseased landscape. However, a pattern of spatial autocorrelation among infected trees should not occur due to the complicated life cycle of blister rust spore development and infection transmission requirements between host pine and alternate host plants—in other words, a healthy pine would not necessarily become infected simply because it is growing next to a diseased pine (Mielke, 1943; Van Arsdel, 1956; Hoff et al., 1980). Yet, research in northern Rocky Mountain treelines show that whitebark pine trees growing within tree islands tended to have more cankers and higher percentages of blister rust infection overall compared to whitebark pine growing solitarily (Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013). Research has also shown a correlation between the length of the tree island patch and the number of blister rust cankers on whitebark pine within the patch (Resler and Tomback, 2008). Additionally, alternate host plants to *Cronartium ribicola* (*Ribes* spp., *C. miniata, P. racemosa*) (McDonald & Hoff, 2001; McDonald *et al*., 2006) are prevalent in some sampled Rocky Mountain treeline communities, and *Ribes* spp. plants in particular have been frequently observed growing within tree islands (Smith et al., 2011; Smith-McKenna et al., 2013; personal observation). Furthermore, the predictive model by Smith et al. (2011) showed that close proximity to *Ribes* spp. (in conjunction with key environmental variables) increased the likelihood in the number of cankers per whitebark pine tree. These findings raise questions regarding the spatial proximity of whitebark pine trees, their relationship with tree islands, alternate hosts, and disease, and whether other factors are correlated to their chance of infection in the ATE.

While spatial proximity of trees may not increase the chance for infection transmission directly, could spatial patterns among whitebark pine trees indicate that other ecological or environmental factors are acting in synergy to produce favorable conditions for blister rust infection? Is spatial autocorrelation among diseased whitebark pine trees occurring in an indirect manner? Are near trees similar to each other in terms of infection, or other characteristics? Do the spatial patterns of diseased whitebark pine treeline communities differ from those in undiseased communities, and is this spatial pattern related to size, growth, and health characteristics of the trees? To answer these research questions I compared spatial locations, infection severity, and size characteristics of multitree and solitary whitebark pine trees sampled east of the Rocky Mountain Continental Divide from two diseased treeline communities in Montana, USA, and one undiseased treeline community in Canada.

While the goal of this study is not to imply that spatial pattern predicts disease occurrence directly, this study explores the notion that spatial pattern may serve as an indicator of other ecological and environmental phenomena that allow disease survival and spread within the ecosystem. In this study I expand on the findings regarding blister rust infected whitebark pine trees and tree island patch size (Resler and Tomback, 2008), tree island vs. solitary growth form (Smith et al., 2011; Smith-McKenna et al., 2013), and proximity to alternate host *Ribes* plants (Smith et al., 2011). My objectives are to 1) investigate the spatial relationships among trees in regards to their neighbor proximity, size, growth habit, and blister rust infection rates; 2) assess any variation in spatial pattern between blister rust-diseased and undiseased whitebark pine treeline communities; and 3) determine if the spatial patterns indicate spatial autocorrelation among the blister rust diseased whitebark pine trees. This study contributes to much needed research in spatially and ecologically complex metacommunities (e.g., Agrawal et al., 2007; Urban et al., 2008; Urban et al., 2012), and uses a landscape pathology approach to assess the spatial connection between whitebark pine treeline communities and blister rust disease.

METHODS

Study Areas

I sampled from whitebark pine treeline communities east of the Continental Divide in three main study areas near whitebark pine's southern, middle, and northern latitudinal range in the Rocky Mountains of North America (Fig. 1). The southernmost study area is located on the Beartooth Plateau in Montana, U.S.A., at treelines within the Line Creek Research Natural Area

(RNA) (~45.0°N, 109.4°W) at elevations from 2960 to 3029 m, referred to here as the Line Creek RNA. The mid-range study area straddles the boundary between Glacier National Park and the Blackfeet Nation (~48.6°N, 113.4°W), in treeline communities located at the bases of Divide and White Calf Mountains of Montana at altitudes ranging 2097 to 2261 m, and is collectively referred to as the Divide Mountain study area. The northernmost study area is located in northern Banff National Park near the Jasper National Park border (~52.2°N, 117.1°W) of Alberta, Canada, in treeline communities near Parker Ridge, Hilda Gulch, and Helen Lake, at elevations ranging 2138 to 2328 m. These communities are collectively referred to as the Parker Ridge study area.

The eastern slopes of the Rocky Mountains tend to have drier, colder, and windier continental climates than western slopes of the Continental Divide (Finklin, 1986). The ATE landscape in all study areas consist of alpine topography sculpted by glaciers, and patterned ground features formed by periglacial processes that shape the microtopography (Johnson and Billings, 1962; Butler and Malanson, 1989). Glaciers and snow fields exist in the mountain peaks surrounding all three treeline study areas. The Canadian sites in the Parker Ridge treeline study area are surrounded by glaciers, with the Columbian Icefield to the north, and valley glaciers such as the Saskatchewan Glacier near Parker Ridge, and the Crowfoot Glacier near Helen Lake (Pole, 2010). The generally poor and rocky soils in all three study areas hinder most vegetative growth except for some hardy treeline conifer species (Mathews, 2003; Pole, 2010).

The sampled communities are from climatically influenced treelines in the alpine treeline ecotone (Fig. 2). Most of the trees displayed a stunted krummholz form less than 1 m in height, and grew either solitarily or in patches of multitree tree island colonies. These communities included both solitary and tree island conifer species consisting primarily of whitebark pine, subalpine fir (*Abies lasiocarpa),* and Engelmann spruce *(Picea engelmanii)*. To a lesser extent, I sampled lodgepole pine (*Pinus contorta*) in the Line Creek RNA, Douglas-fir *(Pseudotsuga menziesii)* in the Divide Mountain study area, and white spruce (*Picea glauca var. albertiana* (S. Brown) Sargent) near Helen Lake in Canada. The alternate host plant *Ribes* spp. was prevalent in all three treeline study areas, and many plants were observed in the sampling plots growing solitarily and within tree islands (Fig. 3).

Treeline Sampling Methodology

Tree metrics and characteristics of the sampled whitebark pine treeline communities were recorded within a total of 85, 15 m x 15 m plots: 30 plots at the Line Creek RNA, 30 plots at the Divide Mountain study area, and 25 plots at the Parker Ridge study area. Plot placement was stratified by aspect and randomly dispersed across each treeline study area to capture a range of landscape variation, tree/tree island sizes, and slope orientation classes representative of each study area. Slope orientation has been linked to blister rust canker infection intensity (e.g., Smith et al., 2011). Therefore, it was appropriate to sample from treeline communities situated on the predominant aspect classes (northeast [0-90°], southeast [90-180°], southwest [180-270°], northwest [270-360°]) in a manner proportional to each study area. Prior to conducting fieldwork I analyzed terrain and aerial imagery in a GIS for each study area, and estimated approximate boundaries of potential treeline sampling areas in order to assess the proportion of the land surface in each aspect class. For example, in the Line Creek RNA study area the 30 plots were dispersed on slopes facing NE (47% of the land surface faces northeast, 14 plots were sampled), SE (27%, 8 plots), SW (13%, 4 plots), and NW (13%, 4 plots). I navigated within each study area using a topographic map and compass, and determined sampling plot centers using random pin tosses at distances greater than 20 m—in addition to hiking accessibility and safety considerations.

In each 15 meter sampling plot I recorded the spatial location of each whitebark pine tree (whether living or dead) using a high resolution Trimble GeoXT global positioning system (GPS) unit. I created GPS polygons to delineate the spatial boundaries of each tree island patch and the sampling plots (Fig. 4). All GPS features were differentially corrected with nearby base stations to achieve submeter accuracy. I inspected each whitebark pine tree for blister rust. When blister rust infection was evident I counted and recorded the number of distinct blister rust cankers separated by healthy tissue on stems and branches following methods from Hoff (1992).

Within each sampling plot, I noted whether the whitebark pine tree grew solitary or as a multitree (a tree within a tree island), and measured and recorded the main stem/bole diameter using calipers. I classified a tree island as two or more adjacent conifer trees with spatially overlapping foliage. Whitebark pine trees not adjacent to trees were classed as solitary trees, and when it was apparent that a cluster of whitebark pine stems/boles originated from a single nutcracker seed cache (stems above ground are within 10-20 cm of each other), I also classified this as a solitary whitebark pine tree (e.g., Resler and Tomback, 2008) and recorded the largest stem diameter.

I measured the canopy area of each solitary whitebark pine tree, and the canopy area of each tree island however, due to time, personnel, and logistical constraints, I did not measure canopy area of each multitree whitebark pine within the tree island. I found canopy area of solitary trees and tree islands to be an important metric, because in addition to providing shelter to other trees and alternate host plants, a tree’s canopy has the potential to intercept wind-dispersed bluster rust spores. Despite a lack of canopy area measurements for multitree whitebark pine, I hypothesized that a tree's stem diameter may indicate the overall size of the tree, such as patch size (canopy area) of the tree. Therefore I tested for correlation and strength, and potential linear relationships between measured stem diameters and canopy area of solitary whitebark pine for each of the treeline study areas using multivariate methods in JMP® Pro (version 10.0, SAS Institute Inc., Cary, NC, USA).

Spatial Pattern Analysis

To examine spatial patterns within treeline communities, and assess patterns of disease, I used the geospatial point and polygon GPS features collected in the field to run proximity analyses in ArcGIS (v.10.1, ESRI, Redlands, CA). I calculated nearest neighbor distances between whitebark pine trees, and between whitebark pine trees and tree islands, within each sampling plot for each treeline study area. I compared distance relationships to characteristics of each whitebark pine tree: number of cankers, stem size, canopy area, and whether the tree grows solitarily or in a tree island. Comparisons for each study area reflect the distance from a whitebark pine tree to the nearest whitebark pine tree or tree island. There were very few tree islands that did not contain whitebark pine, therefore tree islands with at least one whitebark pine tree were considered in this study. For whitebark pine trees within a tree island (a multitree), the nearest neighboring tree island distance is considered zero. Sampling plots with more than one whitebark pine tree were included in the comparative analysis, and I calculated distance relationships among trees of the same sampling plot (i.e., distances do not extend from one sampling plot to another plot). Standard spatial autocorrelation tests, such as the spatial statistical tools in ArcGIS, could not be utilized due to the minimum requirement of 30 neighboring features. Many of my sampling plots contain less than 30 trees. Therefore, I generated bubble plots in JMP® Pro (version 10.0, SAS Institute Inc., Cary, NC, USA) to graph the tree distances and characteristics and visually compare the multilevel relationships between spatial patterns and tree characteristics in the three treeline study areas. I used a Chi-square test of independence to test my interpretations of the bubble plot results, and determine significant relationships between tree distance and characteristics.

RESULTS

Treeline Findings

Of the sampled plots that had at least two whitebark pine trees and recorded GPS spatial positions, I analyzed distance and tree characteristic relationships among 324 whitebark pine trees in the Line Creek RNA, 583 trees at Divide Mountain, and 272 trees at Parker Ridge study areas (see data reported in Table 1). Whitebark pine predominately occurred in solitary form at Parker Ridge (to a greater extent) and Line Creek RNA (to a lesser extent), while at Divide Mountain the majority grew in tree islands. I found a higher percentage of blister rust-infected whitebark pine at Divide Mountain (23.7%) than at Line Creek RNA (19.4%), but found no infected trees at the Parker Ridge study area. Whitebark pine multitrees showed a higher percentage of infection than solitary trees at both Line Creek RNA (58.7%) and Divide Mountain (66.7%), and the majority of cankers were found on multitrees.

Of the sampled solitary whitebark pine, I found a statistically significant strong positive correlation ($r > 0.8$, $p < 0.0001$) between measured tree stem diameters and canopy area for all three treeline study areas (Fig. 5). Measurements of stem diameters of the sampled trees were proportional to the length and width (area) of the tree’s canopy. This relationship shows that the wider the stem diameter, the greater the dimensional area of canopy branch coverage—stem diameter may be an important indicator of patch size, and the potential for intercepting wind-dispersed blister rust spores.

Spatial Pattern Findings

Using bubble plots to visualize multi-level relationships and spatial patterns of tree proximity, growth, and health characteristics, I analyzed nearest neighbor distances between whitebark pine trees and tree islands that contain at least one whitebark pine, and compared these distances to the number of blister rust cankers, stem diameter, solitary/multitree growth form, and canopy area measured in the field (e.g., Figures 6-8). Comparing the number of cankers on a whitebark pine, with the measured distance from this pine to the edge of the nearest neighboring tree island, and neighboring tree island area, yielded interesting results (Fig. 6). Overall, both diseased treelines (Divide Mountain and Line Creek RNA) show that the majority of infected whitebark pine trees with the most cankers were found either in tree islands or in close proximity to tree islands (distances near 0). In the Line Creek RNA, trees with the most cankers are also in large tree islands (sizes ranging from 60 to 100 m^2). Figure 6 shows a clustering spatial pattern for the diseased treelines; trees with similar characteristics (in terms of cankers and growth form) cluster together (the lower left corner of the plots show clustering where distances are shorter)—this is especially apparent for the Divide Mountain treeline. Plotted points for the undiseased treeline, Parker Ridge, demonstrate a random spatial pattern in terms of the relationship between tree island area and neighboring tree island distance. Another important note for Parker Ridge is that the nearest whitebark pine-containing tree islands are less than 50 m^2 in area (most are less than 15 m^2), a considerably smaller size than found in both diseased treeline study areas (see nearest tree island areas reported in Figure 6). Examining tree characteristic relationships with the distance to whitebark pine-containing tree islands is very similar to that of distances to all tree islands (whether they contain whitebark pine or not), because the diseased treelines had very few neighboring tree islands without whitebark pine. For example, in the distance analysis Parker Ridge trees had only 17 nearest neighboring non-whitebark pine tree islands, Line Creek RNA had only 3 nearest non-whitebark pine tree islands, and Divide Mountain had none.

Comparing distances between whitebark pine trees and nearest whitebark pine multitrees, with the stem diameters of those nearest multitrees (Fig. 7), I found a clustering spatial pattern of characteristics in the diseased treelines and a more random spatial pattern at the undiseased treeline. In both diseased treelines, the majority of solitary whitebark pine trees are either not infected or have low canker counts relative to multitrees. Multitrees not only had more cankers than solitary trees, but these infected multitrees also tended to grow closer to multitrees with moderately large stem diameters (see tree characteristics and distance relationships in Figure 7). Trees with the highest canker counts were near multitrees ranging 50-150 mm in diameter at Line Creek RNA; at Divide Mountain, near multitrees 25-130 mm in diameter). A few multitrees grew proximal to very large diameter multitrees (Line Creek RNA, 250-480 mm; Divide Mountain, 200-300 mm) but these were not heavily infected with blister rust, if at all (Divide Mountain). At the undiseased Parker Ridge study area, a dispersed pattern of nearest multitree distances and stem diameters is apparent. Here at Parker Ridge, stem diameters of the nearest multitrees overall are much smaller than in the diseased study areas, with multitree stems ranging only from 1 to 98 mm in diameter.

Figure 8 reveals a spatial pattern of whitebark pine attributes (stem diameters, canker counts, and solitary/multitree growth forms) plotted with the distance to their nearest whitebark pine neighbor. In these plots all three treeline study areas exhibit some amount of spatial clustering noted by the concentrated number of points over relatively short distances (Parker Ridge however, to a lesser extent), with most nearest neighbor distances ranging 0-4 m. Overall, solitary whitebark pine trees of relatively small stem diameters tend to cluster together, compared with multitrees that have larger stem diameters. In both diseased treelines, canker counts are highest for multitrees and these trees also have some of the largest stem diameters—trees that share these characteristics are closer together. In general for the undiseased Parker Ridge treeline, trees with diameters less than 25 mm tend to be clustered with their neighbor (particularly within 2 meters of each other), and most of these trees grow solitary. Above this 25mm threshold, stem diameter measurements become more spread out and variable, and trees larger in diameter show a pattern that becomes more dispersed and random in terms of nearest neighbor distances and stem diameter characteristics, compared with the diseased treelines.

The key points that I interpreted from the bubble plot results, were that whitebark pine trees growing near or in tree islands, tended to have more blister rust cankers—and this trend also appears to be related to the size of the nearest tree island. Using a Chi-square test of independence, both diseased treeline study areas showed that canker intensity on a whitebark pine tree is significantly dependent on both its distance to the nearest tree island (Divide Mountain, $\chi^2 = 46.85$, $df = 6$, $p < 0.001$; Line Creek RNA, $\chi^2 = 48.39$, $df = 5$, $p < 0.001$) and the size of the nearest tree island (Divide Mountain $\chi^2 = 12.51$, $df = 5$, $p < 0.05$; Line Creek RNA, $\chi^2 = 144.15$, $df = 6$, $p < 0.001$).

DISCUSSION

Overall, the characteristics and distance comparisons between trees in the diseased treelines (Line Creek RNA and Divide Mountain) showed spatial patterns that tended towards spatial clustering, while the undiseased treeline (Parker Ridge) predominantly showed patterns of randomness and dispersion. The clustering patterns found at the diseased treelines indicate that spatial autocorrelation may be occurring among blister rust infected pine—perhaps in an indirect manner. Whitebark pine trees with the most cankers tended to grow in tree islands or very close to tree islands, and this trend was also associated with large tree islands and moderately large stem diameters. Of the whitebark pine trees I sampled, stem diameters reflect the size of the tree's canopy—which may increase the potential for trapping spores, sheltering alternate host plants, and moderating microclimates. Field sampling at the undiseased Parker Ridge treeline revealed considerably smaller tree islands, and nearest neighboring multitrees had smaller stem diameters relative to the diseased treelines. Divide Mountain, which had the highest percentage of blister rust infection, also had the most multitrees (many with moderately large stem diameters), and the largest tree island patch areas.

From these findings, it is conceivable that phenomena affecting characteristics of tree growth habit and size, may also improve environmental conditions to favor blister rust infection and canker intensity. The connectivity of closely spaced trees found in tree islands in the ATE could also provide potential sources of inoculum for blister rust disease in terms of: 1) containing a whitebark pine host, 2) sheltering *Ribes* spp., or other alternate host plants, 3) trapping wind-dispersed blister rust spores, and 4) moderating microclimates (Pyatt, unpublished data) suitable for disease development. These findings support those of McDonald (1996) and McDonald and Hoff (2001), who noted that in cold and dry high elevation environments, blister rust infection rates should typically remain low (inhibited by these cold and dry conditions). However, if the environmental conditions are modified to favor spore development (temperatures are moderated, humidity is increased, exposure to sun and frost is minimized) these infection rates may increase.

The mechanisms that drive blister rust spread, as explained by McDonald and Hoff (2001), are further confounded by the light and darkness requirements that influence spore development—and this begs the question as to whether local or long distance spread has more influence on the infection cycle, particularly in high elevation forests. They suggest examining the spatial pattern of infection can lend some insight into the cause of spore distribution. Uniform and random patterns of infection may indicate that blister rust spores were transported over a long distance, and clustered or clumped patterns of infection may indicate that spores came from nearby shrubs—perhaps within the forest stand (McDonald and Hoff, 2001). In this case study of blister rust diseased whitebark pine treeline communities, patch size and connectivity of tree islands appear to allow disease to spread locally—tree islands may harbor the necessary conditions for blister rust spore development, transmission, and infection.

Tree island development can be largely attributed to positive feedbacks, because neighboring trees help ameliorate the harsh abiotic conditions of the ATE and provide facilitative benefits that help increase tree growth and survival (Bekker, 2005). The patch size of the tree or tree island, and the associated positive feedbacks that benefit neighbors, can lead to greater survivability among larger patches with higher population densities of trees (Alftine and Malanson, 2004; Malanson et al., 2009; Harsch and Bader, 2011). Additionally however, there are associated negative feedbacks within these dense patches, in terms of feedback switches to competition (Zeng and Malanson, 2006) and patch influence on patterns of wind, snow, and soil conditions (Holtmeier and Broll, 1992). In reference to a snow fungus that parasitizes many treeline conifers, Marr (1977) commented that larger tree islands trap more snow and create snowdrifts, and the resulting late-lying patches of snow early in the growing season provide favorable conditions for the black-felt fungus (*Herpotrichia nigra* Hartig)—causing death of conifer needles and stems within tree islands. Thus, smaller tree islands (and less snow accumulation in and around them) tend to lack the essential conditions necessary for black-felt fungus development (Marr, 1977). Though blister rust has a very different life-cycle than that of black-felt fungus (e.g., Simms, 1967), the abiotic conditions conducive to blister rust development and pine infection (e.g., Van Arsdel et al., 1956; Van Arsdel 1972) may be similarly linked with tree island abiotic conditions and size. The potential for large tree islands to trap snow and shelter alternate host plants could provide the favorable moisture conditions and inoculum sources for blister rust in the dry and cold environments of the ATE, particularly if the tree island contains, or is proximal to, whitebark pine trees. Coupled with the findings that whitebark pine multitrees and the size of tree islands are positively correlated with blister rust infection (Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013), it appears the sheltering benefits of neighboring trees may also be detrimental. In whitebark pine treeline communities, neighboring trees and the formation of tree islands help boost chances for survival in the harsh abiotic conditions of the alpine treeline ecotone—but this same mechanism may aid in their demise when confronted with an introduced pathogen.

Acknowledgements

I express much gratitude for those who helped me with field data collection, obtain research permits, and funding for this project. This study is based upon work supported by the National Science Foundation Geography and Spatial Sciences Program, Grant 808548, awarded to Lynn Resler, Diana Tomback, and George Malanson. In particular I thank Lauren Franklin, Kathryn Prociv, Jake Slyder, and Dr. Lynn Resler from Virginia Tech, and Paul Resler for their assistance in the field. I also extend thanks to Tara Carolin and the Crown of the Continent Research Learning Center of Glacier National Park, and Mark Magee and the Land Department of the Blackfeet Nation for working with us to obtain research permits for the Divide Mountain study area; Kent Houston, Shoshone National Forest and the Rocky Mountain Research Station for coordinating research permits for the Line Creek Research Natural Area; and Brenda Shepherd, Jasper National Park of Parks Canada, for field and permit logistics in Canada. I would also like to thank the Laboratory for Interdisciplinary Statistical Analysis at Virginia Tech, as well as Stephen Prisley, Laurence Carstensen, Lynn Resler, George Malanson, and Yang Shao for their helpful reviews of this manuscript.

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Fig. 1. Location of three main study areas near the southern, central, and northern portions of whitebark pine's range in the Rocky Mountains of North America.

Fig. 2. Sampled whitebark pine treeline communities in the climatically influenced alpine treeline ecotone. Most trees grow in a stunted krummholz form either solitarily or in tree islands. Treeline study areas are located east of the Continental Divide in the Rocky Mountains of North America and include: Parker Ridge, Canada; Divide Mountain, Glacier National Park, Montana; and Line Creek RNA in the Beartooth Plateau, Montana.

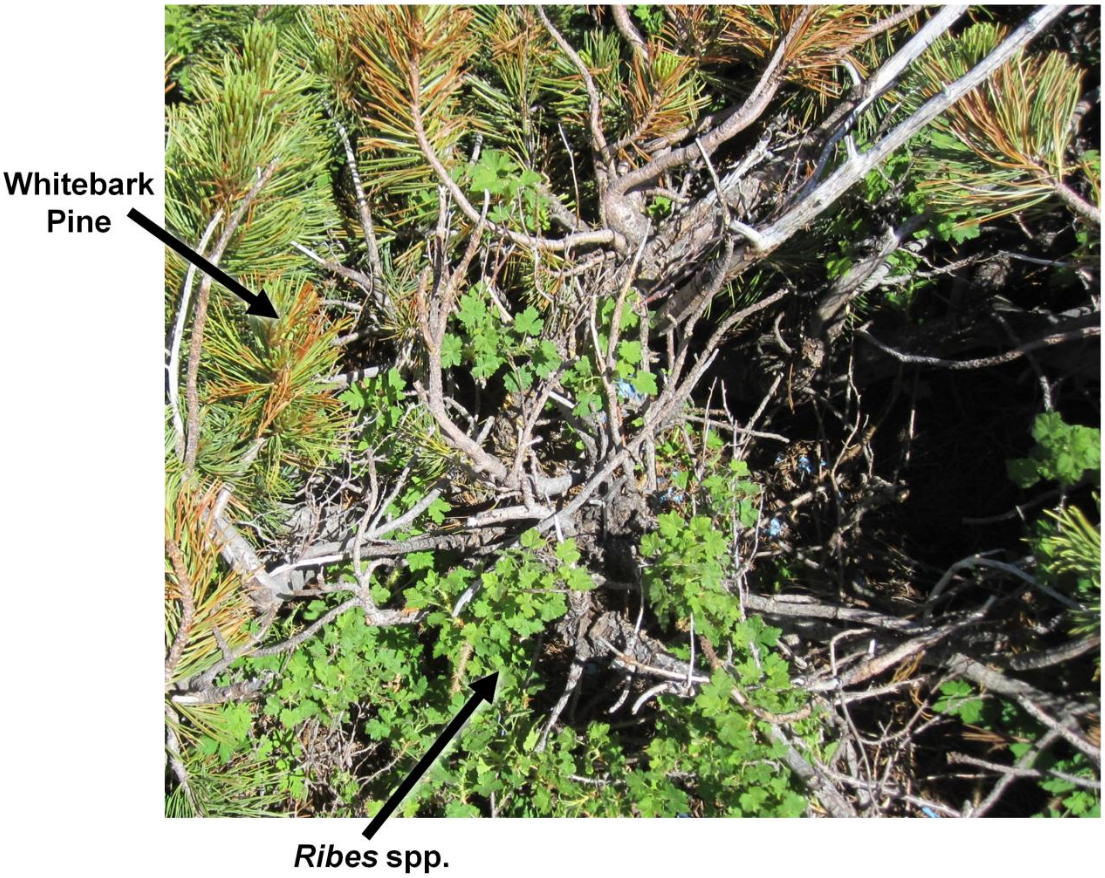

Fig. 3. Photo of an alternate host plant, *Ribes* spp., growing within a whitebark pine tree island. The tree island is located within a sampling plot in the Line Creek RNA treeline study area.

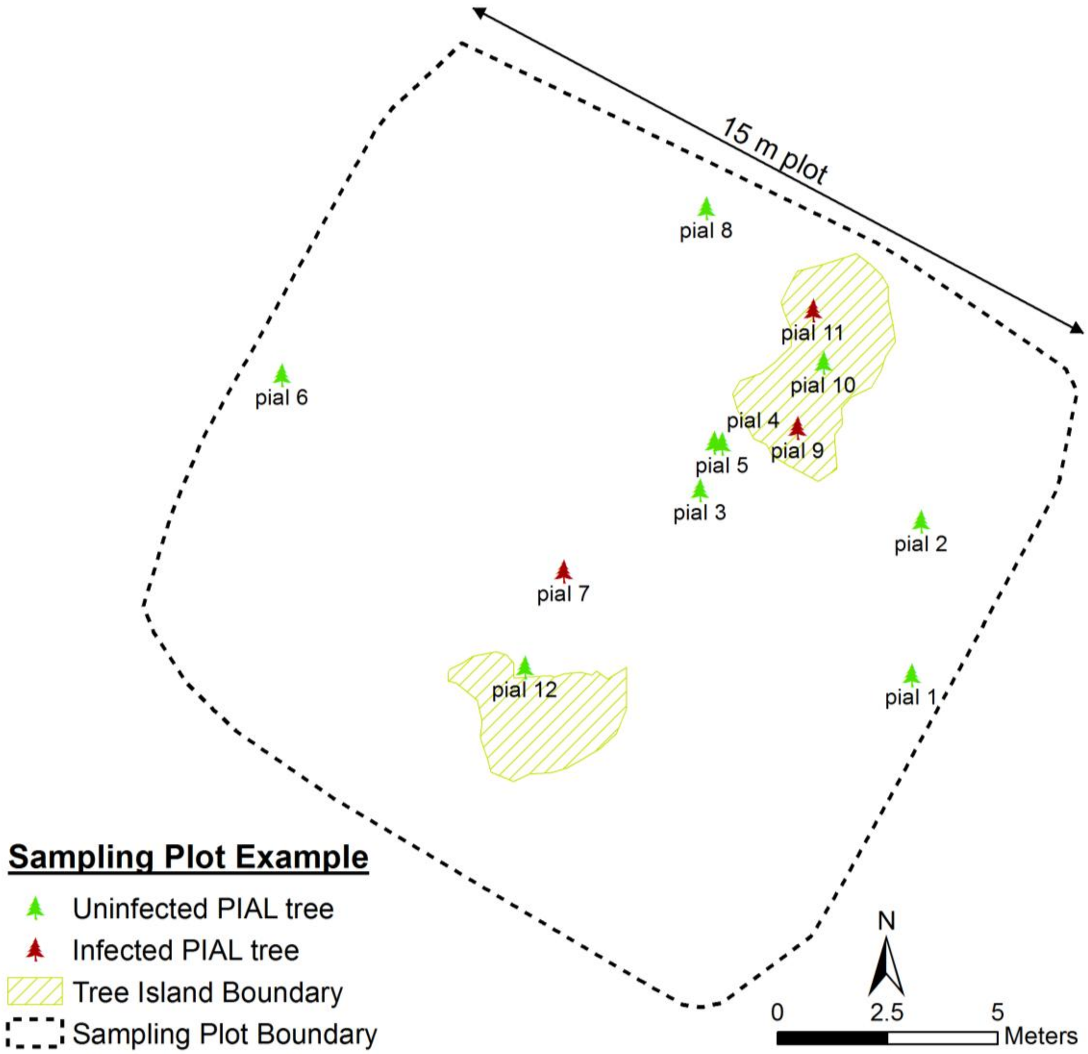

Fig. 4. Example of a sampling plot configuration showing spatial locations of whitebark pine trees (PIAL, *Pinus albicaulis*), and tree islands (Plot #30, Line Creek RNA is shown).

Table 1. Tree and disease statistics for geospatially located, neighboring, whitebark pine trees within three treeline study areas.

Characteristic	**Line Creek RNA**	**Divide Mountain**	**Parker Ridge**
Number of sampling plots	30	30	25
Number of *PIAL** trees analyzed (*N*)	324	583	272
Number of blister rust-infected *PIAL* trees	63	138	0
Number of cankers counted on infected *PIAL* trees	437	505	0
Canker intensity (cankers per infected *PIAL* tree)	6.9	3.7	0
% Blister rust-infected *PIAL* trees	19.4%	23.7%	0%
Number of *PIAL* **solitary** trees	189	267	242
Number of *PIAL* **multitrees**	135	316	30
Number of infected *PIAL* **solitary** trees	26	46	0
Number of infected *PIAL* **multitrees**	37	92	0
Number of cankers on infected *PIAL* **solitary** trees	116	97	0
Number of cankers on infected *PIAL* **multitrees**	321	408	0
% *PIAL* **solitary** trees	58.3%	45.8%	89%
% *PIAL* **multitrees**	41.7%	54.2%	11%
Nearest neighbor distances (m): Mean ± SD (*Median*)			
PIAL – nearest *PIAL* Tree Island distance	1.9 ± 2.8 (*0.8*)	1.1 ± 1.9 (*0*)	3.3 ± 3.1 (*2.6*)
PIAL – nearest *PIAL* multitree distance	2.5 ± 3.2 (*1.1*)	1.5 ± 2.3 (*0*)	4.2 ± 3.3 (*3.5*)
PIAL – nearest *PIAL* distance	2.0 ± 1.7 (*1.5*)	1.3 ± 1.2 (*1.0*)	1.7 ± 2.1 (*1.1*)

**PIAL*: *Pinus albicaulis*, whitebark pine.

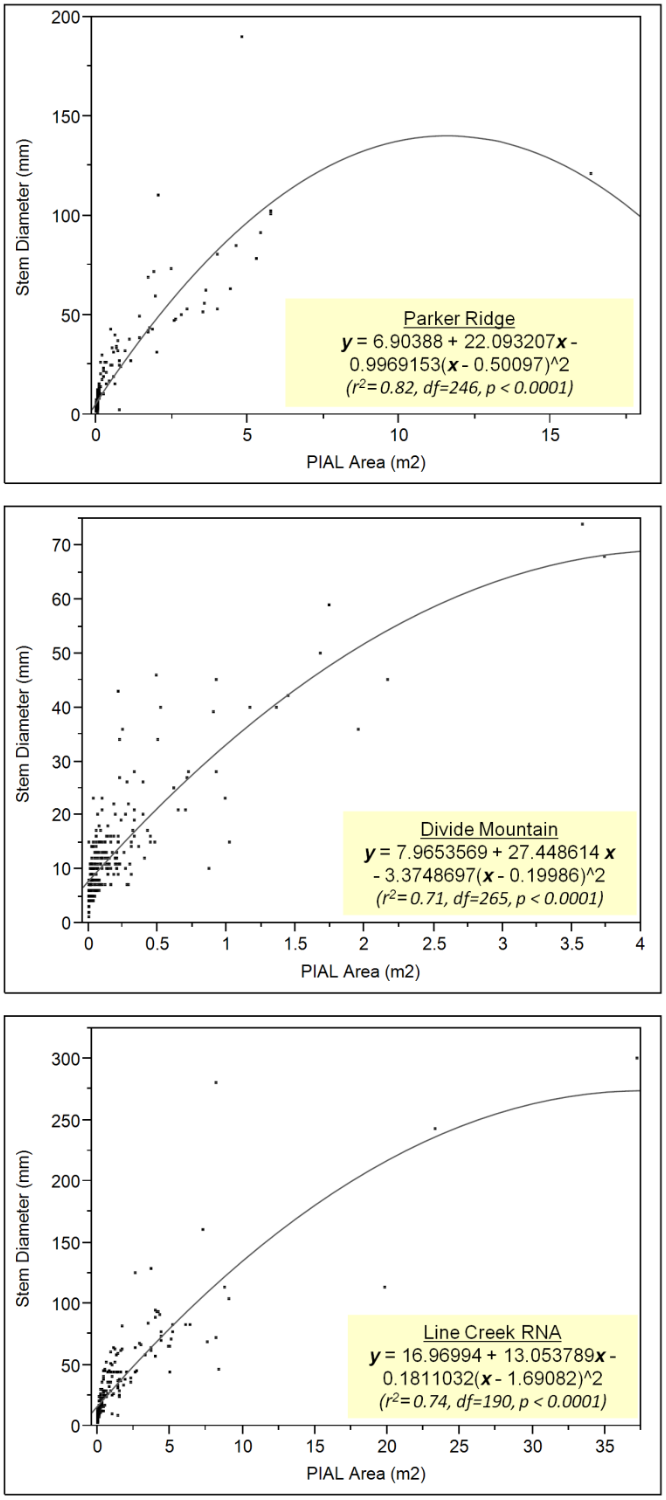

Fig. 5. Linear Regression plots showing the relationship between measured stem diameter and canopy area of solitary whitebark pine trees. All three treeline study areas show a statistically significant strong positive correlation ($r > 0.8$, $p < 0.0001$). Note, measurements are for all sampled solitary whitebark pine, regardless of whether they have neighbors within the same sampling plot. Also note, measurements for three whitebark pine trees in Divide Mountain were not recorded, and are therefore not shown.

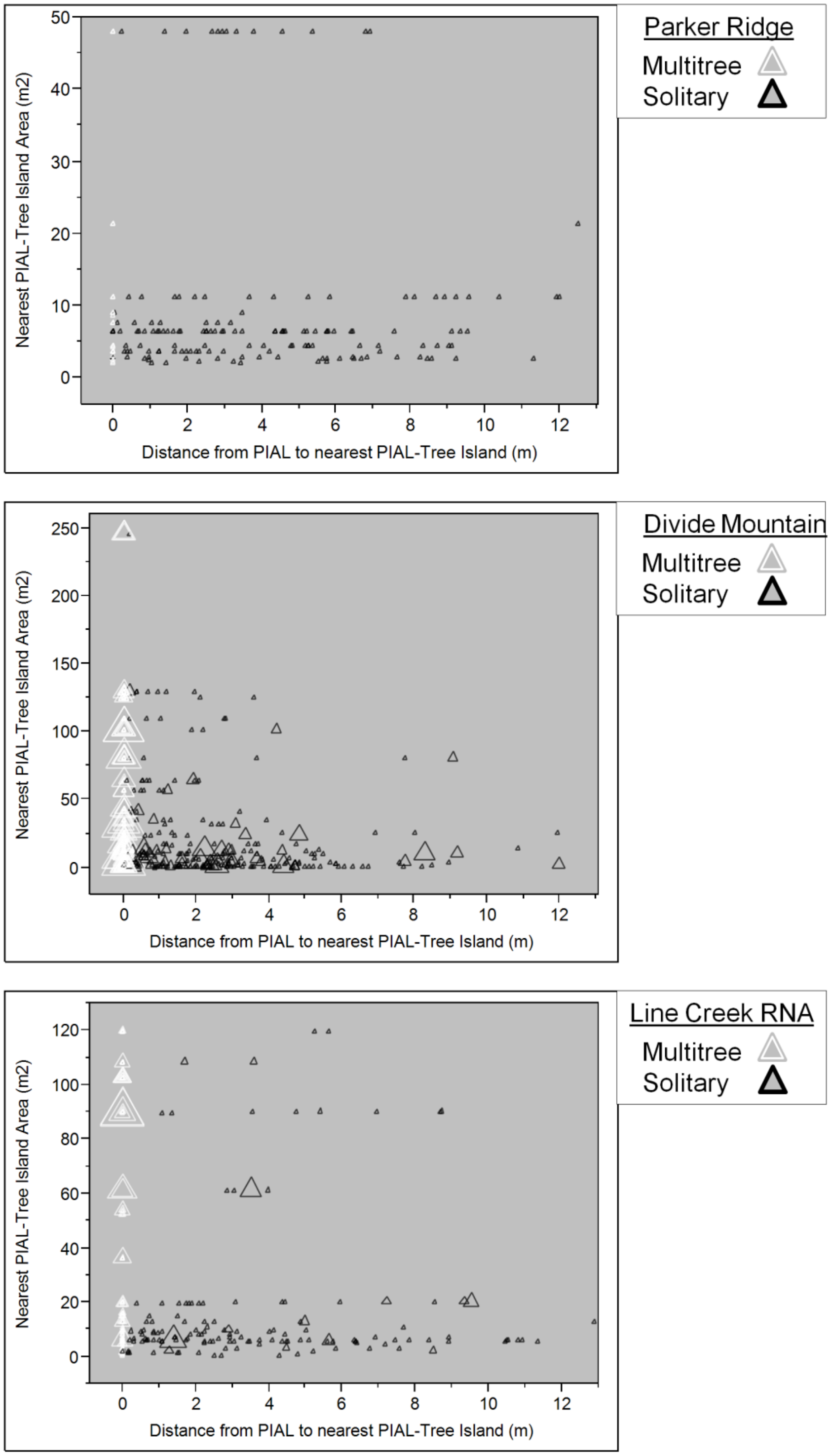

Fig. 6. Bubble plot showing a Tree Island Area vs. Distance relationship: Distance from a whitebark pine (PIAL) tree to the edge of the nearest whitebark pine-containing tree island, compared with that tree island's canopy area. Triangles are sized by canker count (smallest = 0 cankers, see Parker Ridge for size reference), and color coded as either multitree/solitary, and reflect the characteristics of the whitebark pine measured from.

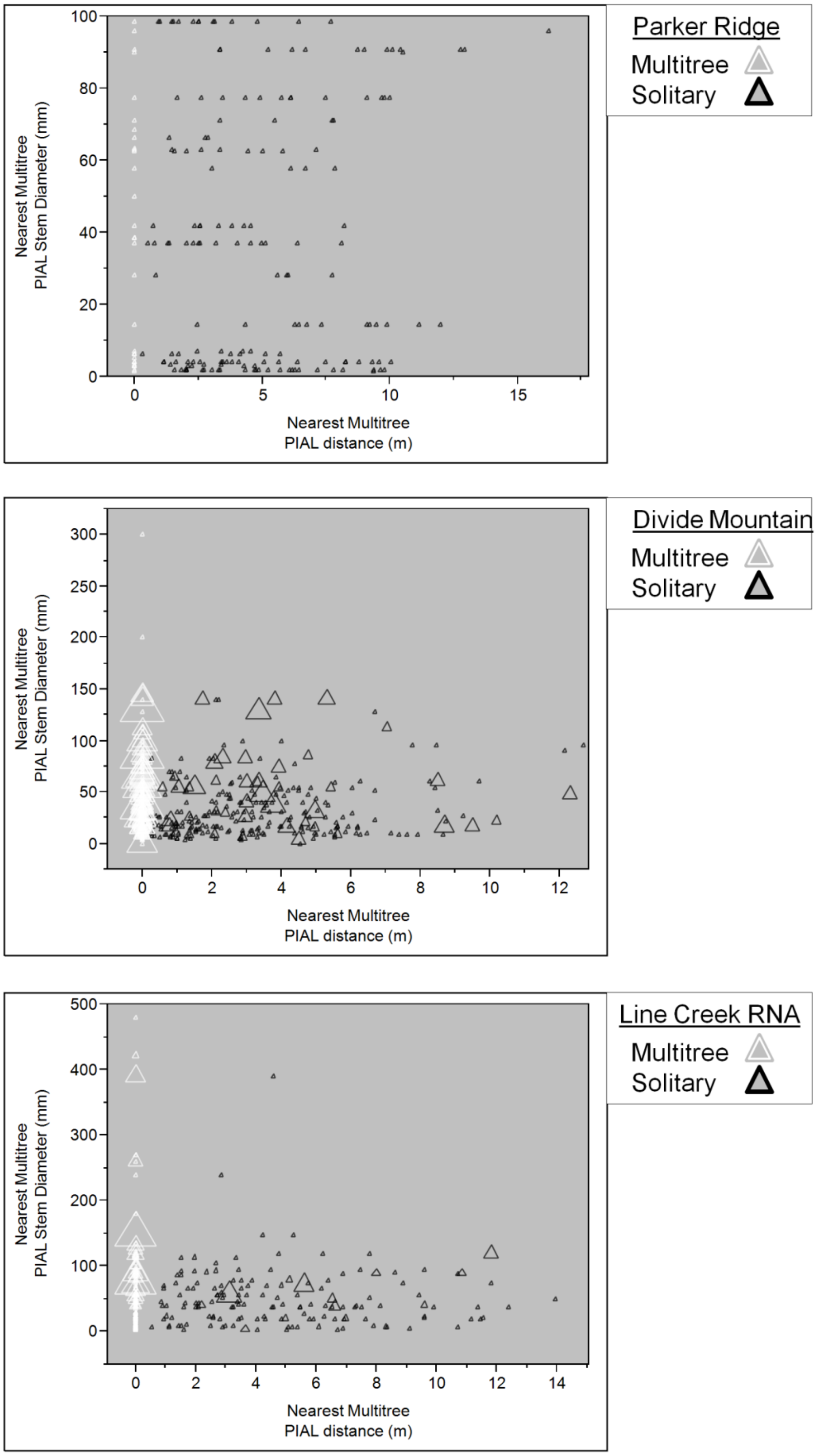

Fig. 7. Bubble plot showing the nearest Multitree Stem Diameter vs. Distance relationship: Distance from a whitebark pine (PIAL) tree to the nearest whitebark pine multitree location in a tree island, compared with that multitree's stem diameter. Triangles are sized by canker count (smallest = 0 cankers, see Parker Ridge for size reference), and color coded as either multitree/solitary, and reflect the characteristics of the whitebark pine measured from.

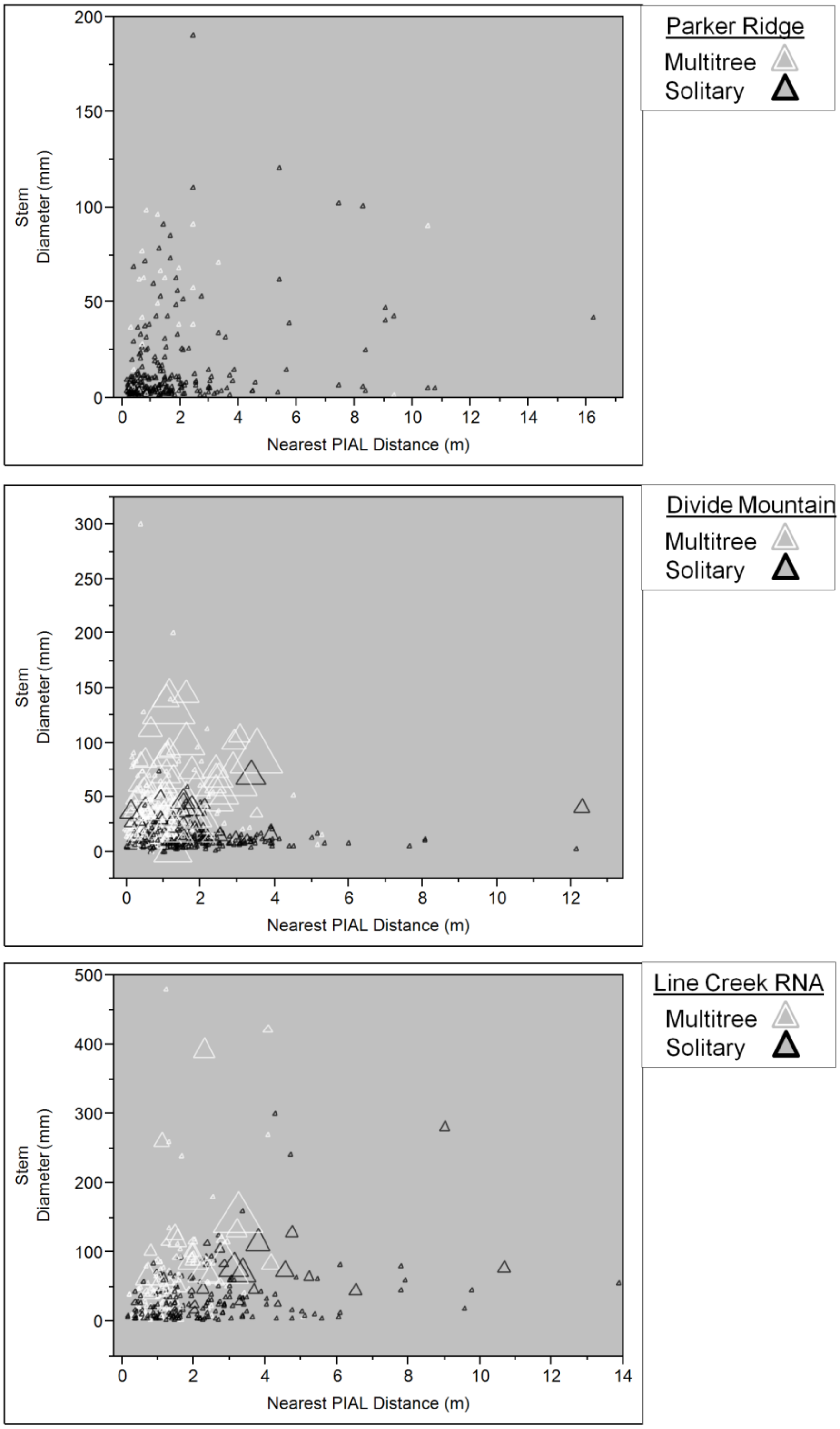

Fig. 8. Bubble plot showing Stem Diameters vs. nearest Distance relationship: Distance from a whitebark pine (PIAL) tree to its nearest whitebark pine neighbor. Stem Diameter, canker count, and multitree/solitary characteristics are for the whitebark pine measured from. Triangles are sized by canker count (smallest = 0 cankers, see Parker Ridge for size reference), and color coded as either multitree/solitary.

Chapter 6: Conclusion

This dissertation explored the potential consequences of the introduced invasive blister rust disease to whitebark pine treeline communities and to treeline position as a bioclimatic indicator, and is the first study to examine the coupled effects of invasive disease and climate change on treeline dynamics. The research presented here contributes to the broader knowledge of how this fungal pathogen may be manifested within the dry, cold, and windy conditions prevalent in the extreme environments of whitebark pine treeline communities. The three studies in this dissertation examined abiotic factors that influence blister rust disease infection in the extreme conditions of whitebark pine treeline environments, explored hypothetical "what if" agent-based model simulation scenarios to determine implications on treeline position, and linked spatial patterns of tree characteristics to disease infection across these fragile treeline landscapes.

This research contributes to much-needed research in spatially and ecologically complex metacommunities and examines the consequences of anthropogenic threats to a species important in promoting biodiversity (Urban et al., 2012). Three major contributions were provided by these studies: 1) a detailed inventory on the presence and intensity of blister rust infection among whitebark pine treeline communities in conjunction with the underlying and surrounding topographic characteristics that influence disease infection at the tree level, 2) an understanding of potential outcomes of climate change and blister rust disease through the development of an agent-based model, and simulation of whitebark pine treeline dynamics under hypothetical "what if" scenarios, 3) findings on the spatial connection between neighboring whitebark pine trees and tree islands, and their size, growth habit, and infection rate, by examining spatial patterns among diseased and undiseased treelines.

The first study (Chapter 3: “Topographic Influences on the Distribution of White Pine Blister Rust in *Pinus albicaulis* Treeline Communities”) involved a fine scale analysis to examine relationships of blister rust infection and topographic variables underlying each whitebark pine tree. Using high resolution GPS units to map the terrain of each sampling plot yielded submeter digital elevation models and unique terrain characteristics for every sampled tree. Out of the two sampled treeline communities, whitebark pine trees growing in the northern study area in Divide Mountain had slightly higher infection rates than those at the Line Creek RNA study area, and in both study areas tree island whitebark pine exhibited more cankers than solitary whitebark pine. The latter finding revealed high canker densities associated with tree island whitebark pine and high canker intensity, and is a similar finding in previous studies (e.g., Resler and Tomback, 2008; Smith et al., 2011). Model results showed that the most influential topographic factors were those that appeared to compensate for the extreme conditions prevalent at each treeline study area. For example, solar radiation likely ameliorates conditions for blister rust development in the extreme cold climates of each treeline study area. At the northerly site at Divide Mountain (which has milder and wetter climates than Line Creek RNA) whitebark pine trees located at sites with higher solar radiation and closer to glaciers tended to have more cankers than those on topographic sites that differ. In the dryer climates of the southerly site at Line Creek RNA, model results suggested terrain with higher solar radiation, and moisture-controlling characteristics such as concave surface curvature, and proximity to streams and lakes were more influential sites for blister rust development on whitebark pine trees. The high topographic position of both study areas appeared strategic places for the associated moisture and wind-dispersal requirements of blister rust spore transmission and infection of whitebark pine. Topographic depressions that provide shelter, in terms of modifying extreme abiotic conditions at treeline, which aid the establishment of whitebark pine trees and development of tree islands, also appear influential to blister rust. Topographic position, microtopography of the tree site, and microclimates within densely populated tree islands, seemed to create favorable conditions that support blister rust infection. In the extreme climates of these treeline study areas east of the Continental Divide, it appears that the same sites that allow for ameliorated conditions, as well as the coexistence of hosts, promote blister rust development while concurrently hindering whitebark pine. Future research in whitebark pine treelines could use these model results to pinpoint treeline landscape factors potential for blister rust severity and mitigate conservation efforts in whitebark pine forest restoration.

Utilizing the knowledge and findings from the first study, empirical data and observations from previous studies, and those from the literature, the second study (Chapter 4: "Feedbacks, disease, and climate influences on whitebark pine treeline dynamics: An agent-based treeline model") involved the development and simulation of a whitebark pine treeline agent-based model. The goal of creating an agent-based model was to assess potential impacts of climate change and blister rust disease infection on treeline pattern and process. From the five hypothetical simulations of untreated, diseased, climate amelioration, climate and disease introduction, and accelerated climate and disease introduction scenarios, it was clear that feedbacks drive treeline dynamics. A logical outcome was that both pine and spruce tree agent populations benefitted under climate amelioration alone, and treeline position advanced to higher slopes. The unknown outcome was that although the introduction of disease and subsequent mortality of pine agents reduces competition from pine, this did not boost spruce agent populations even with an ameliorated climate that should promote the growth of spruce. Rather than spruce replacing the ranks of the absent pine agents, the absence of the pine's facilitative processes proved more detrimental to treeline position, one that could not be remedied even by an ameliorated climate. These results support the notion proposed by Tomback and Resler (2007) that in whitebark pine-dominated treeline communities, blister rust infection and subsequent mortality of whitebark pine will almost certainly have a negative effect on other treeline conifers and the development of tree islands. Climate models that predict treeline advancement to higher altitudes under warming climate scenarios, may predict the wrong outcome when modeling a treeline landscape inflicted with disease. In the case of blister rust infected whitebark pine treeline communities, treelines will likely not respond in the expected upslope advance under warming climate trends. Further development of treeline agent-based models could incorporate differing climate scenarios such as increased precipitation, or the combined effects of drought and blister rust disease on the treeline community. Simulations of additional "what if" scenarios will help assess additional implications to treeline ecosystems, and target the most problematic areas where conservation efforts are needed most.

The goal of the final chapter (Chapter 5: "Spatial Patterns of Whitebark Pine in Treeline Communities, and the Connection with Disease") was to explore spatial relationships between tree proximity and their growth and health characteristics, because spatial patterns of trees are influenced by specific ecological and environmental conditions—and disease patterns may be inferred from these conditions. Examining nearest neighbor distances between trees and tree islands (in relation to their size, growth habit, and health), diseased treelines revealed different spatial patterns than those of the undiseased treeline. In the diseased treelines, whitebark pine trees with larger stem diameter neighbors, and larger tree island neighbors, tended to have more cankers—and in terms of neighbor distance and traits these trees were more clustered. In the undiseased treeline, nearest neighboring tree islands and multitree stem diameters were considerably smaller, and neighbor distance and trait relationships revealed patterns more random and dispersed. The clustered patterns at the diseased treelines indicate that spatial autocorrelation may be occurring among diseased whitebark pine. The fact that infected whitebark pine trees cannot directly infect other pines implies that this pattern of spatial autocorrelation must be occurring indirectly. The connectivity and size of tree islands appeared to support conditions favorable for blister rust disease development, transmission, and infection. Spatial patterns of trees and patterns of disease imply that the environmental phenomena driving growth may also influence disease development at treeline. Patterns at the undiseased treeline showed less clustering, smaller tree sizes, and many more whitebark pine grew in solitary form than in tree islands. The facilitative benefit of neighboring trees and tree islands, and their functional form in providing shelter for conifer trees from the harsh abiotic conditions in extreme landscapes, seem to also harbor adversaries—in terms of harboring alternate host plants as well as moderating abiotic conditions for disease development. Findings reveal an apparent switch from the positive feedbacks that aid in tree island development, to negative feedbacks that diminish tree island development when blister rust disease is introduced. Future research, including the reconnaissance and research of additional diseased and undiseased whitebark pine treeline communities, could uncover other key characteristics integral in blister rust disease pattern at treeline. Future applications of this research could help mitigate strategic plantings of blister rust genetically resistant whitebark pine seedlings, and potentially target microsites prone to blister rust severity—namely, under the shelter of blister rust-plagued whitebark pine tree islands.

With blister rust plaguing most of whitebark pine's distributional range, coupled with mountain pine beetle infestation and fire suppression, the future of this keystone species remains bleak. However, conservation efforts to preserve this threatened species may provide hope for whitebark pine communities. Assisted migration of whitebark pine has been proposed by others, and involves the relocation of species vulnerable to climate change and already at the brink of their distributional limit (McLane and Aitken, 2012). As suggested by Urban et al. (2012) there is biodiversity value in applying assisted migration practices for the preservation of species that are particularly poor dispersers that are under the threat of climate change, and that would otherwise be lost. One viable option for conserving whitebark pine threatened by blister rust involves the restoration efforts of actively planting blister rust resistant whitebark pine seedlings in strategic subalpine locations, and these efforts are ongoing (Keane and Parsons, 2010; Keane et al., 2012). For whitebark pine treeline communities threatened by blister rust, strategic planting of rust-resistant seedlings may be an answer. Precise planting of genetically rust-resistant whitebark pine seedlings at known locations of heavily infected or canker-induced dead whitebark pine could be a key contribution to conservation efforts at treeline. Research that helps pinpoint potential problem areas for blister rust incidence can guide conservation efforts.

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