WHITEBARK PINE AT TREELINE IN THE GREATER YELLOWSTONE ECOSYSTEM: PREVALENCE, FACILITATION, AND BIOPHYSICAL CHARACTERISTICS OF LEEWARD MICROSITES

by

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B.S., University of Colorado Denver, 2013

A thesis submitted to the

Faculty of the Graduate School of the

University of Colorado in partial fulfillment

of the requirements for the degree of

Master of Science

Biology Program

2017

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Thesis directed by Professor Diana Tomback

Abstract

Facilitative interactions are particularly important in the climatically stressful alpine treeline ecotone (ATE), the transition zone from closed canopy forest to alpine tundra. Within some ATEs on the harsh Eastern slope in the Rocky Mountains, whitebark pine (*Pinus albicaulis*)—a foundation and keystone species—plays a central role in tree island development by facilitating the survival and growth of leeward conifers more frequently than other species. However, the structure, composition, and dynamics of ATE formation are not well known for some geographic regions of western North America, including the Greater Yellowstone Ecosystem (GYE). Although facilitative interactions are considered important to treeline community development, comparisons of biophysical attributes among the leeward microsites of nurse objects and trees are also lacking. We conducted an exploratory study of four treeline communities in the GYE to investigate (1) the prevalence of whitebark pine, (2) the proportional occurrence of whitebark pine as a tree island initiator, (3) whether solitary whitebark pine abundance predicts its prevalence as a tree island initiator, (4) whether whitebark pine better ameliorates local biophysical conditions relative to other plants or objects, (5) the relationship between common nurse objects and solitary/tree island initiator establishment, and (6) the presence and severity of *Cronartium ribicola*, an invasive pathogen that attacks and kills

whitebark pine, in these communities. We found that whitebark pine is the most prevalent solitary conifer and tree island component, and initiates tree island formation in direct proportion to its abundance as a solitary tree. We also found that whitebark pine leeward microsites did not consistently experience the most moderate microclimate compared to spruce, fir, rock and unprotected leeward microsites; differences in microclimatic conditions by microsite type depended substantially on the general climatic conditions observed at each study area. Among our study areas, *C. ribicola* infection rates ranged from less than 1% to 18%. Our findings suggest that whitebark pine is an important treeline species in the Greater Yellowstone Ecosystem. Losses of whitebark pine from infection by *C. ribicola* will lead to proportional changes in the composition and structure of ATE communities in the GYE, including decline in tree island formation on the landscape.

The form and content of this abstract are approved. I recommend its publication

Approved: Diana F. Tomback

DEDICATION

To my wife, Elizabeth Rose Pansing, whose intelligence, grace, and adventurous spirit rouse me to follow my heart. To my father, Edward James Wagner, whose passion for grand questions and profound contemplation always inspires me to think boldly. For my mother, Susan Lynn Knoll, whose boundless energy has always been contagious, and whose love and empathy make her the matriarch of our family. To my step-father, Gary Evertt Knoll, whose patience and fortitude give me balance. Finally, to the giants who came before me, whose shoulders never tire.

> "If God were to hold all Truth concealed in his right hand, and in his left only the steady and diligent drive for Truth, albeit with the proviso that I would always and forever err in the process, and to offer me the choice, I would with all humility take the left hand." –Gotthold Ephraim Lessing (Anti-Goese, 1778)

ACKNOWLEDGEMENTS

This product would not have been possible without Dr. Diana Tomback. Her determination, support, and guidance have been a sustained source of inspiration. My respect and appreciation for Dr. Raibatak Das, whose statistical knowledge was invaluable to this project. My utmost appreciation for Dr. Rafael Moreno-Sanchez, whose positivity was contagious, and whose background helped place this work in context. My sincerest gratitude to Dr. Michael Wunder for assisting in the development of my quantitative skills, and for being a person I aspire to emulate. I am profoundly grateful to Bill Lee, Jimmy Smail, Tanner Shuler, Daniel Byron, Scott Berkenfield, Ellen Jungck, and Carl Crittenden of the United States Forest Service (USFS) for assisting with logistical planning and execution. A special thanks to Kent Houston (USFS), whose professional support made this project possible. This project would not have been nearly as enjoyable without the help and humor of my friend, T. Ryan McCarley. Finally, my sincerest respect and appreciation to my friends and colleagues in the Department of Integrative Biology at the University of Colorado Denver; their tenacity and desire to make this world a better place has profoundly influenced this project, and my life.

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LIST OF ABBREVIATIONS

1. ATE Alpine Treeline Ecotone—the region of transition from closed-canopy upper subalpine forest to treeless alpine tundra.

2. GYE Greater Yellowstone Ecosystem—a temperate zone area in the northern Rocky Mountains that encapsulates swaths of southwestern Montana, eastern Idaho, and northwestern Wyoming. It is defined by a large community of interacting organisms.

3. WPBR White Pine Blister Rust—a disease caused by the invasive fungal pathogen *Cronartium ribicola*.

3. HDI Highest Density Interval—the Bayesian analog to frequentist confidence intervals. HDI boundaries are fixed, and the estimated parameter is a random variable. This is in contrast to frequentist confidence intervals, which have random variable boundaries and a fixed parameter value.

Chapter I

ECOLOGICAL FOUNDATIONS

Overview

Landscape pathology examines how pathogens shape the distribution and dynamics of plant communities on a local scale (Holdenrieder et al., 2004). Across the range of five-needle white pines, infection by white pine blister rust—a disease caused by the exotic fungal pathogen, *Cronartium ribicola*—has caused extensive damage and mortality (Ellison et al., 2005; Schwandt et al., 2010; Tomback & Achuff, 2010; Bockino and Tinker, 2012). One of the most widely-distributed of the white pines, whitebark pine (*Pinus albicaulis* Engelm.) has experienced rapid decline in the western U.S. and Canada due to mortality from: 1) blister rust; 2) mountain pine beetle outbreaks; and 3) fire exclusion. A keystone and foundation species, whitebark pine fosters biodiversity and ecosystem stability (Tomback et al., 2001; Ellison et al., 2005; Tomback & Achuff, 2010; Tomback et al., 2011). This ecological role results from whitebark pine's seed dispersal by Clark's nutcrackers (*Nucifraga columbiana*), hardy seedlings, and high tolerance for cold and windy sites (Tomback et. al., 2011).

Under harsh conditions, whitebark pine may participate in positive interactions with neighboring plants (Callaway, 1998), in which leeward conifers may experience a moderated microclimate in the lee of whitebark pine, at no cost to the windward participant—an interaction referred to as facilitation (Stachowicz, 2001; Butler et al., 2007). This interaction contributes to tree island initiation (Resler and Tomback 2008; Tomback et al. 2014), allowing treeline communities to develop under harsh environments. Because whitebark pine's ecosystem function may be diminishing due to

mortality from white pine blister rust, community structure, whitebark pine's ecological role, and climatic variables must be used to assess treeline dynamics.

Climate change is expected to alter forest tree distributions both latitudinally and in elevation. Depending on the species composition and landscape structure, some alpine treeline ecotones (ATEs) will have a greater ability to respond to climatic change, while others may be less equipped (Harsch et al., 2009). Upward movement of whitebark pine communities is predicted as a response to climate change (e.g., Schrag et al. 2007). However, damage and mortality to newly established recruits due to infection by white pine blister rust may counter the effects of warming in communities (Tomback and Resler, 2007). At this time, the combined effects of pathogen disturbance and increasing temperature on ATEs are largely unknown, and we need to examine the interactions among disease, vegetation, and climate change.

Research previously conducted by: 1) D. F. Tomback and her students—University of Colorado Denver; 2) L.M. Resler and her student Emily Smith-McKenna—Virginia Polytechnic Institute and State University; and 3) G. P. Malanson—University of Iowa—have examined the proportional abundance of whitebark pine, its role in tree island development, and the incidence of blister rust in selected areas across the Central and Northern Rocky Mountains, from 45° to about 54° latitude. This work shows that geographic variation exists in the importance of facilitation by whitebark pine in tree island development.

Whitebark pine has been found to be a majority tree island initiator and dominant conifer in the ATE at several study locations in the Rocky Mountains—Stanley Glacier, Kootenay National Park, British Columbia; Lee Ridge and Divide Mountain, Glacier

National Park, Montana; and Wyoming Creek, Custer National Forest, Wyoming (Resler and Tomback 2008, Tomback et al. 2014). However, whitebark pine is not a majority tree island initiator in other ATE communities—Tibbs Butte, Shoshone National Forest, Wyoming; Gibbon Pass, Banff National Park, Alberta; and Willmore Wilderness, Alberta—although it is abundant in these areas (Tomback et al. 2014, Tomback and Resler, in preparation). The abundance and ecological role of whitebark pine in facilitation of tree islands in the ATE remains unknown in its southeastern-most range (i.e., 42° latitude), the southern Wind River Mountains. Specific questions for this region are: What is the proporitonal abundance of whitebark pine? What is the incidence of blister rust? What is the extent of whitebark pine's ecological role? Do the microclimatic conditions differ from documented study locations in whitebark pine's central and northernmost range, and if so, how? Does whitebark pine provide better microsite protection than other conifers or unprotected microsites, and if so, which conditions? What do we predict in terms of the future movement of the ATE in the presence of blister rust and climate change?

Background

The Alpine Treeline Ecotone

The alpine-treeline ecotone (ATE) is the transition from closed canopy forest to treeless alpine tundra (e.g., Holtmeier, 2009). Compared to subalpine forest, the environment within the ATE is characterized by low temperatures and high winds, where species experience frozen soils, elevated frost exposure, increased solar radiation, high rates of evapotranspiration, and amplified nutrient scarcity (Körner and Paulsen, 2004, Holtmeier, 2009). In this zone, upright growth forms of trees are unable to develop due to

wind-blasting, and tissue formation is limited by low temperatures (Körner, 2008). When tree anatomy and physiology are impeded significantly by these climatic extremes, dwarfed morphologies—known as krummholz growth forms—result. These stunted forms respond to slightly higher temperatures close to the ground (Körner & Paulsen 2004; Hoch & Körner, 2009), and often grow in the lee of biotic or abiotic structures—termed nurse objects—that provide shelter from the wind (e.g., Resler and Tomback 2008, Castro et al. 2011). As elevations increase, trees reach their upper distributional limit due to stress from these harsh conditions, giving way to herbaceous alpine species (Malanson et al., 2011).

Facilitation

Within many ecosystems that exist under climatically stressful conditions, positive associations can occur among neighboring plants in which one individual experiences localized protection from climatic stress at no cost to others (Stachowicz, 2001; Butler et al., 2007). As conifers struggle to germinate, establish, and grow in the ATE, these facilitative interactions among neighbors become more important than competition for resources (Callaway et al., 2002). Competitive interactions among spatially associated individuals at lower elevations are facilitative in this zone and often result in the formation of tree islands—groups of two or more krummholz trees in close proximity (Marr, 1977). These emergent structures occur when a conifer successfully establishes in the open or in the lee of a nurse object such as a rock, shrub, or terrace riser (Resler et al., 2005; Resler, 2006; Resler and Tomback, 2008). Other conifers will then germinate, establish, and grow in close leeward proximity to the initiating conifer, enjoying moderated climatic conditions (e.g. decreased wind speed; Pyatt et al. 2016).

These conifers then ameliorate the microclimate in their lee. This positive feedback of climate moderation and survival among neighbors occurs until tree island size is ultimately limited by topography or nutrient scarcity (Resler, 2006). The result is a landscape containing clusters of environmentally dwarfed trees above the continuous forest limit, described as island-krummholz (Harsch and Bader, 2011).

Treeline Dynamics

The position and stability of the ATE is controlled by environmental and climatic influences on conifer regeneration, recruitment, and growth. Harsch and Bader (2011) sum up the mechanisms that affect performance as: 1) growth limitation—a result of impaired biosynthesis in response to low growing season temperature, short growing season duration, or nutrient deficiency; 2) dieback—a result of physical damage due to high snow load, frost, frozen soil, excess radiation, and high wind; and 3) seedling mortality—a result of physical damage caused by high snow load, frost, frozen soil, excess radiation, heat stress, high temperatures, and low precipitation. With all these environmental challenges—coupled with geomorphic barriers to establishment—trees struggle to survive at the highest elevations. The prevailing theory is that the elevational boundaries of the ATE are governed by climatic conditions during the growing season—July through September (Körner & Paulsen, 2004; Hoch & Körner, 2009; Harsch & Bader, 2011). Therefore, moderation of the environmental and climatic variables of the growing season—temporary or long-term—that limit growth and tree establishment may allow the ATE to move upward in latitude and elevation (Schrag, et al., 2007).

In the next 100 years, global ambient temperatures are predicted to increase approximately 2.5°C (Grace et al, 2002). Because ATE communities are among the first

to display signs of climatic stress, it has been hypothesized that many of them will serve as first indicators of climate change (Smith et al., 2009). It has already been demonstrated that 52% of all ATEs have advanced in elevation since 1900 A.D.—with only 1% receding (Harsch et al., 2009). Research linking past temperature changes to ATE movement (Lloyd and Graumlich 1997), and ATE position to worldwide isotherms (Körner and Paulsen 2004) has provided evidence that the formation and maintenance of these ecosystems is largely temperature controlled. As the minimum growing season temperature rises over time, growth and seedling establishment are expected to increase, and dieback due to freezing or frost at higher elevations should decrease (Körner, 2008). At the current rate of climate change, ATEs are expected to move upward in elevation an average of 140—700 m (Grace et al., 2002). Bioclimatic envelope models also predict these distributional changes (McKenney et al., 2007; Warwell et al., 2007).

At the highest elevations and latitudes, the environmental and climatic variables of the ATE are too extreme for the majority of conifer species (Hättenschwiler and Smith, 1999). Pyatt et al. (2016) demonstrated that micosites in the lee of conifers provide ameliorated climatic conditions compared to rock and unprotected microsites. Successful establishment and community structure in harsh conditions is dependent upon facilitation via the formation of tree islands.

Whitebark Pine: A keystone and Foundation Species

One of the most widely-distributed of the white pines in the U.S. and Canada, whitebark pine (Family Pinaceae, Subgenus *Strobus*.) has been designated as a keystone and foundation species in subalpine ecosystems and the ATE (Tomback et al., 2001). It's a keystone species because it fosters more biodiversity than its proportional abundance

would suggest (e.g., Mills et al. 1993, Power et al. 1996, Soule´ et al. 2003). Additionally, whitebark pine often defines community structure, creating stable conditions for other species (Tomback et al., 2011). Due to its high tolerance for low temperatures, high wind speeds, and hardy seedlings, whitebark pine is able to play a key functional role as tree island initiator in many ATEs across the western United States (Tomback and Achuff 2010; McKinney and Tomback, 2011). Other important ecosystem services provided by whitebark pine include facilitating the growth of other conifers (Callaway, 1998), the regulation of runoff by slowing snow melt (Farnes, 1990), decreasing soil erosion via root systems (Arno and Hammerly, 1984), contributing to early-successional regeneration following fires, resulting in community development (Tomback and Linhart, 1990; Tomback et al., 2001), and providing seeds that serve as an essential component of the diets of a number of birds and small mammals (Tomback and Kendall, 2001). The benefits of whitebark pine that pertain to watershed hydrology are also of the utmost importance to society. Farmers, ranchers, and Native Americans—who inhabit many regions downstream of these mountain communities—benefit from the protraction of snowmelt, which normalizes the levels of streams and creeks (Farnes 1990). Water levels in reservoirs utilized in urban communities are also maintained by the control of runoff (Smith et al., 2009).

Among the many consequences of krummholz growth is a sharp decrease in cone and viable seed production (Grace et al., 2002). Species employing a wind-dispersal strategy, such as Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) experience a high probability of sun-scorching and predation of seeds by granivorous birds and mammals in the ATE, reducing the

likelihood of germination. In contrast, whitebark pine is an ornithochorous conifer—meaning it relies on the assistance of birds for the dispersal of seeds—and has evolved a special mutualism with a corvid, the Clark's nutcracker (*Nucifraga columbiana*) (Tomback, D.F., 1982). To utilize whitebark pine seeds for food in the winter and spring, nutcrackers break off the tough scales of the cones with their beaks, place seeds in a sublingual pouch, and transport them up to 32.6 kilometers (Lorenz et al. 2011) before burying small 'caches'—groups of seeds numbering 1-15—in the ground (Hutchins and Lanner, 1982; Tomback 1982). This process results in the transport of many whitebark pine seeds from subalpine forest to the ATE every year (Tomback, 1986; Tomback and Linhart, 1990). Unrecovered whitebark pine seeds may germinate and establish either in open or sheltered microsites and become the initiating conifer of tree islands. In a relative vigor study, Blakeslee (2012) was able to determine that whitebark pine has greater vigor at treeline than other ATE conifers—Engelmann spruce and subalpine fir—by analyzing shoot length measurements. This means that whitebark pine may have superior hardiness to harsh conditions and may regenerate, establish, and survive more frequently than other, less-hardy species.

Threats

Twentieth century globalization and climate change have caused: 1) native mountain pine beetle (*Dendroctonus ponderosae*) outbreaks of unprecedented severity; 2) the spread of the invasive fungal pathogen *C. ribicola*, which causes the disease white pine blister rust; and 3) wildfire suppression, resulting in the extensive loss of trees through successional replacement across the range of whitebark pine (Tomback and Achuff, 2010). In some areas, whitebark pine mortality rates approach one-hundred

percent (Smith et al., 2009). Additionally, these factors may diminish whitebark pine's role in affected ATE communities, resulting in unpredictable changes in ecosystem function, stability, and biodiversity.

Mountain Pine Beetle. Mountain pine beetles—native to western North America—are parasitic insects that attack pine trees periodically, killing mature trees within weeks of successful infestation (Cole and Amman, 1969). Although pine species that comprise a large portion of lower-elevation forest - lodgepole (*Pinus contorta* Douglas ex Loudon) and ponderosa (*Pinus ponderosa* Lawson and C. Lawson) pine - are primary hosts, all mature western pines qualify as targets (Tomback et al., 2011). During particularly severe outbreaks, these pests can advance to higher elevation forest communities (Perkins and Swetnam, 1996). Outbreaks are limited in severity and scope by climatic conditions that regulate mountain pine beetle life cycles. Over the last 20 years, climate change has resulted in unprecedented mountain pine beetle proliferation (Logan et al., 2010), resulting in epidemic-level mortality of mature whitebark pine in the central and northern Rocky Mountains (Gibson et al., 2008; Schwandt et al., 2010).

Fire Exclusion. Whitebark pine is an early successional tree on productive sites, and is less shade-tolerant than other subalpine and treeline conifers (Arno, 1986). Throughout the 20th century, fire exclusion has inhibited the natural 'successional clock' and led to the replacement of whitebark pine by Engelmann Spruce and subalpine fir, fundamentally altering forest structure. In forests that have been 'protected' from fire, the result has been a decrease in biodiversity.

White Pine Blister Rust. Whitebark pine trees are infected by *C. ribicola* when wind-dispersed basidiospores enter needle stomata (McDonald and Hoff, 2001). Rust

mycelia spread from the needles into the living wood and produce the characteristic 'cankers' and branch swelling associated with blister rust once aecial sacs break through the bark (Fig. I.1; McDonald and Hoff, 2001). These sporulating cankers girdle branches and stems by inhibiting nutrient and water flow; the tree dies if cankers girdle the bole of the tree (McDonald and Hoff, 2001). New spores are dispersed—via wind—as the sacs of aeciospores of the sporulating cankers rupture (McDonald and Hoff, 2001).

Unlike mountain pine beetle and fire suppression, white pine blister rust affects regeneration, recruitment, and growth by attacking seedlings and saplings in addition to mature trees. Whitebark pine require up to 50 years to reach reproductive maturity (McCaughey and Schmidt, 1990), this means that once blister rust is introduced into a location, loss in cone production may last indefinitely. Additionally, the loss of seedlings and saplings—which die more readily than a fully mature tree—drastically reduce the regeneration capacity of a community. Unlike mountain pine beetles, blister rust may also affect krummholz whitebark pine, altering whitebark pine's ecosystem services in the ATE. Because climate change is expected to alter treeline dynamics, the effects of blister rust may affect treeline response to climate warming. What could result is a diminished ecological function in whitebark pine across its range, or net forest loss.

Tables and Figures



Fig. 1.1: White pine blister rust infection. Blisters containing aeciospores on the branches and bole of a whitebark pine.

Chapter II

WHITEBARK PINE AT TREELINE IN THE GREATER YELLOWSTONE ECOSYSTEM: PREVALENCE, FACILITATION, AND POTENTIAL DISRUPTION BY AN INTRODUCED PATHOGEN

Abstract

Facilitative interactions are particularly important in the climatically stressful alpine treeline ecotone (ATE), the transition zone from closed canopy forest to alpine tundra. Within some ATEs on the harsh eastern slope in the Rocky Mountains, whitebark pine (*Pinus albicaulis*)—a foundation and keystone species—plays a central role in tree island development by facilitating the survival and growth of leeward conifers more frequently than other species. However, white pine blister rust (WPBR)—a disease caused by an invasive fungal pathogen *Cronartium ribicola*—is resulting in extensive mortality across whitebark pine's range. The structure, composition, and dynamics of ATE formation are not well known for some geographic regions of western North America. The effect of disturbance to ATE whitebark pine is also understudied. We conducted an exploratory study of four treeline communities in the Greater Yellowstone Ecosystem (GYE) to investigate (1) the prevalence of whitebark pine, (2) the proportional occurrence of whitebark pine as a tree island initiator, (3) whether solitary whitebark pine abundance predicts its prevalence as a tree island initiator, (4) whether differences in climate correspond to geographic differences in whitebark pine's frequency of occurrence as a tree island initiator, (5) the relationship between common nurse objects and solitary/tree island initiator establishment, and (6) the presence and severity of white pine blister rust in these communities. We found that whitebark pine is the most prevalent

solitary conifer and tree island component, and initiates tree island formation in direct proportion to its proportional community abundance as a solitary tree. Among our study areas, *Cronartium ribicola* infection rates ranged from less than 1% to 18%. Our findings suggest that losses of whitebark pine from infection by *C. ribicola* will lead to profound changes in composition and structure of ATE communities in the GYE, including decline in tree island formation on the landscape.

Introduction

Temperate zone treeline communities provide important ecosystem services, such as snow retention and soil stabilization (Farnes 1990, Geddes et al. 2005, Tomback et al. 2016a), and wildlife habitat, including refuge for disturbance-sensitive species (e.g., Mattson 1997). The structure and composition, as well as dynamics of treeline formation in the alpine-treeline ecotone (ATE)—the transition between open subalpine forest and tundra—are not well known for some geographic regions of western North America. However, within a number of treeline communities in the Central and Northern Rocky Mountains, and particularly those on the harsh, eastern Rocky Mountain Front, whitebark pine (*Pinus albicaulis* Engelm, Family Pinaceae, Subgenus *Strobus*) functions as a majority tree island initiator, facilitating the survival and growth of leeward conifers more frequently than other species (e.g., Resler and Tomback 2008, Tomback et al. 2014, Tomback et al. 2016a).

There is now a general consensus that facilitation—protective interactions between individuals of the same or different species (Callaway et al. 2002)—is an important biotic process shaping plant community structure and composition in abiotically stressful environments (Bertness and Callaway 1994, Antonsson et al. 2009).

The ATE experiences extreme winds (Marr 1977), cold and variable temperatures (Körner and Paulsen, 2004), poorly developed soils (Arno and Hammerly 1984), aridity (Holtmeier 2003), nutrient scarcity (Holtmeier 2003), high solar radiation (Maher et al. 2005), and truncated growing seasons (Arno and Hammerly 1984).

ATE community development relies on the initial establishment of solitary trees in unprotected microsites, or in protected microsites leeward of *nurse objects* such as rocks and topographic niches (Resler et al. 2005; Fig. 2.1). Once established, these windward conifers create favorable leeward microsites by alleviating wind speeds (Hättenschwiler and Smith 1999, Alftine and Malanson 2004, Pyatt et al. 2016), reducing solar radiation (Germino et al. 2002; Pyatt et al. 2016), decreasing soil temperature variation (Pyatt et al. 2016), and/or increasing soil moisture (Pyatt et al. 2016). Tree islands form when conifers become established in these leeward microsites, building a patch of krummholz trees (Marr 1977). Whitebark pine is often the most prevalent solitary conifer growing at treeline (Resler and Tomback 2008, Tomback et al. 2014, 2016); its prevalence as a solitary conifer predicts its frequency as a tree island initiator among different study areas (Tomback et al. 2016a).

A moderately shade-intolerant and slow-growing conifer, whitebark pine competes poorly on productive sites, resulting in successional losses to faster-growing, shade-tolerant trees (Arno and Hoff 1990, Arno 2001). However, its slow growth and comparatively high carbon gain and water-use efficiency relative to other conifers (Callaway et al. 2000, Bansal et al. 2011), coupled with hardy seedlings, contribute to its general tolerance of stressful conditions common to the ATE, including cold temperatures, aridity, nutrient-poor soils, and high solar radiation (Arno and Hoff 1990,

Tomback et al. 2001b). Whitebark pine's recruitment success at high-elevations may also be attributed to the seed storing behavior of its coevolved mutualist, Clark's nutcracker (*Nucifraga columbiana*; Tomback 1982). Nutcrackers bury whitebark pine seeds in small caches near protective objects, such as rocks, tree trunks, and fallen trees (Tomback 1978); they also transport seeds from parent trees up to 32.6 kilometers for caching (Lorenz et al. 2011). This process results in the dispersal of whitebark pine seeds from upper subalpine forest to treeline and tundra elevations (Tomback 1986).

Whitebark pine is one of the most widely distributed five-needle white pines in the U.S. and Canada (Tomback and Achuff 2010), and serves as a foundation and keystone species in many high-elevation forest communities across the Central and Northern Rocky Mountains (Tomback et al. 2001a, Ellison et al. 2005). A foundation species is a locally abundant and regionally common ecosystem constituent that also creates stable local conditions for others, thereby regulating ecosystem dynamics and disproportionately determining community spatial structure (Dayton 1972, Ellison et al. 2005, Ellison 2014). These Foundation species govern community assembly trajectories by modulating processes fundamental to the establishment and maintenance of associated flora and fauna (Ellison et al. 2014). Similarly, keystone species contribute disproportionately to biodiversity, influencing community composition more than their relative abundance would suggest (Soulé et al., 2003). Loss of foundation and keystone species through disease and other disturbance can destabilize ecosystems and have cascading effects on community structure and composition (Ellison et al. 2005).

The keystone and foundation functions of whitebark pine are discussed in detail elsewhere (Tomback et al. 2001a, Tomback and Kendall 2001, Tomback and Achuff

2010, Tomback et al. 2011). They result from four major features of whitebark pine: large, nutritious seeds; seed dispersal by nutcrackers; hardy, robust seedlings; and tolerance of cold and windy sites (McKinney and Tomback 2011). The foundation functions include early establishment by whitebark pine after fire on poor seedbeds, or on harsh, exposed sites, leading to facilitation and establishment of other conifers; substrate stabilization against erosion at high elevations; snow retention and protraction of snow melt and regulation of downstream flows (e.g., Farnes 1990, Tomback et al. 2016a). The keystone function includes providing wildlife habitat at the highest elevations and providing a significant wildlife food source for a number of granivorous birds and mammals, including grizzly (*Ursus arctos*) and black bears (*Ursus americanus*) (e.g., Tomback and Kendall 2001, Mattson et al. 2001). The extirpation of whitebark pine from subalpine and treeline communities is predicted to result in significant changes in community structure, function, and biodiversity (Tomback and Kendall 2001, Tomback and Resler 2007, McKinney and Tomback 2011, Tomback et al. 2011, Tomback et al. 2016a).

Throughout most of whitebark pine's range, the disease white pine blister rust, caused by the exotic fungal pathogen *Cronartium ribicola*, has resulted in extensive damage and mortality (McDonald and Hoff 2001, Schwandt et al. 2010). White pine blister rust may infect all life stages of whitebark pine, from seedlings to mature trees. Stem infections kill trees; but branch infections reduce cone production and thus potential regeneration (McDonald and Hoff 2001). *Cronartium ribicola* infection threatens the foundation and keystone functions of whitebark pine (Tomback et al. 2001a, Tomback and Achuff 2010). When high infection rates from *Cronartium ribicola* as well as

whitebark pine mortality from blister rust were first detected in whitebark pine-dominated ATE communities, the potential for disruption of structure and function and even altered response to climate warming were explored (Tomback and Resler 2007, Resler and Tomback 2008, Smith-McKenna et al. 2014).

In the Greater Yellowstone Ecosystem (GYE), *Cronartium ribicola* has infected an overall mean of 20 to 30% of the whitebark pine throughout the region (Jean et al. 2011). In this region, whitebark pine is widely-represented in upper subalpine forests (Renkin and Despain 1992, McCaughey and Schmidt 2001), both as a successional component on productive sites and self-replacing component on exposed sites with undeveloped soils. However, the prevalence and developmental role of whitebark pine in ATE communities in the GYE, as well as the ATE structure and function, have been relatively unstudied, as is the prevalence of *Cronartium ribicola*. Elsewhere (Tomback et al. 2016a), we present information that whitebark pine is generally prevalent in ATEs in the GYE but varies in occurrence and in its role as tree island initiator. We also provide information on variation in the occurrence of white pine blister rust in ATEs. Here, we provide more detailed information on community assessments and examine them in relation to mesoclimate conditions.

For this study, we examined four ATE communities in the GYE from the Beartooth Plateau to the southeastern limits of whitebark pine's range in the Wind River Range to determine (1) the prevalence of whitebark pine in treeline communities, (2) the importance of whitebark pine in facilitating tree island initiation, (3) whether solitary whitebark pine abundance predicts its prevalence as a tree island initiator, (4) whether differences in climate correspond to geographic differences in whitebark pine's frequency

of occurrence as a tree island initiator, (5) the relationship between common nurse objects and solitary/tree island initiator establishment, and (6) whether blister rust is present, and, if so, the rate of infection in these communities.

Methods

Study Areas

We performed community composition and climatic assessments in four ATEs in the GYE, two east and two west of the Continental Divide (Table. 2.1, Fig. 2.2). Within all study areas, conifer species included whitebark pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). At Tibbs Butte, the terrain followed a continuous upslope gradient with a few exposed rocks, and undeveloped soils stemming from a bedrock of Precambrian granite (Bevan 1923). Conifers and tree islands were scattered in occurrence. Dominant understory vegetation included *Geum rossii* (R. Br.) Ser., *Potentilla diversifolia* Lehm., and *Saxifraga* spp. (Tomback et al. 2016a).

Paintbrush Divide, Grand Teton National Park, Wyoming, consists of a steady rocky slope that becomes steeper with increasing elevation from SW to NE. *Arctostaphylos uva-ursi* (L.) Spreng., *Myosotis asiatica* (Vesterg.) Schischkin & Sergievskaja, *Senecio* spp., and *Silene acaulis* (L.) Jacq. are the understory dominants (Tomback et al. 2016a).

The Hurricane Pass study area, Grand Teton National Park, Wyoming, has sparse rocks, and undeveloped soils supporting a diverse array of understory vegetation; dominants included included *Dryas octopetala* L., *Senecio* spp., *Silene acaulis* (L.) Jacq., and Graminoids species (Tomback et al. 2016a).

Our southernmost study area was located on Mutiny Ridge in the Wind River Range, Shoshone National Forest, Wyoming, approximately 1.5 km west of Christina Lake. The study area comprised 117 ha on northeast, southeast, and southwest aspects from 3200 to 3400 m elevation. The terrain in the Mutiny Ridge ATE consists of a rock field with soils derived from Precambrian (Archean) crystalline bedrock, including granodiorite, porphyritic quartz monzonite, and magmatic gneiss (e.g., Frost et al. 2000). The understory vegetation includes *Geum rossii (R. Br.) Ser.*, *Pteryxia hendersonii (J.M. Coult. & Rose) Mathias & Constance*, *Phlox pulvinata (Wherry) Cronquist*, and *Silene acaulis (L.) Jacq* (Tomback et al. 2016a).

Community Assessments

In July 2014 and 2015, we established assessment plots within each study area as follows: Tibbs Butte (n = 12), Paintbrush Divide (n = 20), Hurricane Pass (n = 20), and Mutiny Ridge (n = 30). Plots were constructed at random locations generated using the splancs package in R (version 3.1.0, R Core Team 2014; Rowlingson and Diggle 2014). If random points were outside the ATE (i.e., in subalpine forest or alpine tundra), or resulted in plots without any conifers, we created the sampling plot in the nearest krummholz growth. We were cognizant that data collected within the same plot lack spatial independence. Each plot was the sampling unit; we used a plot size of 225 m^2 to minimize environmental variation within each plot, following the methods of Smith-McKenna et al (2013).

We assessed all conifers found completely or partly inside each plot. We identified each tree to species, and classified the ecological role of each as tree island initiator, leeward tree island component, or solitary tree. Tree islands comprised two or

more contiguous conifers with spatially overlapping canopies. Conifers in tree islands were classified as tree island initiators or leeward conifers; initiators were the most windward conifer, and leeward trees were all other trees within the tree island. For this study, there was only one initiating conifer per tree island, and thus the number of initiators equaled the number of tree islands for a given plot. To determine prevailing wind direction, and corresponding windward and leeward designations, we observed wind-flagged branches of krummholz trees within the plot and in the immediate vicinity. Trees spatially isolated from other conifers (i.e., lacking overlap of branches, and often scattered throughout the plot) were classified as solitary. We identified nurse objects as any potentially protective object found directly windward of solitary trees or tree island initiators, including rocks, topographic depressions, and shrubs; we designated conifers with the apparent absence of a nurse object as *unprotected*. Because each whitebark pine germinates from a cache of seeds buried by a Clark's nutcracker (Tomback 1982), some trees may occur as multi-genet tree clusters (Tomback and Linhart 1990). Additionally, Engelmann spruce and subalpine fir may have multiple stems of the same genotype due to clonal reproduction (Grime 1977). Following the methods of Resler and Tomback (2008), we characterized all multi-stem growth forms as a single individual.

We recorded the following information for each plot: number of conifers by ecological role (i.e., solitary, initiator, or leeward), number of conifers by species, and nurse object for each solitary conifer and tree island initiator (i.e., rocks, topographic depressions, shrubs, and unprotected). Additionally, we recorded the number of blister rust-infected whitebark pine by thoroughly examining all stems and canopies for evidence of infection. The criteria for an *infected* blister rust designation included at least

one active canker, or three of the five following characteristics: 1) inactive cankers, 2) stem swelling, 3) branch flagging/dead foliage, 4) rodent gnawing, and 5) oozing sap (Burns et al. 2008).

Mesoclimate Assessments

To estimate differences in climate variables among study areas, we used open source Precipitation Elevation Regressions on Independent Slopes Model (PRISM) data from the last 30 years (1985-2015; PRISM Climate Group, 2015). For each study site, we estimated the average daily growing season temperature and average growing season precipitation. Although literature definitions of growing season length differ, a global study by Körner and Paulsen (2004) found a narrow growing season temperature range in ATEs, and determined the lower limit for plant tissue growth to be 5°C. This temperature is also the threshold at which tissue growth is interrupted in cold-adapted trees (Alvarez-Uria and Körner, 2007). Thus, we defined the growing season as the temporal period between average daily air temperatures of >5°C for >5 consecutive days and average daily air temperatures of <5°C for >5 consecutive days (Frich et al. 2002).

Data Analysis

We converted raw counts for conifer ecological role (i.e., solitary, initiator, and leeward), species, nurse object association (rocks, topographic depressions, shrubs, and unprotected), and blister rust infection incidence (infected vs. uninfected) to proporitonal abundances for each assessment plot. We used R (version 3.2.4, R core team 2016) to conduct all statistical analyses.

Proportional abundance parameter estimates. To estimate overall conifer proportional abundance parameters by ecological role, species, nurse object association,

and blister rust infection incidence for each study area, we bootstrapped the raw proportional abundance data—that is, sampled randomly with replacement over the size of the sample (e.g., 20 on Paintbrush Divide)—for 5000 iterations to generate a sampling distribution of mean proportional abundances for each variable. We calculated the mean of each sampling distribution to identify the proportional abundance parameter estimate ($\hat{p}$). Finally, we used the 0.025 and 0.975 quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% high density interval (HDI).

Mean differences in proportional abundance parameter estimates. We calculated pairwise differences in proportional abundance for conifer ecological role, species, nurse object association, and blister rust infection incidence groups for each assessment plot. For example, comparing ecological roles at the species level, we calculated the difference in proporitonal abundance between whitebark pine and Engelmann spruce, whitebark pine and subalpine fir, and Engelmann spruce and subalpine fir for each assessment plot. We also calculated the difference in proportional abundance between tree island initiators and solitary trees within species. Next, we bootstrapped the pairwise proportional abundance difference data—that is, sampled randomly with replacement over the size of the sample (e.g., 20 on Paintbrush Divide)—for 5000 iterations to generate a sampling distribution of mean difference proportional abundances for each within-group comparison. We calculated the mean of each mean-difference-in-proportional-abundance sampling distribution to identify the parameter estimate ($\hat{p}_{\text{difference}}$). We made Bonferroni adjustments based on the number of pairwise

comparisons to determine which sampling distribution quantiles to use as the HDI lower and upper boundaries. The formula for these adjustments is the following:

$$HDI = (1 - \frac{\alpha}{n}) * 100 \quad (1)$$

The number of pairwise comparisons is denoted by *n*; our α for all analyses in this study was 0.05. For three pairwise comparisons (i.e., species-specific comparisons including whitebark pine, Engelmann spruce, and subalpine fir as well as ecological role comparisons including initiator, leeward, and solitary conifers), we estimated the 98.3% HDI by calculating the 0.0083 and 0.9917 quantiles of each sampling distribution. For six pairwise comparisons (i.e., conifer nurse object associations including rocks, topographic depressions, shrubs, and unprotected; climactic variables across study areas), we estimated the 99.17% HDI by calculating the 0.0042 and 0.9958 quantiles of each sampling distribution as the lower and upper boundary. For all pairwise difference estimates, we concluded that proportional abundances did not differ (i.e., no mean difference) if the estimated HDI included zero.

Growing season temperature and precipitation parameter estimates. We determined the duration of each growing season from 1985 to 2015 for all study sites by trimming the imported PRISM daily mean temperature and precipitation data according to the temperature parameters defined in methods. Then, we calculated the mean daily growing season air temperature and precipitation corresponding to each year. We bootstrapped—that is, sampled randomly with replacement over the size of the sample (30 seasons; 1985 through 2015)—for 5000 iterations to generate a sampling distribution of means corresponding to each climatic parameter (i.e., average daily temperature and precipitation). We calculated the mean of each sampling distribution to estimate average

daily temperature ($\hat{T}$) and precipitation ($\hat{P}$) across all growing seasons. Finally, we estimated the 95% HDI by calculating the 0.025 and 0.975 quantiles of each sampling distribution as the lower and upper boundary.

Differences in mean growing season climatic parameter estimates. Once the average daily growing season temperature and precipitation sampling distributions had been generated, we calculated pairwise differences in means between all study areas. Then, we calculated the mean of each difference-in-mean-growing-season temperature ($\hat{T}_{\text{difference}}$) and precipitation ($\hat{P}_{\text{difference}}$) sampling distribution to identify the parameter estimate. For six pairwise comparisons (i.e. Tibbs Butte vs. Paintbrush Divide, Tibbs Butte vs. Hurricane Pass, Tibbs Butte vs. Mutiny Ridge, Paintbrush Divide vs. Hurricane Pass, Paintbrush Divide vs. Mutiny Ridge, and Hurricane Pass vs. Mutiny Ridge), we estimated the 99.17% HDI by calculating the 0.0042 and 0.9958 quantiles of each sampling distribution as the lower and upper boundary, respectively. For all pairwise difference estimates, we concluded climatic conditions did not differ (i.e., no difference in means) if the estimated HDI included zero.

Results

All raw count and proportional abundance data for conifer ecological role, species, nurse object association, and blister rust infection incidence are available in Appendix A, Tables A.1 through A.8. For consistency with other studies assessing whitebark pine's prevalence and functional role at treeline (e.g., Resler and Tomback 2008, Tomback et al. 2014, Tomback et al. 2016a), we report basic descriptive statistics on raw data in Table 2.2.

Community Structure and Composition

Tibbs Butte. On average, 0.956 (95% HDI: 0.880, 1.000) of all conifers in the Tibbs Butte study area were solitary, and 0.044 (95% HDI: 0.000, 0.120) were tree island members (i.e., initiators or leeward conifers). Average solitary tree density was 7.322 (95% HDI: 3.583, 12.583) trees per plot. Mean tree island density was 0.259 (95% HDI: 0.000, 0.667) tree islands per plot. Of all conifers observed regardless of ecological role, whitebark pine comprised 0.914 (95% HDI: 0.843, 0.975), followed by Engelmann spruce at 0.076 (95% HDI: 0.014, 0.148) and subalpine fir at 0.011 (95% HDI: 0.000, 0.031; Fig. 2.3a). Overall, whitebark pine was significantly more abundant than Engelmann spruce and subalpine fir (Fig. 2.3b)

Solitary trees were comprised of 0.926 (95% HDI: 0.855, 0.988) whitebark pine, followed by 0.074 (95% HDI: 0.012, 0.145) Engelmann spruce, and 0.000 (95% HDI: 0.000, 0.000) subalpine fir. We found that whitebark pine was the most prevalent solitary conifer.

Whitebark pine comprised 0.775 (95% HDI: 0.750, 0.800) of leeward tree island conifers; Engelmann spruce accounted for 0.123 (95% HDI: 0.000, 0.250), and subalpine fir comprised 0.101 (95% HDI: 0.000, 0.200). Whitebark pine was the most common leeward tree island conifer.

The three tree island initiators we observed on Tibbs Butte included 2 whitebark pine, 1 subalpine fir, and 0 Engelmann spruce (Appendix A, Table A.1). Both whitebark pine tree island initiators were located within the same assessment plot. On average, tree island initiator species composition was 0.504 (95% HDI: 0.000, 1.000) whitebark pine, 0.496 (95% HDI: 0.000, 1.000) subalpine fir, and 0.000 (95% HDI: 0.000, 0.000)

Engelmann spruce. Pairwise mean differences between tree island initiator species abundances revealed no differences.

Paintbrush Divide. At Paintbrush Divide, 0.620 (95% HDI: 0.482, 0.751) of all conifers were solitary, and 0.380 (95% HDI: 0.249, 0.518) were tree island members. Average solitary tree density was 14.030 (95% HDI: 10.100, 18.000) trees per plot. Mean tree island density was 2.144 (95% HDI: 1.450, 2.950) tree islands per plot. Whitebark pine comprised 0.579 (95% HDI: 0.441, 0.707) of all conifers observed, followed by Engelmann spruce at 0.276 (95% HDI: 0.170, 0.395) and subalpine fir at 0.145 (95% HDI: 0.073, 0.229; Fig. 2.3a). Whitebark pine was significantly more abundant than Engelmann spruce and subalpine fir (Fig. 2.3b).

Whitebark pine comprised 0.646 (95% HDI: 0.521, 0.753) of solitary trees, followed by 0.271 (95% HDI: 0.160, 0.405) Engelmann spruce, and 0.082 (95% HDI: 0.040, 0.130) subalpine fir. We found that whitebark pine was the majority solitary conifer, constituting more solitary trees than Engelmann spruce and subalpine fir. We also found there were more solitary Engelmann spruce than solitary subalpine fir.

For leeward conifers, whitebark pine comprised 0.666 (95% HDI: 0.474, 0.833), Engelmann spruce 0.201 (95% HDI: 0.067, 0.363), and subalpine fir 0.132 (95% HDI: 0.037, 0.271). Our analysis revealed that whitebark pine was the majority leeward conifer.

We observed 43 tree island initiators, which included 28 whitebark pine, 9 Engelmann spruce, and 6 subalpine fir (Appendix A, Table A.1). Average tree island initiator species proportional abundance was 0.561 (95% HDI: 0.353, 0.757) whitebark pine, 0.248 (95% HDI: 0.100, 0.419) Engelmann spruce, and 0.191 (95% HDI: 0.033,

0.382) subalpine fir. We found no differences in species proportional abundance for tree island initiators.

Hurricane Pass. On average, 0.537 (95% HDI: 0.404, 0.676) of the conifers at Hurricane Pass were solitary; 0.463 (95% HDI: 0.323, 0.596) were tree island members. Average solitary tree density was 6.987 (95% HDI: 4.900, 9.200) trees per plot. Mean tree island density was 2.406 (95% HDI: 1.500, 3.450) tree islands per plot. Whitebark pine comprised 0.419 (95% HDI: 0.298, 0.539) of all conifers observed, followed by Engelmann spruce at 0.326 (95% HDI: 0.231, 0.428) and subalpine fir at 0.255 (95% HDI: 0.173, 0.343; Fig. 2.3a). We found no species to be an overall majority conifer at Hurricane Pass (Fig. 2.3b).

In our examination of the species composition of solitary trees, we found whitebark pine comprised 0.480 (95% HDI: 0.334, 0.627), followed by 0.325 (95% HDI: 0.218, 0.437) for Engelmann spruce, and 0.194 (95% HDI: 0.092, 0.311) for subalpine fir. We found that no species comprised a higher proportion of solitary trees than any other species.

We found that whitebark pine composed an average 0.419 (95% HDI: 0.247, 0.596) of leeward tree island conifers, followed by Engelmann spruce at 0.307 (95% HDI: 0.157, 0.489), and subalpine fir at 0.273 (95% HDI: 0.119, 0.453). No species comprised a higher proportion of leeward tree island conifers than any other species.

Our sample at Hurricane Pass included 48 tree island initiators: 16 whitebark pine, 17 Engelmann spruce, and 15 subalpine fir (Appendix A, Table A.1). On average, tree island initiator species composition was 0.263 (95% HDI: 0.127, 0.417) whitebark pine, 0.415 (95% HDI: 0.237, 0.598) subalpine fir, and 0.322 (95% HDI: 0.151, 0.561)

Engelmann spruce. Pairwise mean differences among tree island initiator species revealed no differences.

Mutiny Ridge. At Mutiny Ridge, we found that 0.745 (95% HDI: 0.618, 0.860) of all conifers were solitary, and 0.255 (95% HDI: 0.140, 0.382) were tree island members. Average solitary tree density was 8.256 (95% HDI: 5.167, 12.067) trees per plot. Mean tree island density was 1.367 (95% HDI: 0.667, 2.267) tree islands per plot. In total, whitebark pine comprised 0.904 (95% HDI: 0.856, 0.945) of all conifers observed, followed by subalpine fir at 0.064 (95% HDI: 0.028, 0.109) and Engelmann spruce at 0.032 (95% HDI: 0.015, 0.052; Fig. 2.3a). We found that whitebark pine was the overall majority conifer (Fig. 2.3b).

Of the solitary trees in the Christina Lake ATE, whitebark pine comprised 0.924 (95% HDI: 0.882, 0.962), followed by 0.041 (95% HDI: 0.014, 0.074) subalpine fir, and 0.035 (95% HDI: 0.014, 0.059) Engelmann spruce. Whitebark pine was the majority solitary tree.

We also found whitebark pine constituted an average 0.955 (95% HDI: 0.900, 0.995) of leeward tree island conifers; Engelmann spruce accounted for 0.031 (95% HDI: 0.000, 0.086), and subalpine fir comprised 0.014 (95% HDI: 0.000, 0.037). We found whitebark pine was the majority leeward tree island constituent.

The 41 tree island initiators we observed at Mutiny Ridge included 33 whitebark pine, 4 subalpine fir, and 4 Engelmann spruce (Appendix A, Table A.1). Average tree island initiator species composition was 0.652 (95% HDI: 0.409, 0.873) whitebark pine, 0.283 (95% HDI: 0.071, 0.538) subalpine fir, and 0.065 (95% HDI: 0.000, 0.163)

Engelmann spruce. We found there were more whitebark pine tree island initiators than Engelmann spruce.

Tree Island Development

To determine whether solitary whitebark pine proportional abundance predicted its prevalence as a tree island initiator, we examined the difference in proportional abundance between tree island initiators and solitary trees within species. At Tibbs Butte, Paintbrush Divide, and Mutiny Ridge, we found there were no differences between the estimated proportion of tree island initiators and solitary trees for any species (Fig. 2.4). At Hurricane Pass, however, our results indicated whitebark pine initiated fewer tree islands than would be expected given its proportional abundance as a solitary tree; subalpine fir initiated more tree islands than would be expected given its proportional abundance as a solitary tree.

Facilitation by Nurse Objects

Tibbs Butte. Our sample collected at Tibbs Butte contained 91 conifers that were either solitary trees or tree island initiators (Appendix A, Table A.1). Of these, 0.545 (95% HDI: 0.383, 0.703) were in geomorphic depressions, 0.237 (95% HDI: 0.094, 0.417) were leeward of woody plants, 0.174 (95% HDI: 0.080, 0.273) were protected by rocks, and 0.045 (95% HDI: 0.000, 0.098) were unprotected (Fig. 2.5a). There were significantly more conifers protected by geomorphic depressions than rocks, and significantly more conifers protected by geomorphic depressions than those that were unprotected (Fig. 2.5b).

Paintbrush Divide. There were 324 conifers that were either solitary trees or tree island initiators at Paintbrush Divide (Appendix A, Table A.1). Of these, 0.532 (95%

HDI: 0.381, 0.684) were protected by rocks, 0.429 (95% HDI: 0.284, 0.579) were unprotected, 0.029 (95% HDI: 0.000, 0.068) were in geomorphic depressions, and 0.010 (95% HDI: 0.000, 0.027) were in the lee of woody plants (Fig. 2.5a). We found that rocks protected more conifers than woody vegetation and geomorphic depressions. We also found there were more unprotected conifers than those protected by woody plants or geomorphic depression (Fig. 2.5b).

Hurricane Pass. The Hurricane pass sample encompassed 188 trees that were either solitary or tree island initiators (Appendix A, Table A.1). Of these, 0.413 (95% HDI: 0.268, 0.562) were unprotected, 0.338 (95% HDI: 0.207, 0.489) were protected by rocks, 0.193 (95% HDI: 0.068, 0.342) were in geomorphic depressions, and 0.055 (95% HDI: 0.008, 0.124) were in the lee of woody plants (Fig. 2.5a). We found there were more conifers protected by rocks than geomorphic shelters, and more unprotected conifers than those protected by geomorphic depressions (Fig. 2.5b).

Mutiny Ridge. At Mutiny Ridge, 288 trees were either solitary or tree island initiators (Appendix A, Table A.1). Of these, 0.689 (95% HDI: 0.570, 0.800) were protected by rocks, 0.174 (95% HDI: 0.092, 0.274) were unprotected, 0.086 (95% HDI: 0.038, 0.142) were in the lee of woody plants, and 0.051 (95% HDI: 0.023, 0.082) were in geomorphic depressions (Fig. 2.5a). We found there were more conifers protected by rocks than those that were unprotected, or protected by geomorphic depressions or woody plants (Fig. 2.5b).

Blister Rust Assessments

Mean blister rust infection was 0.006 (95% HDI: 0.000, 0.018) at Tibbs Butte, 0.180 (95% HDI: 0.099, 0.273) at Paintbrush Divide, 0.143 (95% HDI: 0.062, 0.242) at

Hurricane Pass, and 0.019 (95% HDI: 0.005, 0.038) at Mutiny Ridge—a range of less than 1%, to 18%. There were no differences between white pine blister rust infection in solitary and tree island whitebark pine at any study area.

Mesoclimate Assessments

For our study locations, the mean daily growing season temperature from 1985 to 2015 was 8.51°C (95% HDI: 8.05°C, 8.97°C) at Tibbs Butte, 9.90°C (95% HDI: 9.49°C, 10.28°C) at Paintbrush Divide, 8.95°C (95% HDI: 8.50°C, 9.38°C) at Hurricane Pass, and 9.13°C (95% HDI: 8.70°C, 9.54°C) at Mutiny Ridge (Fig. 2.6a). When examining pairwise differences in mean daily growing season temperature between study locations, we found Paintbrush Divide was warmer than Hurricane Pass and Tibbs Butte (Fig. 2.6b). Average daily growing season precipitation was 1.65mm (95% HDI: 1.44mm, 1.87mm) on Tibbs Butte, 2.02mm (95% HDI: 1.78mm, 2.27mm) on Paintbrush Divide, 2.14mm (95% HDI: 1.85mm, 2.43mm) on Hurricane Pass, and 1.42mm (95% HDI: 1.21mm, 1.62mm) on Mutiny Ridge (Fig. 2.6a). We found Paintbrush Divide and Hurricane Pass received more precipitation than Mutiny Ridge (Fig. 2.6b).

Discussion

We designed this exploratory study of community structure and composition at four ATE communities in the GYE to examine specifically (1) the prevalence of whitebark pine, (2) the proportional occurrence of whitebark pine as a tree island initiator, (3) whether solitary whitebark pine abundance predicts its prevalence as a tree island initiator, (4) whether differences in climate correspond to geographic differences in whitebark pine's frequency of occurrence as a tree island initiator, (5) the relationship

between common nurse objects and solitary/tree island initiator establishment, and (6) the presence and severity of white pine blister rust in these communities.

Whitebark Pine and Tree Island Development in the GYE

Results of this study confirm whitebark pine's importance in ATE community structure and composition in the Greater Yellowstone Ecosystem. We found that whitebark pine was the overall majority conifer at Tibbs Butte ($\bar{p}$ = 0.914), Paintbrush Divide ($\bar{p}$ = 0.579), and Mutiny Ridge ($\bar{p}$ = 0.904). It was also the most abundant solitary conifer at all study areas except Hurricane Pass, and by a wide margin for study areas outside Grand Teton National Park ($\bar{p}$ > 0.853 more than any other conifer). Additionally, whitebark pine comprised the majority of leeward tree island conifers at Tibbs Butte ($\bar{p}$ = 0.775), Paintbrush Divide ($\bar{p}$ = 0.665), and Mutiny Ridge ($\bar{p}$ = 0.955). The preceding evidence supports the notion that the prevalence of whitebark pine in the ATE is increased relative to other conifer species, particularly on the arid and windy sites east of the Continental Divide. It also highlights the importance of mechanisms that may drive whitebark pine's elevated proportional abundance, namely, efficient seed dispersal by Clark's nutcrackers to protected sites (Tomback 1978) and whitebark pine's relatively high tolerance of abiotic stress (e.g., Arno and Hoff 1990).

We also found that solitary trees and conifers that serve as tree island initiators in ATEs within the GYE often establish leeward of nurse objects (i.e. rocks, topographic depressions, and shrubs), and the proportional occurrence of common nurse objects types found windward of solitary conifers and tree island initiators differs by study area. This study did not assess whether the proportional occurrence of nurse objects as windward facilitators differs from the proportion of nurse objects available on the landscape. We

recommend future studies account for the proportional abundance of nurse objects types available when assessing the relative importance of certain nurse objects to solitary conifer establishment.

Given that whitebark pine functions as the majority tree island initiator in many ATEs across the Central and Northern Rocky Mountains (Tomback et al. 2016a), we hypothesized that it would serve this role in the southeastern-most limit of its range. Yet, our results indicated that whitebark pine did not serve as majority tree island initiator at any study area. If whitebark pine is the majority conifer in regards to overall, solitary, and leeward compositon at Tibbs Butte, Paintbrush Divide, and Mutiny Ridge, why is it not the majority tree island initiator at these locations? One explanation may lie in the high proportional abundance of solitary whitebark pine, which Resler et al. (2014) hypothesized as indicative of an early stage in ATE development or a steady age structure with rapid new establishment. High proportional abundance of leeward whitebark pine supports the conjecture that whitebark pine readily establishes leeward of solitary conifers, most likely because nutcrackers place seeds near objects disproportionately (Tomback 1978), and whitebark pine early life stage survival is increased near rocks and trees relative to unprotected microsites in some ATEs (Pansing et al. in review). Another answer may be that other ATE conifers, namely Engelmann spruce and subalpine fir, are unable to establish leeward of whitebark pine due to seed dispersal limitations, or lower tolerances to stressful conditions (Bansal et al. 2011), even with windward facilitation

Finally, use of a study design that applies assessment plots may have led to a low number of tree islands sampled (n = 3, n = 43, n = 48, and n = 41 at Tibbs Butte, Paintbrush Divide, Hurricane Pass, and Mutiny Ridge, respectively), decreasing the

precision of our estimates to a degree that precluded our ability to detect mean differences in proportional abundance between species. Previous plot- or transect-based studies have overlooked this issue of intra-plot spatial interdependence and combined tree island totals across replicates (e.g., Resler and Tomback 2008, Tomback et al. 2014)—a form of pseudoreplication (Hurlbert 1984); this work invoked a more rigorous approach. Indeed, had we combined tree island totals across assessment plots and conducted multinomial goodness of fit tests under the null hypothesis that tree island initiator species proportional abundances were equal ($\bar{p}_{whitebark\ pine} = \bar{p}_{subalpine\ fir} = \bar{p}_{Engelmann\ spruce} = 0.333$; e.g. Resler and Tomback 2008, Tomback et al. 2014), we would have designated whitebark pine a majority tree island initiator at Paintbrush Divide ($X^2 = 19.86$, $df = 2$, $p \approx 0.000$), and Mutiny Ridge ($X^2 = 41.02$, $df = 2$, $p \approx 0.000$). In future examinations of tree island initiator species proportional abundances, we recommend two possible approaches: (1) forego assessment plots and transects in favor of a simple random sampling strategy that employs tree islands as replicates, or (2) use hierarchical models that account for spatial dependence among observations to increase the precision.

The Relationship of Solitary Trees to Tree Island Initiators

Our second objective was to determine whether solitary conifer species proportional abundances would predict tree island initiator species proporitonal abundances, as they did previously in Tomback et al. (2016a). Our results support those findings. With the exception of whitebark pine and subalpine fir at Hurricane Pass, the mean difference effect size between solitary and tree island initiator proportional abundances did not deviate from zero for any species at any study area. These results

provide support for the general notion that ATE conifer species facilitate subsequent conifer establishment (Marr 1977), and thereby initiate tree island development at a rate proportional to their proportional abundance as solitary trees. Mean differences in proportional abundance among species, therefore, relate primarily to differences in establishment and survival (Malanson et al. 2007).

At Hurricane Pass, however, whitebark pine initiated 0.207 (95% HDI: 0.028, 0.393) fewer tree islands than would be expected given its proportional abundance as a solitary tree; subalpine fir initiated 0.175 (95% HDI: 0.025, 0.334) more. These results may be explained by long-known physiological differences between whitebark pine and subalpine fir. Griggs (1938) noted that subalpine fir survive and better grow in moist, snowy environments in relation to other timberline species. Little (1994) found subalpine fir establishment and survival to be limited by low soil moisture, especially on southern aspects. Indeed, our pairwise comparisons of climactic conditions between study sites revealed that Hurricane Pass received, on average, 0.489 mm and 0.720 mm per day more precipitation than Tibbs Butte and Mutiny Ridge, respectively. Our findings suggest that local climactic conditions, particularly mean daily growing season precipitation, may influence species' functional ecology and tree island composition at high-elevations in some communities in the Greater Yellowstone Ecosystem.

The Impact of *C. ribicola* Invasion

The spread of *C. ribicola* and the resulting incidence of white pine blister rust in ATEs within the Shoshone National Forest and Grand Teton National Park have the potential to disrupt tree island development and community structure and composition. As a stress-tolerant foundation species, whitebark pine establishes on cold, arid sites, and

facilitates the leeward establishment of other conifers in locations less conducive to the survival of other species (Resler and Tomback 2008, Tomback et al. 2016b). Resler and Tomback (2008), working south of the Canadian border on Divide Mountain and Lee Ridge on the eastern slope of Glacier National Park, documented whitebark pine mortality from blister rust in the ATE; they reported an overall infection level of 33.7%. In fact, this northern region along with the southern Canadian Rocky Mountains have the highest blister rust infection levels (83%) recorded for whitebark pine overall (Smith et al. 2013). In this study, we found that ATE white pine blister rust incidences ranged from <1% at Tibbs Butte in Shoshone National Forest to 18% at Paintbrush Divide in Bridger-Teton National Forest. The blister rust incidence of 83% among subalpine whitebark pine communities in Grand Teton National Park was as high as the northern surveys (Bockino and Tinker 2012), and explains the high blister rust incidence at treeline in this region. The progressive loss of solitary whitebark pine to white pine blister rust, therefore, may ultimately limit tree island development on the ATE landscape, significantly affecting community structure and biodiversity.

Given whitebark pine's ecological role as majority solitary tree and leeward tree island component in three-out-of-four study areas, ATE conifer communities in the Greater Yellowstone Ecosystem will likely experience severe changes in structure and composition resulting from mortality by white pine blister rust, as described by Tomback and Resler (2007): First, the seed sources for ATE conifer regeneration and community development are trees from lower elevations (Malanson et al. 2007). As *C. ribicola* spreads through stands in the upper subalpine, trees succumbing to white pine blister rust infection will produce fewer seeds (e.g., Hoff et al. 2001). As a result, Clark's

nutcrackers will have fewer opportunities to disperse to the ATE (e.g., Tomback, 1986). McKinney et al. (2009) and Barringer et al. (2012) demonstrated that the probability of nutcracker seed dispersal or stand visitation decreases with decreased cone production in subalpine whitebark pine stands; there may also be a threshold below which the probability of nutcracker visitation declines steeply. Recent studies in the GYE have estimated subalpine blister rust incidences range from 20% to 30%. Second, white pine blister rust kills whitebark pine in the ATE, and mortality of solitary whitebark pine will reduce the number of trees available to facilitate the establishment of other conifers, precluding tree island development (Tomback and Resler 2007). Proportionally, whitebark pine's ecosystem function within these ecosystems may also be reduced, altering its functional ecology, impacting community assembly trajectories, and reducing the ecosystem services provided by treeline communities.

Conclusions

Here, for the study areas sampled in the GYE, we found evidence that whitebark pine is generally the most prevalent solitary conifer and tree island component in treeline communities, and whitebark pine initiates tree island development at a rate directly proportional to its proportional abundance as a solitary tree. Our findings suggest that declines in ATE whitebark pine are imminent, stemming from community invasion by the pathogen *C. ribicola*. Whitebark pine mortality will likely lead to a serious decline in ATE conifer abundance, a proportional loss of tree islands on the landscape, and reduction in whitebark pine's ecological role and general ecosystem services in ATE communities in the Greater Yellowstone Ecosystem .

Tables and figures

Table 2.1 Study areas across the Greater Yellowstone Ecosystem (GYE). The GYE comprises the southernmost distribution of whitebark pine in the Rocky Mountains.

Study Area	National Forest	Latitude & Longitude	Aspects	Elevation [m]	Area Sampled [ha]
Tibbs Butte	Shoshone	44°56'46.48" N 109°26'39.76" W	NE	2,983 – 3,238	4.2
Paintbrush Divide	Bridger-Teton	43°47'32.90" N 110°49'17.96" W	NE, NW, SW	3,055 – 3,289	121
Hurricane Pass	Bridger-Teton	43°43'55.06" N 110°50'31.45" W	NE, SE, SW	3,045 – 3,078	92
Mutiny Ridge	Shoshone	42°35'33.56" N 108°58'07.44" W	NE, SE, SW	3,200 – 3,400	117

Table 2.2 Descriptive statistics. Minimum, median, and maximum statistics for per-plot conifer counts by ecological role and species for all study areas. ABLA = *A. lasiocarpa*, PIEN = *P. Engelmannii*, PIAL = *P. albicaulis*.

Study area	Ecological role	Descriptive statistics											
		ABLA			PIEN			PIAL			Total		
		Min	Med	Max	Min	Med	Max	Min	Med	Max	Min	Med	Max
Tibbs Butte	initiator	0	0.5	1	0	0.0	0	0	1.0	2	1	1.5	2
	leeward	0	0.5	1	0	0.5	1	3	3.5	4	4	4.5	5
	solitary	0	0.0	0	0	0.0	3	1	4.0	32	1	5	32
Paintbrush Divide	initiator	0	0.0	3	0	0.0	2	0	1.0	5	1	2	7
	leeward	0	0.0	3	0	1.0	2	0	4.0	17	1	4	20
	solitary	0	1.0	3	0	4.0	17	0	8.5	23	3	14	34
Hurricane Pass	initiator	0	1.0	3	0	1.0	3	0	1.0	5	1	2	8
	leeward	0	1.0	6	0	1.0	3	0	2.0	14	1	4	17
	solitary	0	1.0	6	0	2.0	11	0	1.0	9	1	6	18
Mutiny Ridge	initiator	0	0.0	1	0	0.0	2	0	2.0	10	1	2	10
	leeward	0	0.0	1	0	0.0	1	1	5.0	55	1	5.5	55
	solitary	0	0.0	6	0	0.0	6	1	5.5	33	1	6	45



Fig. 2.1 Facilitation in action. Krummholz whitebark pine (*Pinus albicaulis*) established leeward of a rock at Tibbs Butte, Shoshone National Forest, Wyoming. Photograph credit: E.R. Pansing.

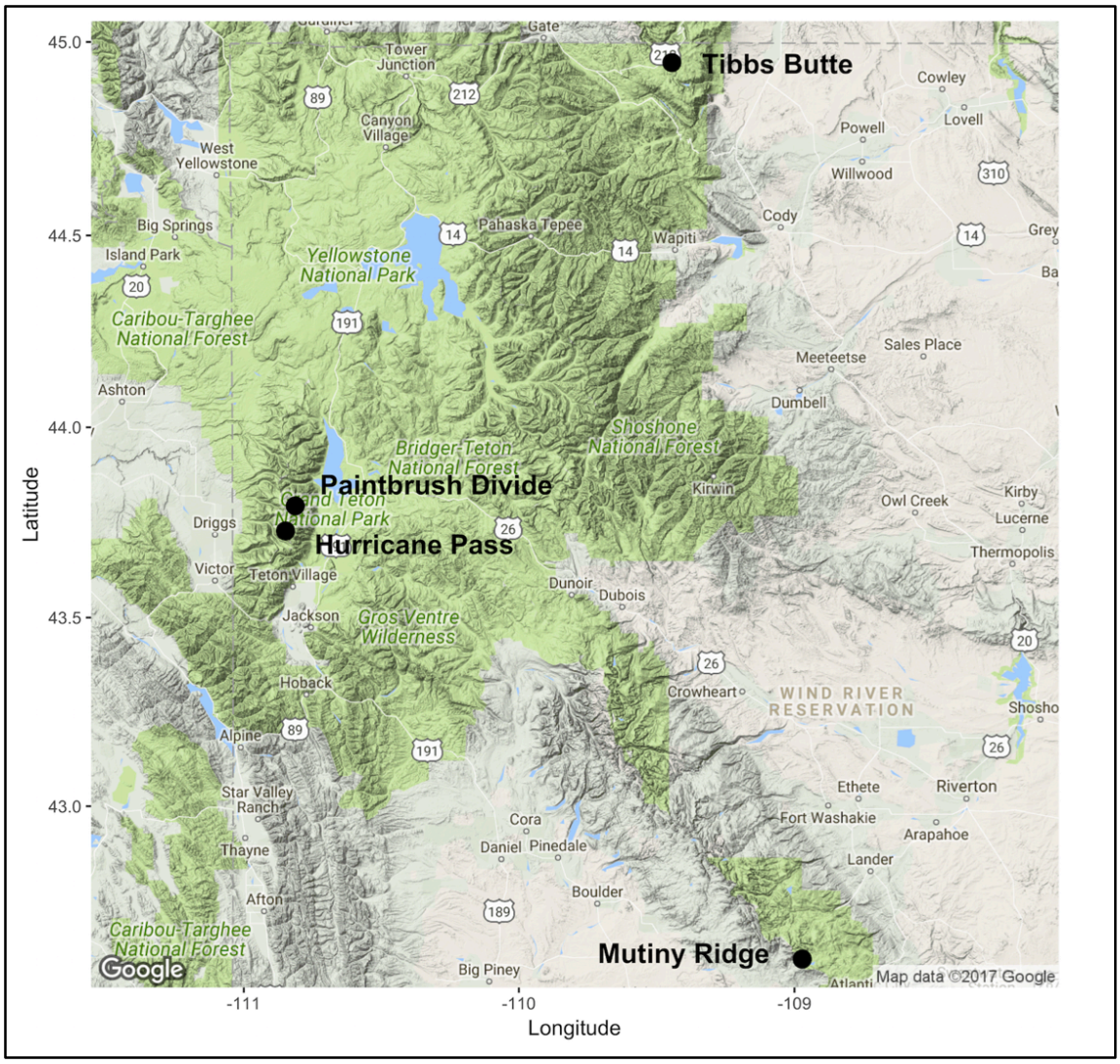


Fig. 2.2. Study areas across the Greater Yellowstone Ecosystem. Study areas are in the southernmost distribution of whitebark pine in the Rocky Mountains. Map created using ggmap package in R (Kahle and Wickham 2013).

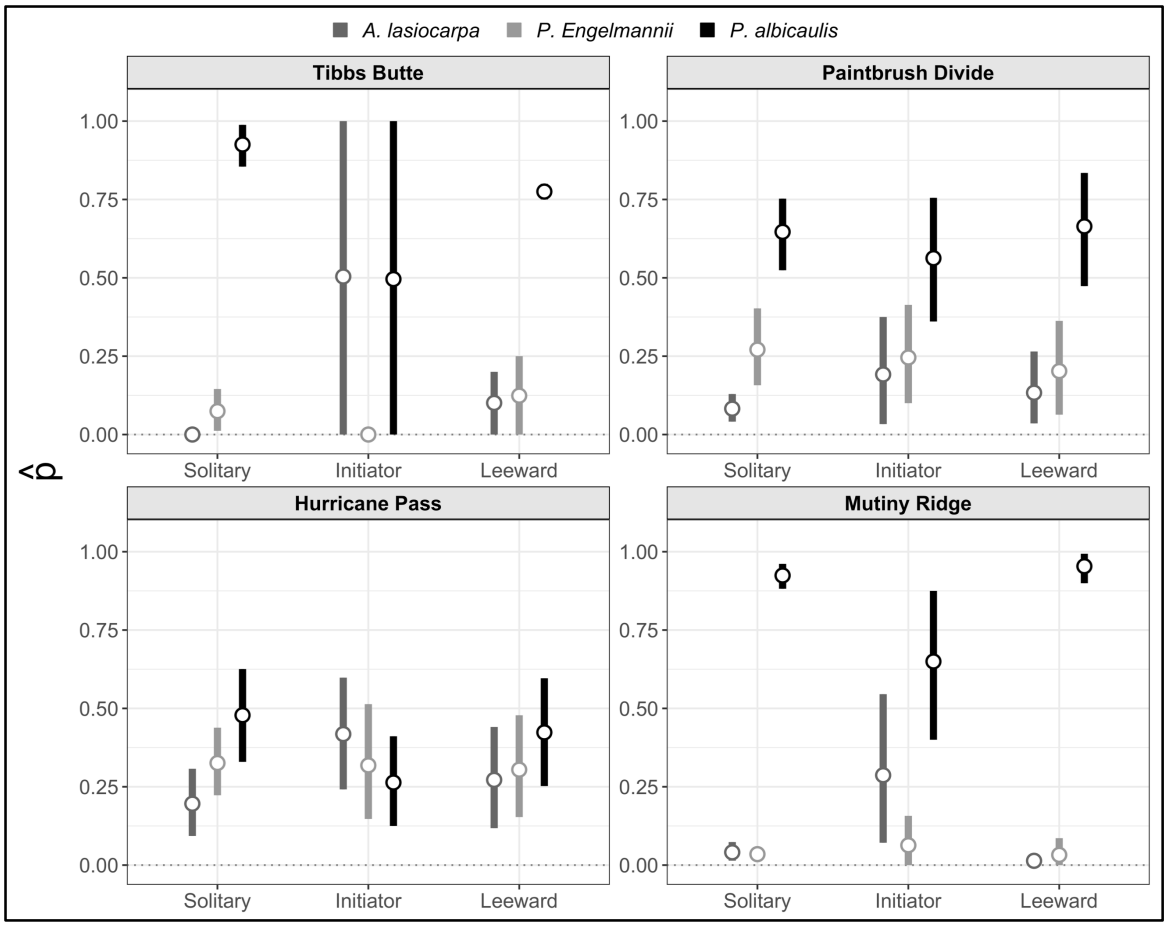


Fig. 2.3a. Parameter estimates. Bootstrapped parameter estimates and 95% HDIs for the proportional abundance of solitary, initiator, and leeward conifers by species for each study area.

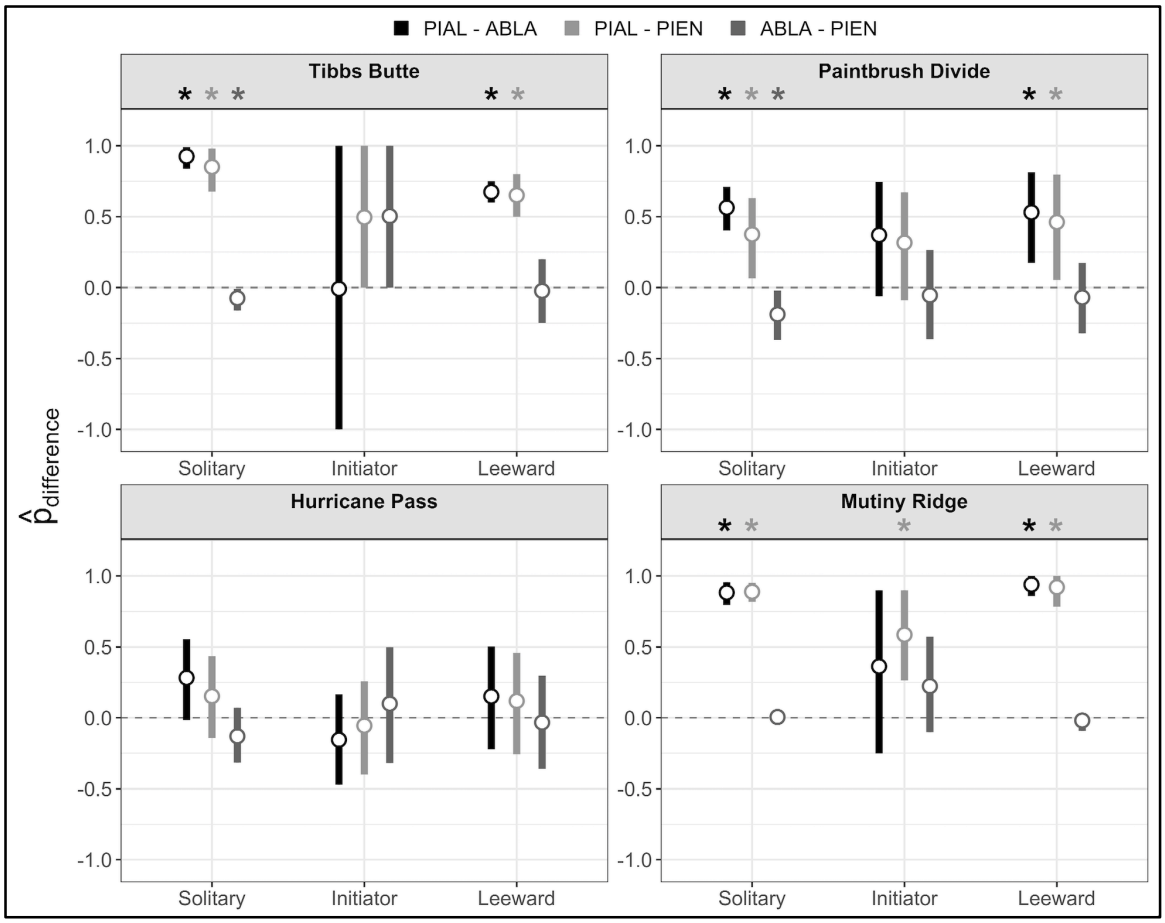


Fig. 2.3b. Parameter estimates for mean differences. Bootstrapped estimates and 98.3% HDIs for mean differences in proportional abundance of solitary, initiator, and leeward conifers by species for each study area. PIAL = *P. Albicaulis*, ABLA = *A. lasiocarpa*, and PIEN = *P. engelmannii*. We concluded no mean difference if the HDI included zero; fields in which there was a difference are marked with an asterisks (*).

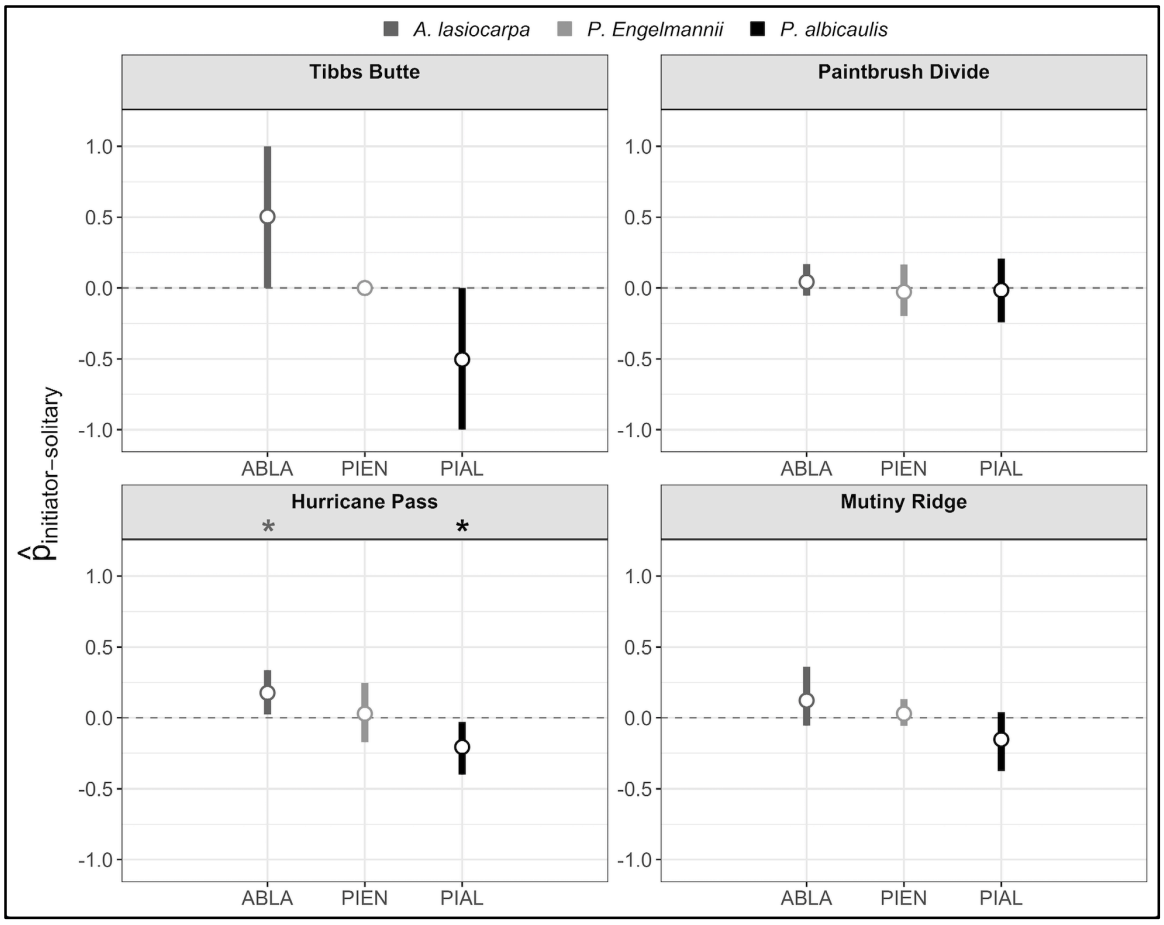


Fig. 2.4. Mean difference parameter estimates: solitary minus initiator conifers. Bootstrapped mean differences in proportional abundance between tree island initiators and solitary trees by species at each study area. Estimates are indicated by open circles, and lines delineate 95% HDIs. We concluded that no mean difference occurred between distributions if the HDI included zero. Fields in which there was a difference are marked with an asterisks (*).

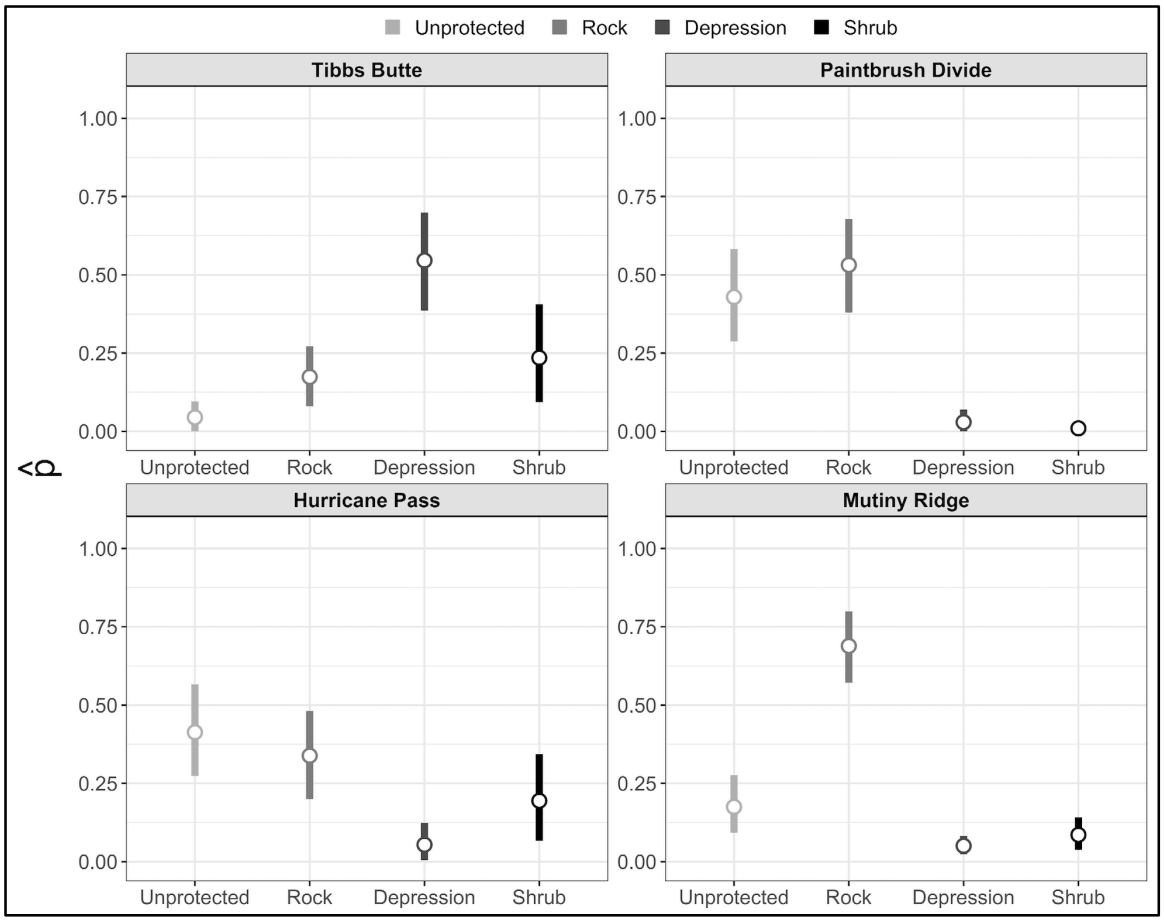


Fig. 2.5a. Parameter estimates for nurse objects. Bootstrapped proportional abundance of nurse objects found facilitating solitary and tree island initiator conifers, by study site. Estimates are indicated by open circles, and lines delineate 95% HDIs.

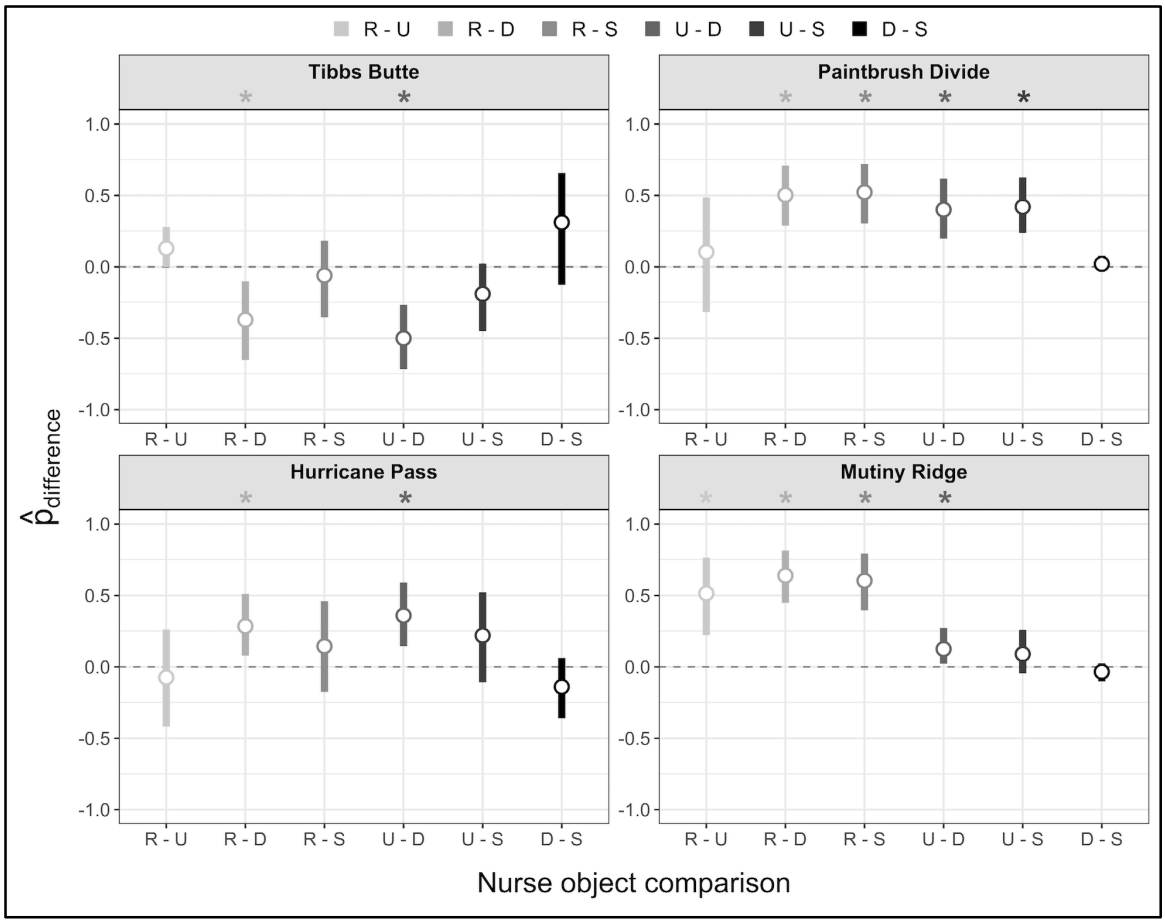


Fig. 2.5b. Mean difference parameter estimates for nurse objects. Bootstrapped mean differences in proportional abundance of nurse objects found protecting solitary conifers and tree island initiators, by study area. R = Rock, U = Unprotected, D = Depression, and S = Shrubs. Estimates are indicated by open circles, and lines delineate 99.17% HDIs. We concluded that no mean difference occurred if the HDI included zero. Fields in which there was a difference are marked with an asterisks (*).

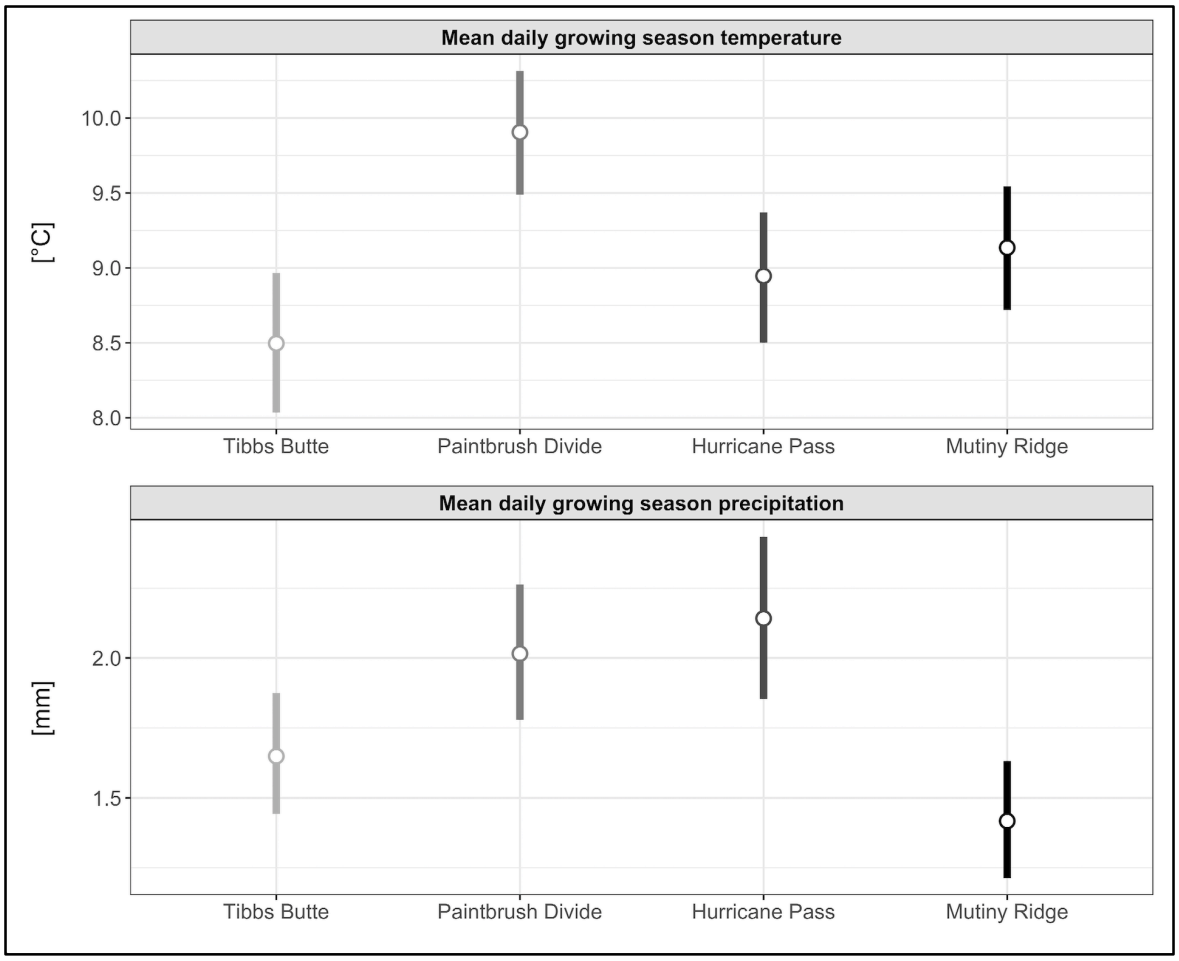


Fig. 2.6a. Parameter estimates for climate. Bootstrapped mean daily growing season temperature (top) and precipitation (bottom), by study area. We estimated climactic parameters using PRISM data from the last 30 years (1985-2015). Estimates are indicated by open circles, and lines delineate 95% HDIs.

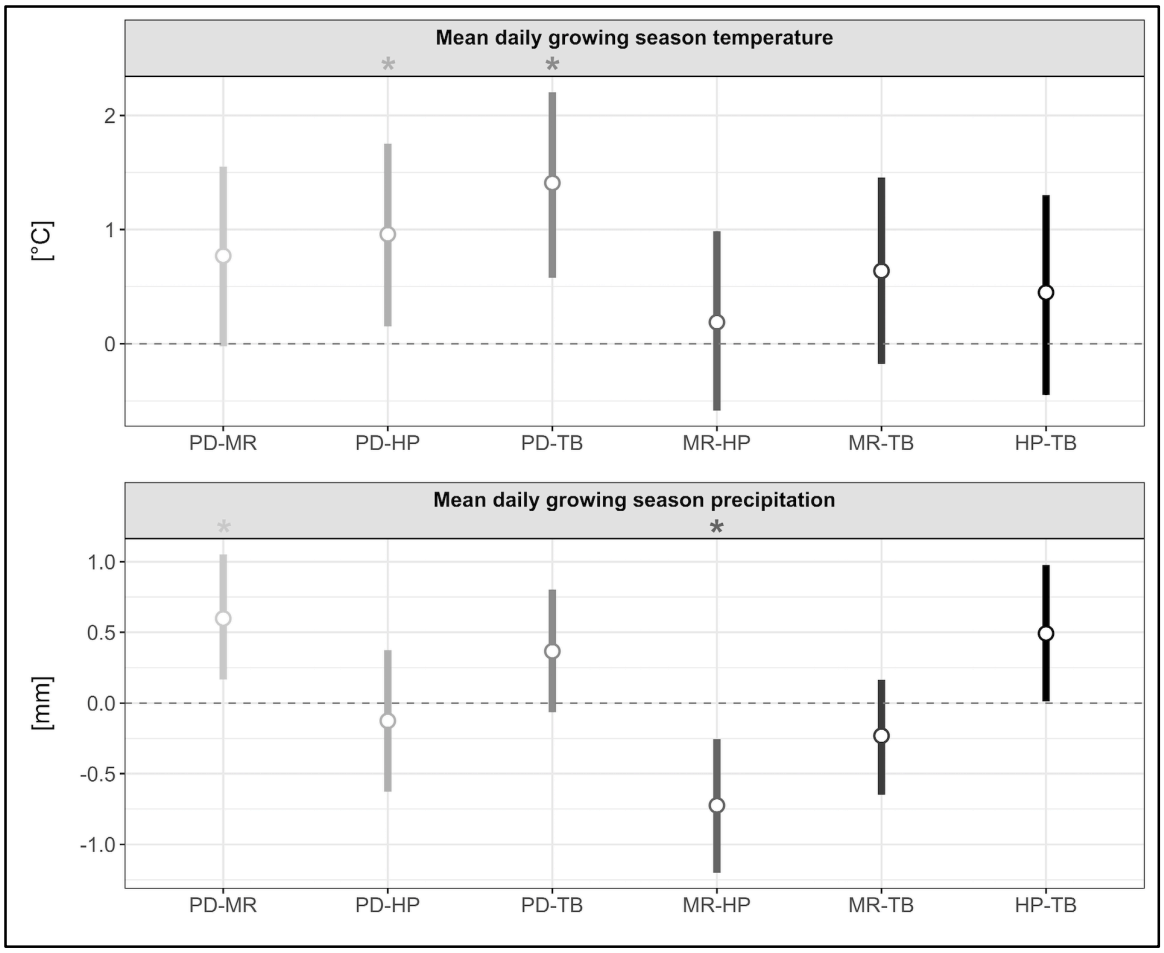


Fig. 2.6b. Difference in mean parameter estimates for climate. Bootstrapped pairwise differences in mean growing season temperature (top) and precipitation (bottom) between study area. Estimates are indicated by open circles, and lines delineate 99.17% HDIs. We concluded that no difference in means occurred if the HDI included zero. Fields in which there was a difference are marked with an asterisks (*). TB = Tibbs Butte, PD = Paintbrush Divide, HP = Hurricane Pass, MR = Mutiny Ridge.

Appendix A

Table A.1. Raw conifer species count data for all study areas. ABLA = *A. Lasiocarpa*, PIEN = *P. Engelmannii*, PIAL = *P. Albicaulis*.

Study Area	Ecological Role	ABLA	PIEN	PIAL	Total
Tibbs Butte	Initiator	1	0	2	3
	Leeward	1	1	7	9
	Solitary	0	6	82	88
	Total	**2**	**7**	**91**	**100**
Paintbrush Divide	Initiator	6	9	28	43
	Leeward	11	11	81	103
	Solitary	17	89	175	281
	Total	**34**	**109**	**284**	**427**
Hurricane Pass	Initiator	15	17	16	48
	Leeward	22	20	54	96
	Solitary	32	47	61	140
	Total	**69**	**84**	**131**	**284**
Mutiny Ridge	Initiator	4	4	33	41
	Leeward	2	3	143	148
	Solitary	14	13	220	247
	Total	**20**	**20**	**396**	**436**

Table A.2. Raw conifer species count and proportional abundance data for Tibbs Butte.

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
TB	1	initiator	NA	NA	NA	NA	NA	NA
TB	2	initiator	NA	NA	NA	NA	NA	NA
TB	3	initiator	1	0	0	1.0	0.000	0.000
TB	4	initiator	NA	NA	NA	NA	NA	NA
TB	5	initiator	NA	NA	NA	NA	NA	NA
TB	6	initiator	0	0	0	0.0	0.000	1.000
TB	7	initiator	NA	NA	NA	NA	NA	NA
TB	8	initiator	NA	NA	NA	NA	NA	NA
TB	9	initiator	NA	NA	NA	NA	NA	NA
TB	10	initiator	NA	NA	NA	NA	NA	NA
TB	11	initiator	NA	NA	NA	NA	NA	NA
TB	12	initiator	NA	NA	NA	NA	NA	NA
TB	1	leeward	NA	NA	NA	NA	NA	NA
TB	2	leeward	NA	NA	NA	NA	NA	NA
TB	3	leeward	1	0	0	0.2	0.000	0.800
TB	4	leeward	NA	NA	NA	NA	NA	NA
TB	5	leeward	NA	NA	NA	NA	NA	NA
TB	6	leeward	0	1	0	0.0	0.250	0.750
TB	7	leeward	NA	NA	NA	NA	NA	NA
TB	8	leeward	NA	NA	NA	NA	NA	NA
TB	9	leeward	NA	NA	NA	NA	NA	NA
TB	10	leeward	NA	NA	NA	NA	NA	NA
TB	11	leeward	NA	NA	NA	NA	NA	NA
TB	12	leeward	NA	NA	NA	NA	NA	NA
TB	1	solitary	0	0	0	0.0	0.000	1.000
TB	2	solitary	0	3	0	0.0	0.300	0.700
TB	3	solitary	0	0	0	0.0	0.000	1.000
TB	4	solitary	0	1	0	0.0	0.333	0.667
TB	5	solitary	0	1	0	0.0	0.111	0.889
TB	6	solitary	0	0	0	0.0	0.000	1.000
TB	7	solitary	0	0	0	0.0	0.000	1.000
TB	8	solitary	0	0	0	0.0	0.000	1.000
TB	9	solitary	0	0	0	0.0	0.000	1.000
TB	10	solitary	0	0	0	0.0	0.000	1.000
TB	11	solitary	0	0	0	0.0	0.000	1.000
TB	12	solitary	0	1	0	0.0	0.143	0.857

Table A.3. Raw conifer species count and proportional abundance data for Paintbrush Divide.

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
PD	1	initiator	0	0	1	0.000	0.000	1.000
PD	2	initiator	NA	NA	NA	NA	NA	NA
PD	3	initiator	0	1	3	0.000	0.250	0.750
PD	4	initiator	0	1	2	0.000	0.333	0.667
PD	5	initiator	0	1	1	0.000	0.500	0.500
PD	6	initiator	1	1	0	0.500	0.500	0.000
PD	7	initiator	1	0	0	1.000	0.000	0.000
PD	8	initiator	NA	NA	NA	NA	NA	NA
PD	9	initiator	0	0	4	0.000	0.000	1.000
PD	10	initiator	0	1	0	0.000	1.000	0.000
PD	11	initiator	3	0	1	0.750	0.000	0.250
PD	12	initiator	0	1	0	0.000	1.000	0.000
PD	13	initiator	0	2	5	0.000	0.286	0.714
PD	14	initiator	0	0	1	0.000	0.000	1.000
PD	15	initiator	0	1	2	0.000	0.333	0.667
PD	16	initiator	0	0	4	0.000	0.000	1.000
PD	17	initiator	NA	NA	NA	NA	NA	NA
PD	18	initiator	0	0	2	0.000	0.000	1.000
PD	19	initiator	1	0	0	1.000	0.000	0.000
PD	20	initiator	0	0	2	0.000	0.000	1.000
PD	1	leeward	0	0	1	0.000	0.000	1.000
PD	2	leeward	NA	NA	NA	NA	NA	NA
PD	3	leeward	0	0	4	0.000	0.000	1.000
PD	4	leeward	0	1	2	0.000	0.333	0.667
PD	5	leeward	1	2	17	0.050	0.100	0.850
PD	6	leeward	1	1	0	0.500	0.500	0.000
PD	7	leeward	0	1	0	0.000	1.000	0.000
PD	8	leeward	NA	NA	NA	NA	NA	NA
PD	9	leeward	0	1	8	0.000	0.111	0.889
PD	10	leeward	0	0	4	0.000	0.000	1.000
PD	11	leeward	1	0	9	0.100	0.000	0.900
PD	12	leeward	0	1	0	0.000	1.000	0.000
PD	13	leeward	3	0	11	0.214	0.000	0.786
PD	14	leeward	0	0	1	0.000	0.000	1.000
PD	15	leeward	1	1	8	0.100	0.100	0.800
PD	16	leeward	1	1	5	0.143	0.143	0.714
PD	17	leeward	NA	NA	NA	NA	NA	NA
PD	18	leeward	2	2	9	0.154	0.154	0.692
PD	19	leeward	1	0	0	1.000	0.000	0.000
PD	20	leeward	0	0	2	0.000	0.000	1.000
PD	1	solitary	0	6	16	0.000	0.273	0.727
PD	2	solitary	2	4	8	0.143	0.286	0.571
PD	3	solitary	0	7	12	0.000	0.368	0.632
PD	4	solitary	1	8	15	0.042	0.333	0.625
PD	5	solitary	0	2	12	0.000	0.143	0.857
PD	6	solitary	NA	NA	NA	NA	NA	NA
PD	7	solitary	NA	NA	NA	NA	NA	NA
PD	8	solitary	1	0	6	0.143	0.000	0.857
PD	9	solitary	2	9	23	0.059	0.265	0.676

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
PD	10	solitary	0	0	7	0.000	0.000	1.000
PD	11	solitary	1	0	3	0.250	0.000	0.750
PD	12	solitary	0	11	0	0.000	1.000	0.000
PD	13	solitary	0	4	6	0.000	0.400	0.600
PD	14	solitary	3	17	2	0.136	0.773	0.091
PD	15	solitary	1	6	16	0.043	0.261	0.696
PD	16	solitary	2	1	7	0.200	0.100	0.700
PD	17	solitary	2	11	9	0.091	0.500	0.409
PD	18	solitary	0	1	9	0.000	0.100	0.900
PD	19	solitary	1	0	2	0.333	0.000	0.667
PD	20	solitary	1	2	22	0.040	0.080	0.880

Table A.4. Raw conifer species count and proportional abundance data for Hurricane Pass.

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
HP	1	initiator	1	0	0	1.000	0.000	0.000
HP	2	initiator	0	1	0	0.000	1.000	0.000
HP	3	initiator	2	1	2	0.400	0.200	0.400
HP	4	initiator	0	3	5	0.000	0.375	0.625
HP	5	initiator	1	0	1	0.500	0.000	0.500
HP	6	initiator	1	0	2	0.333	0.000	0.667
HP	7	initiator	3	1	1	0.600	0.200	0.200
HP	8	initiator	1	0	0	1.000	0.000	0.000
HP	9	initiator	1	0	0	1.000	0.000	0.000
HP	10	initiator	NA	NA	NA	NA	NA	NA
HP	11	initiator	NA	NA	NA	NA	NA	NA
HP	12	initiator	1	2	2	0.200	0.400	0.400
HP	13	initiator	0	0	1	0.000	0.000	1.000
HP	14	initiator	1	0	1	0.500	0.000	0.500
HP	15	initiator	1	2	0	0.333	0.667	0.000
HP	16	initiator	0	2	0	0.000	1.000	0.000
HP	17	initiator	NA	NA	NA	NA	NA	NA
HP	18	initiator	1	0	0	1.000	0.000	0.000
HP	19	initiator	0	2	0	0.000	1.000	0.000
HP	20	initiator	1	3	1	0.200	0.600	0.200
HP	1	leeward	0	1	6	0.000	0.143	0.857
HP	2	leeward	1	0	0	1.000	0.000	0.000
HP	3	leeward	1	3	4	0.125	0.375	0.500
HP	4	leeward	6	2	4	0.500	0.167	0.333
HP	5	leeward	2	1	1	0.500	0.250	0.250
HP	6	leeward	2	2	5	0.222	0.222	0.556
HP	7	leeward	2	1	11	0.143	0.071	0.786
HP	8	leeward	0	0	2	0.000	0.000	1.000
HP	9	leeward	0	1	0	0.000	1.000	0.000
HP	10	leeward	NA	NA	NA	NA	NA	NA
HP	11	leeward	NA	NA	NA	NA	NA	NA
HP	12	leeward	1	2	14	0.059	0.118	0.824
HP	13	leeward	0	1	0	0.000	1.000	0.000
HP	14	leeward	2	1	0	0.667	0.333	0.000
HP	15	leeward	0	2	3	0.000	0.400	0.600
HP	16	leeward	2	0	0	1.000	0.000	0.000
HP	17	leeward	NA	NA	NA	NA	NA	NA
HP	18	leeward	0	0	1	0.000	0.000	1.000
HP	19	leeward	0	2	0	0.000	1.000	0.000
HP	20	leeward	3	1	3	0.429	0.143	0.429
HP	1	solitary	NA	NA	NA	NA	NA	NA
HP	2	solitary	6	11	1	0.333	0.611	0.056
HP	3	solitary	2	5	1	0.250	0.625	0.125
HP	4	solitary	1	2	5	0.125	0.250	0.625
HP	5	solitary	2	0	1	0.667	0.000	0.333
HP	6	solitary	6	3	7	0.375	0.188	0.438
HP	7	solitary	0	2	2	0.000	0.500	0.500
HP	8	solitary	2	1	8	0.182	0.091	0.727
HP	9	solitary	2	4	0	0.333	0.667	0.000

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
HP	10	solitary	0	4	1	0.000	0.800	0.200
HP	11	solitary	0	0	5	0.000	0.000	1.000
HP	12	solitary	0	2	7	0.000	0.222	0.778
HP	13	solitary	0	1	5	0.000	0.167	0.833
HP	14	solitary	0	1	1	0.000	0.500	0.500
HP	15	solitary	3	4	9	0.188	0.250	0.562
HP	16	solitary	0	0	1	0.000	0.000	1.000
HP	17	solitary	4	4	1	0.444	0.444	0.111
HP	18	solitary	4	1	0	0.800	0.200	0.000
HP	19	solitary	0	1	1	0.000	0.500	0.500
HP	20	solitary	0	1	5	0.000	0.167	0.833

Table A.5. Raw conifer species count and proportional abundance data for Mutiny Ridge.

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
MR	1	initiator	1	0	0	1.000	0.000	0.000
MR	2	initiator	0	2	3	0.000	0.400	0.600
MR	3	initiator	0	2	2	0.000	0.500	0.500
MR	4	initiator	0	0	2	0.000	0.000	1.000
MR	5	initiator	1	0	0	1.000	0.000	0.000
MR	6	initiator	NA	NA	NA	NA	NA	NA
MR	7	initiator	0	0	3	0.000	0.000	1.000
MR	8	initiator	1	0	0	1.000	0.000	0.000
MR	9	initiator	NA	NA	NA	NA	NA	NA
MR	10	initiator	NA	NA	NA	NA	NA	NA
MR	11	initiator	1	0	0	1.000	0.000	0.000
MR	12	initiator	0	0	10	0.000	0.000	1.000
MR	13	initiator	0	0	4	0.000	0.000	1.000
MR	14	initiator	NA	NA	NA	NA	NA	NA
MR	15	initiator	NA	NA	NA	NA	NA	NA
MR	16	initiator	NA	NA	NA	NA	NA	NA
MR	17	initiator	NA	NA	NA	NA	NA	NA
MR	18	initiator	NA	NA	NA	NA	NA	NA
MR	19	initiator	NA	NA	NA	NA	NA	NA
MR	20	initiator	0	0	2	0.000	0.000	1.000
MR	21	initiator	0	0	1	0.000	0.000	1.000
MR	22	initiator	NA	NA	NA	NA	NA	NA
MR	23	initiator	NA	NA	NA	NA	NA	NA
MR	24	initiator	NA	NA	NA	NA	NA	NA
MR	25	initiator	NA	NA	NA	NA	NA	NA
MR	26	initiator	NA	NA	NA	NA	NA	NA
MR	27	initiator	0	0	1	0.000	0.000	1.000
MR	28	initiator	NA	NA	NA	NA	NA	NA
MR	29	initiator	NA	NA	NA	NA	NA	NA
MR	30	initiator	0	0	5	0.000	0.000	1.000
MR	1	leeward	0	0	4	0.000	0.000	1.000
MR	2	leeward	1	1	17	0.053	0.053	0.895
MR	3	leeward	1	0	6	0.143	0.000	0.857
MR	4	leeward	0	0	3	0.000	0.000	1.000
MR	5	leeward	0	0	9	0.000	0.000	1.000
MR	6	leeward	NA	NA	NA	NA	NA	NA
MR	7	leeward	0	1	2	0.000	0.333	0.667
MR	8	leeward	0	0	1	0.000	0.000	1.000
MR	9	leeward	NA	NA	NA	NA	NA	NA
MR	10	leeward	NA	NA	NA	NA	NA	NA
MR	11	leeward	0	0	3	0.000	0.000	1.000
MR	12	leeward	0	0	55	0.000	0.000	1.000
MR	13	leeward	0	0	15	0.000	0.000	1.000
MR	14	leeward	NA	NA	NA	NA	NA	NA
MR	15	leeward	NA	NA	NA	NA	NA	NA
MR	16	leeward	NA	NA	NA	NA	NA	NA
MR	17	leeward	NA	NA	NA	NA	NA	NA
MR	18	leeward	NA	NA	NA	NA	NA	NA
MR	19	leeward	NA	NA	NA	NA	NA	NA

Study area	Plot	Ecological role	ABLA	PIEN	PIAL	Prop ABLA	Prop PIEN	Prop PIAL
MR	20	leeward	0	0	2	0.000	0.000	1.000
MR	21	leeward	0	0	9	0.000	0.000	1.000
MR	22	leeward	NA	NA	NA	NA	NA	NA
MR	23	leeward	NA	NA	NA	NA	NA	NA
MR	24	leeward	NA	NA	NA	NA	NA	NA
MR	25	leeward	NA	NA	NA	NA	NA	NA
MR	26	leeward	NA	NA	NA	NA	NA	NA
MR	27	leeward	0	0	1	0.000	0.000	1.000
MR	28	leeward	NA	NA	NA	NA	NA	NA
MR	29	leeward	NA	NA	NA	NA	NA	NA
MR	30	leeward	0	1	16	0.000	0.059	0.941
MR	1	solitary	1	1	6	0.125	0.125	0.750
MR	2	solitary	0	0	30	0.000	0.000	1.000
MR	3	solitary	6	6	33	0.133	0.133	0.733
MR	4	solitary	3	1	12	0.188	0.062	0.750
MR	5	solitary	NA	NA	NA	NA	NA	NA
MR	6	solitary	0	0	4	0.000	0.000	1.000
MR	7	solitary	0	0	23	0.000	0.000	1.000
MR	8	solitary	NA	NA	NA	NA	NA	NA
MR	9	solitary	0	0	1	0.000	0.000	1.000
MR	10	solitary	0	0	6	0.000	0.000	1.000
MR	11	solitary	0	0	1	0.000	0.000	1.000
MR	12	solitary	0	0	4	0.000	0.000	1.000
MR	13	solitary	0	1	12	0.000	0.077	0.923
MR	14	solitary	1	0	2	0.333	0.000	0.667
MR	15	solitary	0	0	1	0.000	0.000	1.000
MR	16	solitary	0	0	4	0.000	0.000	1.000
MR	17	solitary	0	0	2	0.000	0.000	1.000
MR	18	solitary	0	0	5	0.000	0.000	1.000
MR	19	solitary	1	1	6	0.125	0.125	0.750
MR	20	solitary	0	1	6	0.000	0.143	0.857
MR	21	solitary	0	0	3	0.000	0.000	1.000
MR	22	solitary	0	0	1	0.000	0.000	1.000
MR	23	solitary	0	0	6	0.000	0.000	1.000
MR	24	solitary	0	0	1	0.000	0.000	1.000
MR	25	solitary	0	1	7	0.000	0.125	0.875
MR	26	solitary	0	0	7	0.000	0.000	1.000
MR	27	solitary	1	0	13	0.071	0.000	0.929
MR	28	solitary	0	1	4	0.000	0.200	0.800
MR	29	solitary	1	0	5	0.167	0.000	0.833
MR	30	solitary	0	0	15	0.000	0.000	1.000

Table A.6. Raw nurse object count data by plot for all study areas.

Study area	Plot	Topographic depression	None	Rock	Shrub
TB	1	1	3	1	4
TB	2	0	4	4	2
TB	3	0	3	6	2
TB	4	0	0	2	1
TB	5	2	1	6	0
TB	6	7	6	20	1
TB	7	0	0	2	0
TB	8	0	0	1	0
TB	9	0	0	1	1
TB	10	0	1	1	0
TB	11	0	0	0	1
TB	12	0	2	4	1
PD	1	3	14	0	0
PD	2	2	6	0	0
PD	3	3	13	0	0
PD	4	6	12	0	0
PD	5	6	8	0	0
PD	6	2	0	0	0
PD	7	1	0	0	0
PD	8	1	3	2	0
PD	9	4	20	3	0
PD	10	4	4	0	0
PD	11	4	1	1	1
PD	12	0	1	0	0
PD	13	12	1	0	0
PD	14	1	2	0	0
PD	15	15	3	0	1
PD	16	2	9	0	0
PD	17	9	0	0	0
PD	18	6	5	0	0
PD	19	0	3	0	0
PD	20	1	23	0	0
HP	1	1	0	0	0
HP	2	1	0	0	1
HP	3	5	1	0	0
HP	4	4	4	0	3
HP	5	2	1	0	0
HP	6	3	7	0	0
HP	7	0	7	0	0
HP	8	2	7	0	0
HP	9	1	0	0	0
HP	10	0	1	0	0
HP	11	1	2	1	0
HP	12	6	4	0	2
HP	13	1	4	1	0
HP	14	3	0	0	0
HP	15	2	2	1	7
HP	16	1	1	0	1
HP	17	0	0	0	1

Study area	Plot	Topographic depression	None	Rock	Shrub
HP	18	0	0	0	1
HP	19	2	1	0	0
HP	20	3	1	6	0
MR	1	4	6	0	0
MR	2	10	18	6	1
MR	3	14	29	5	1
MR	4	9	8	1	0
MR	5	1	0	0	0
MR	6	1	2	1	0
MR	7	6	11	2	7
MR	8	0	1	0	0
MR	9	0	1	0	0
MR	10	0	5	0	1
MR	11	0	2	0	0
MR	12	2	10	0	2
MR	13	0	17	0	0
MR	14	0	2	0	1
MR	15	0	1	0	0
MR	16	0	4	0	0
MR	17	0	2	0	0
MR	18	1	3	0	1
MR	19	1	1	2	4
MR	20	1	7	0	1
MR	21	0	4	0	0
MR	22	1	0	0	0
MR	23	0	6	0	0
MR	24	0	1	0	0
MR	25	2	2	2	2
MR	26	1	5	1	0
MR	27	3	11	1	0
MR	28	0	5	0	0
MR	29	0	6	0	0
MR	30	2	4	3	11

Table A.7. Raw nurse object proportional abundance data by plot for all study areas.

Study area	Plot	Prop Topographic depression	Prop None	Prop Rock	Prop Shrub
TB	1	0.111	0.333	0.111	0.444
TB	2	0	0.4	0.4	0.2
TB	3	0	0.273	0.545	0.182
TB	4	0	0	0.667	0.333
TB	5	0.222	0.111	0.667	0
TB	6	0.206	0.176	0.588	0.029
TB	7	0	0	1	0
TB	8	0	0	1	0
TB	9	0	0	0.5	0.5
TB	10	0	0.5	0.5	0
TB	11	0	0	0	1
TB	12	0	0.286	0.571	0.143
PD	1	0.176	0.824	0	0
PD	2	0.25	0.75	0	0
PD	3	0.188	0.812	0	0
PD	4	0.333	0.667	0	0
PD	5	0.429	0.571	0	0
PD	6	1	0	0	0
PD	7	1	0	0	0
PD	8	0.167	0.5	0.333	0
PD	9	0.148	0.741	0.111	0
PD	10	0.5	0.5	0	0
PD	11	0.571	0.143	0.143	0.143
PD	12	0	1	0	0
PD	13	0.923	0.077	0	0
PD	14	0.333	0.667	0	0
PD	15	0.789	0.158	0	0.053
PD	16	0.182	0.818	0	0
PD	17	1	0	0	0
PD	18	0.545	0.455	0	0
PD	19	0	1	0	0
PD	20	0.042	0.958	0	0
HP	1	1	0	0	0
HP	2	0.5	0	0	0.5
HP	3	0.833	0.167	0	0
HP	4	0.364	0.364	0	0.273
HP	5	0.667	0.333	0	0
HP	6	0.3	0.7	0	0
HP	7	0	1	0	0
HP	8	0.222	0.778	0	0
HP	9	1	0	0	0
HP	10	0	1	0	0
HP	11	0.25	0.5	0.25	0
HP	12	0.5	0.333	0	0.167
HP	13	0.167	0.667	0.167	0
HP	14	1	0	0	0
HP	15	0.167	0.167	0.083	0.583
HP	16	0.333	0.333	0	0.333

Study area	Plot	Prop Topographic depression	Prop None	Prop Rock	Prop Shrub
HP	17	0	0	0	1
HP	18	0	0	0	1
HP	19	0.667	0.333	0	0
HP	20	0.3	0.1	0.6	0
MR	1	0.4	0.6	0	0
MR	2	0.286	0.514	0.171	0.029
MR	3	0.286	0.592	0.102	0.02
MR	4	0.5	0.444	0.056	0
MR	5	1	0	0	0
MR	6	0.25	0.5	0.25	0
MR	7	0.231	0.423	0.077	0.269
MR	8	0	1	0	0
MR	9	0	1	0	0
MR	10	0	0.833	0	0.167
MR	11	0	1	0	0
MR	12	0.143	0.714	0	0.143
MR	13	0	1	0	0
MR	14	0	0.667	0	0.333
MR	15	0	1	0	0
MR	16	0	1	0	0
MR	17	0	1	0	0
MR	18	0.2	0.6	0	0.2
MR	19	0.125	0.125	0.25	0.5
MR	20	0.111	0.778	0	0.111
MR	21	0	1	0	0
MR	22	1	0	0	0
MR	23	0	1	0	0
MR	24	0	1	0	0
MR	25	0.25	0.25	0.25	0.25
MR	26	0.143	0.714	0.143	0
MR	27	0.2	0.733	0.067	0
MR	28	0	1	0	0
MR	29	0	1	0	0
MR	30	0.1	0.2	0.15	0.55

Table A.8. Raw white pine blister rust count and proportional abundance data by plot, all study areas.

Study area	Plot	Uninfected	Infected	Prop Uninfected	Prop Infected
TB	1	9	0	1	0
TB	2	7	0	1	0
TB	3	13	1	0.9286	0.07143
TB	4	2	0	1	0
TB	5	8	0	1	0
TB	6	36	0	0.973	0
TB	7	2	0	1	0
TB	8	1	0	1	0
TB	9	2	0	1	0
TB	10	2	0	1	0
TB	11	1	0	1	0
TB	12	6	0	1	0
PD	1	17	1	0.9444	0.05556
PD	2	8	0	1	0
PD	3	17	2	0.8947	0.1053
PD	4	19	0	1	0
PD	5	28	2	0.9333	0.06667
PD	6	0	0	NA	NA
PD	7	0	0	NA	NA
PD	8	5	1	0.8333	0.1667
PD	9	29	6	0.8286	0.1714
PD	10	9	2	0.8182	0.1818
PD	11	5	8	0.3846	0.6154
PD	12	0	0	NA	NA
PD	13	14	8	0.6364	0.3636
PD	14	4	0	1	0
PD	15	20	6	0.7692	0.2308
PD	16	14	2	0.875	0.125
PD	17	9	0	1	0
PD	18	11	9	0.55	0.45
PD	19	1	1	0.5	0.5
PD	20	25	1	0.9615	0.03846
HP	1	2	4	0.3333	0.6667
HP	2	1	0	1	0
HP	3	5	2	0.7143	0.2857
HP	4	10	4	0.7143	0.2857
HP	5	1	2	0.3333	0.6667
HP	6	13	1	0.9286	0.07143
HP	7	12	2	0.8571	0.1429
HP	8	10	0	1	0
HP	9	0	0	NA	NA
HP	10	1	0	1	0
HP	11	4	1	0.8	0.2
HP	12	22	1	0.9565	0.04348
HP	13	5	1	0.8333	0.1667
HP	14	2	0	1	0
HP	15	11	1	0.9167	0.08333
HP	16	1	0	1	0
HP	17	1	0	1	0

Study area	Plot	Uninfected	Infected	Prop Uninfected	Prop Infected
HP	18	1	0	1	0
HP	19	1	0	1	0
HP	20	7	1	0.7778	0.1111
MR	1	10	0	1	0
MR	2	41	9	0.82	0.18
MR	3	35	6	0.8537	0.1463
MR	4	16	1	0.9412	0.05882
MR	5	9	0	1	0
MR	6	4	0	1	0
MR	7	28	0	1	0
MR	8	1	0	1	0
MR	9	1	0	1	0
MR	10	6	0	1	0
MR	11	4	0	1	0
MR	12	64	5	0.9275	0.07246
MR	13	30	1	0.9677	0.03226
MR	14	2	0	1	0
MR	15	1	0	1	0
MR	16	4	0	1	0
MR	17	2	0	1	0
MR	18	5	0	1	0
MR	19	6	0	1	0
MR	20	9	1	0.9	0.1
MR	21	13	0	1	0
MR	22	1	0	1	0
MR	23	6	0	1	0
MR	24	1	0	1	0
MR	25	7	0	1	0
MR	26	7	0	1	0
MR	27	15	0	1	0
MR	28	4	0	1	0
MR	29	5	0	1	0
MR	30	36	0	1	0

Chapter III

FACILITATION IN TREELINE WHITEBARK PINE COMMUNITIES: BIOPHYSICAL DIFFERENCES AMONG LEEWARD MICROSITES DEPEND ON LARGER-SCALE CLIMATE INDICES

Abstract

In many treeline communities across the Northern and Central Rocky Mountains, whitebark pine (*Pinus albicaulis* Engelm, Family Pinaceae, Subgenus *Strobus*.)—a widely distributed five-needle white pine in the U.S. and Canada—is the most common tree island initiator, facilitating the survival and growth of leeward conifers more frequently than other species. Recent comparisons of biophysical characteristics of leeward microsites suggest that conifers offer a more moderated microclimate than rocks or exposed microsites, but that that whitebark pine's leeward microclimate may be similar or slightly harsher than spruce microsites, except for moisture and sky exposure. We assessed differences in leeward microclimate in two treeline communities on the harsh Rocky Mountain eastern front to test whether whitebark pine better ameliorates local conditions relative to other nurse plants or objects. Using a simple random sampling design, as opposed to a block study, we found that whitebark pine leeward microsites did not consistently experience the most moderate microclimate. Differences in microclimatic conditions by microsite type depended substantially on the general climatic conditions observed at each study area. Whitebark pine microsites experienced the lowest minimum, mean, and maximum daily soil moisture compared to all other microsite types at moister locations, but among the highest soil moisture levels in more arid conditions. We also found an inverse relationship between wind/gust speed severity and differences

in wind-protection by microsite type. Where wind and gust speeds were lower, microsites sheltered by conifers experienced lower wind and gust speeds compared to rocks and unprotected sites. Extreme wind and gust speeds, however, precluded ameliorative effects based on microsite type.

Introduction

The link between local processes and community spatial structure is one of the central principles of landscape ecology (Callaway 1995, Turner et al. 2001). In plant communities, decades of cross-sectional observations and experiments have revealed that ecosystem structure emerges from a complex combination of negative and positive associations (Callaway and Walker 1997). Although many factors tilt the balance among these interactions, including the life stages and physiologies of constituent individuals (Callaway and Walker 1997), there is a general consensus that facilitation helps shape population and community structure in environments experiencing harsh abiotic stress (e.g., Bertness and Callaway 1994, Choler et al. 2001, Callaway et al. 2002, Antonsson et al. 2009). Facilitative interactions among plants (Callaway 1995)—nurse plant syndromes—have been observed in many stressful environments, including deserts (Arriaga et al. 1993), salt marshes (Bertness and Hacker 1994) and alpine tundra (Whitehead, 1951). Similarly, where abiotic conditions reduce the likelihood of seed germination and seedling growth and survival, common geomorphic objects such as rocks and topographic niches— nurse objects or conditions—may also increase establishment and survival success (Castro et al. 2011).

The magnitude of effect that facilitation has in governing community assembly in harsh environments relies on the moderation of climatic conditions at the local scale

(Maher et al. 2005). The term "microclimate" refers to the site-specific, fine-scale abiotic conditions that are subject to variation attributable to small differences in air and soil temperature, light intensity, humidity, moisture, and wind/gust speeds (Spittlehouse and Sathers 1990). The *modus operandi* of sheltering individuals in nurse plant and nurse object syndromes is the amelioration of microclimates to a degree that promotes plant germination and seedling survival (Pyatt et al. 2016). Mechanisms by which plants can be facilitative in harsh environments include solar radiation reduction (Germino et al. 2002), wind speed moderation (Baumeister and Callaway 2006), soil temperature amelioration (Chambers 2001), and soil nutrient provision (Callaway et al. 1991); McIntire et al. (2016) found solar radiation and wind speed to be most important limitations on seedling establishment above treeline.

Facilitative interactions are particularly important in the climatically stressful alpine treeline ecotone (ATE), the transition zone from closed canopy forest to alpine tundra (Callaway et al. 2002, Resler and Tomback 2008, Tomback et al. 2016a). Compared to lower elevations, conditions in the ATE typify abiotic stress for plants (e.g., Grime 1977). Extreme winds (Marr 1977, McIntire et al. 2016), cold and variable temperatures (Körner and Paulsen, 2004), poorly developed soils (Arno and Hammerly 1984), aridity (Holtmeier 2009), nutrient scarcity (Stevens and Fox 1991), high solar radiation and sky exposure (Stevens and Fox 1991, Maher et al. 2005), and truncated growing seasons (Arno and Hammerly 1984) decrease the likelihood of conifer seed germination and early-seedling survival (e.g., Pansing et al. 2017). Harsch and Bader (2011) summarize the mechanisms that impede conifer survival in the ATE as: (1) growth limitation—impaired biosynthesis in response to low growing season

temperature, short growing season duration, or nutrient deficiency, (2) dieback—physical damage due to high snow load, frost, frozen soil, excess radiation, and high wind; and 3) seedling mortality—a result of physical damage caused by high snow load, frost, frozen soil, excess radiation, heat stress, high temperatures, and low precipitation.

ATE conifer community development relies on the initial establishment of solitary trees in unprotected microsites, or leeward of nurse objects (Resler et al. 2005). Once established, these conifers create favorable leeward microsites by alleviating wind speeds (Hättenschwiler and Smith 1999), reducing solar radiation and sky exposure (Germino et al. 2002, Maher et al. 2005), decreasing soil temperature variation (Pyatt et al. 2016), and/or increasing water availability (Callaway 1998). Tree islands form when conifers become established in the leeward microsites, building a patch of krummholz trees (Marr 1977). The capacity to survive, establish, and grow as a solitary tree allows whitebark pine to contribute significantly to community structure and biodiversity in these ecosystems (Resler and Tomback 2008).

Seed germination and early life-stage survival patterns give rise to ATE conifer community structure over time (e.g., Maher and Germino 2006, Pansing et al. 2017), and are governed largely by local climatic conditions during the growing season—July through September (e.g., Körner and Paulsen, 2004; Hoch and Körner, 2009; Harsch and Bader, 2011). Air and soil temperatures do not limit tissue growth, but rather the investment of photo-assimilates into structural growth (i.e., sink activity; Germino and Smith 1999); low air and soil temperatures slow physiological processes, including root growth (Landhäusser et al. 1996). Elevated sky exposure, radiation, and wind speeds decrease humidity and soil moisture (Holtmeier, 2009). High winds desiccate and

damage branches (Marr 1977). Although much is known about the climatic conditions governing treeline dynamcs (e.g., Harsch and Bader 2011) and nurse plant object syndromes (e.g., Resler and Tomback 2008), studies comparing the differences in microclimate provided by nurse objects and/or nurse plants (such as Pyatt et al 2016) are lacking.

In many ATEs across the Northern and Central Rocky Mountains, whitebark pine (*Pinus albicaulis* Engelm, Family Pinaceae, Subgenus *Strobus*.)—one of the most widely-distributed five-needle white pines in the U.S. and Canada—serves as a foundation species, facilitating the survival and growth of leeward conifers more frequently than other species (e.g., Resler and Tomback 2008; Tomback et al. 2016a). Due to its slow growth, high water-use efficiency (Callaway et al. 2000) and elevated carbon gain relative to other conifers (Bansal et al. 2011), whitebark pine tolerates stressful conditions in the ATE. Whitebark pine seedlings are also robust and tolerant of a variety of conditions, including poor soils and harsh seedbeds (Arno and Hoff 1990, Tomback et al. 2001, McCaughey and Tomback 2001). Whitebark pine's survival and recruitment success at high-elevations may also be attributable to a coevolved mutualism with the corvid Clark's nutcracker (*Nucifraga columbiana*; Tomback 1982). Nutcrackers often bury whitebark pine seeds in small *caches* near protective objects, such as rocks, tree trunks, and fallen trees (Tomback 1978); they may also transport seeds from parent trees up to 32.6 kilometers in distance (Lorenz et al. 2011). This process results in the dispersal of whitebark pine seeds from upper subalpine forest to the highest elevations (Tomback 1986). Unrecovered seed caches may germinate and establish in open or sheltered microsites, facilitate leeward conifer recruitment, and eventually become the

initiating conifer of tree islands. Additionally, nutcrackers cache near nurse objects disproportionately; seed caches in geomorphic niches or leeward of rocks boost whitebark pine survival in the ATE (Tomback 1978, Tomback 1982, Maher et al. 2005, Resler et al. 2005, Resler and Tomback 2008, Pyatt et al 2016).

Pyatt et al. (2016) postulated two explanations for whitebark pine's prevalence as a tree island initiator: (1) whitebark pine may present more frequent opportunities for microclimate amelioration, given its landscape abundance, or (2) it may provide better quality microclimate amelioration compared to other nurse plants, or nurse objects. Using a block design, they compared biophysical attributes in microsites leeward of whitebark pine, Engelmann spruce (*Picea engelmannii*), rocks, and in unprotected (exposed) microsites. They found whitebark pine and Engelmann spruce microsites experienced higher daily soil temperature minima, lower daily soil temperature maxima, lower daily photosynthetically active radiation (PAR), and lower daily mean wind speeds than rock and unprotected microsites.

Here, we examined growing season microclimate for two ATE communities on the harsh Rocky Mountain eastern front to test whether microsites leeward of conifers, and particularly *P. albicaulis*, experience less extreme and variable microclimates than those of similarly sized rocks, or those in open, unprotected microsites (e.g., Pyatt et al. 2016), but using a simple random sampling design. In both these treeline communities, whitebark pine is the predominant treeline conifer, and a locally abundant tree island initiator (Wagner, chapt. 2). In both communities examined by Pyatt et al. (2016), whitebark pine was the most frequent tree island initiator (Tomback et al. 2016a). In this study, we hypothesized that whitebark pine leeward microsites, in comparison to other

microsite types, would be characterized by (1) higher minimum and lower maximum growing season air and soil temperatures (2) higher levels of percent relative humidity and soil moisture, and (3) lower wind and gust speeds. To test these hypotheses, we compared differences in biophysical variables among four microsite types at both study areas, for the growing season, following the methods of Pyatt et al. (2016). Our focus was comparative performance of four microsite types at opposite ends of the Greater Yellowstone Ecosystem over part of the growing season in each study area.

Methods

Study Areas

We performed microclimate assessments in two ATEs at northernmost and southernmost locations in the Greater Yellowstone Area (GYE, Fig. 3.1), which is situated in northwestern Wyoming. In both study areas, conifer species included whitebark pine, Engelmann spruce, and subalpine fir (*Abies lasiocarpa*), which occurred either solitarily or as members of tree islands (Wagner, chapt. 2). At Tibbs Butte, Shoshone National Forest, the study area comprised approximately 4.2 ha on the northeast aspect, from 2,983 to 3,238 m elevation. The topography consisted of a continuous upslope gradient, and the terrain featured large, scattered rocks, and undeveloped soils stemming from a bedrock of Precambrian granite (Bevan 1923). Conifers were scarce and primarily solitary. Dominant understory vegetation included *Geum rossii* (R. Br.) Ser., *Potentilla diversifolia* Lehm., and *Saxifraga* spp. (Tomback et al. 2016a).

Our southernmost study site was located 250 km south of Tibbs Butte on Mutiny Ridge in the Wind River Range, Shoshone National Forest, approximately 1.5 km west of

Christina Lake. The Mutiny Ridge ATE terrain is strewn with numerous large rocks and scattered pockets of soil; the bedrock consists of Precambrian (Archean) crystalline minerals, including granodiorite, porphyritic quartz monzonite, and magmatic gneiss (e.g., Frost et al. 2000). Dominant vegetation includes *Geum rossii (R. Br.) Ser.*, *Pteryxia hendersonii (J.M. Coult. and Rose) Mathias and Constance*, *Phlox pulvinata (Wherry) Cronquist*, and *Silene acaulis (L.) Jacq* (Tomback et al. 2016a). The study area included 117 ha on northeast, southeast, and southwest aspects (3,200—3,400 m elevation).

Wagner (chapt 2) performed mesoclimate comparisons between these two study areas using open source Precipitation Elevation Regressions on Independent Slopes Model (PRISM) data for the years 1985 through 2015 (PRISM Climate Group, 2015). He found no significant differences in mean daily growing season temperature and precipitation between the study areas.

Study Design

We defined a microsite as a cylindrical space 20 cm in diameter and 15 cm in height directly leeward of a conifer or rock, or on open ground with no windward protection (Pyatt et al. 2016). At each study area, we recorded microclimatic conditions directly leeward of the two most prevalent conifer species (Tibbs Butte: whitebark pine and subalpine fir; Mutiny Ridge: whitebark pine and Engelmann spruce), rocks, and in unprotected (exposed) microsites. The heights, lengths, and widths of nurse trees and rocks depended on local availability and are depicted in Appendix B, Fig. B.1. We found no mean difference in nurse object height between Tibbs Butte and Mutiny Ridge. There were also no mean differences in nurse object height by microsite type.

In 2014, we established twenty microclimatic weather stations at Tibbs Butte and in 2015 at Mutiny Ridge. Each microsite type (i.e., *P. albicaulis*, *A. lasiocarpa*, rock, and unprotected on Tibbs Butte; *P. albicaulis*, *P. Enelmannii*, rock, and unprotected on Mutiny Ridge) had five replicates, resulting in a sample population of 20 leeward microsites, stratified by type. We employed a simple random sampling design, selecting microsite locations based on random positions generated using the splancs package in R (version 3.1.0, R Core Team 2014; Rowlingson and Diggle 2014). We also randomized the assignment of each nurse object to its corresponding random location. We determined leeward microsite position by the direction of wind-flagging on branches of nearby conifers. We defined the leeward microsite as directly opposite the source of wind causing the most prevalent branch flagging. At both study sites, we selected microsites not protected by objects other than the nurse object specified; those microsites designated to be unprotected were not protected by any nearby object. Microsites at Tibbs Butte typically supported a higher percent ground cover (75%–100%) than Mutiny Ridge (50%–75%).

Microclimatic Assessments

Using Onset Computer HOBO sensors and Micro Station Data Loggers, we measured the following microclimate characteristics at each microsite for part of the growing season, from August 2nd to September 5th (2014 for Tibbs Butte and 2015 for Mutiny Ridge): air temperature (°C) 10 cm above the ground (S-TMB-M002), percent relative humidity 10 cm above the ground (S-TMB-M002), soil temperature (°C) 3 cm below ground (S-TMB-M017), soil moisture ($m^3\ m^{-3}$) 6 cm below ground (S-SMC-M00), wind speed ($m\ s^{-1}$) 10 cm above ground (S-WSA-M003), and gust speeds ($m\ s^{-1}$) 10 cm

above ground (S-WSA-M003; Pyatt et al. 2016). The wind and gust speed sensor was an anemometer. We constructed protective housing using PVP piping and vinyl gutters to prevent damage to the sensors and cables during the recording interval (Pyatt et al. 2016; Fig. 3.2). For placement of the air temperature and percent relative humidity sensor, we used a protective radiation shield mounted on a 7.6 cm wooden block; the apparatus was attached to a metal stake for stability (Pyatt et al. 2016). The soil temperature and soil moisture sensors were placed directly in the ground on opposite sides of the microsite (approximately 20 cm apart) and at least 4 cm from other sensors to avoid interference. The anemometer was staked near the center of the microsite. All the sensors delivered data to a Micro Station Data Logger established 1 m away from the microsite; the data logger was mounted on a vinyl gutter pipe 30 cm above the ground (Pyatt et al. 2016).

To record all microclimate variables, we launched the Micro Station Data Loggers using HOBOware Pro software (version 3.3.0), and set each to record in 15-minute intervals. For wind speed, data loggers averaged automatically over each 15-minute interval from one minute observations. Gust speeds were designated as the highest wind speed over any 3 second period within each 15-minute logging interval (Pyatt et al. 2016). On Tibbs Butte, all 20 Micro Station Data Loggers began recording on August 2, 2014 at 12:00am MST and were stopped on September 5, 2014 at 11:45pm MST. On Mutiny Ridge, all 20 Micro Station Data Loggers began recording on August 2, 2015 at 12:00am MST and were stopped on September 5, 2015 at 11:45pm MST. The recording duration was 35 days at both study areas for each year.

Data Analysis

We used R (version 3.2.4, R core team 2016) to conduct all statistical analyses. For response variables (i.e., air temperature, percent relative humidity, soil temperature, soil moisture, wind speed, and gust speed) at each microclimate weather station, we computed the following statistics prior to data analysis: (1) daily minimum, mean, and maximum for air temperature, percent relative humidity, soil temperature, and soil moisture, (2) daily mean and maximum for wind speed, and (3) daily maximum for gust speed.

Model selection. We began the process of estimating growing season microclimatic parameters by microsite type at each study area by fitting intercept ($y = \beta_o + \epsilon$), linear ($y = \beta_o + \beta_1 x + \epsilon$), and quadratic ($y = \beta_o + \beta_1 x + \beta_2 x^2 + \epsilon$) models to each response variable statistic at each station. In these models, *y* corresponds to the response variable statistic, *x* corresponds to time (in days), β's are parameter estimates, and ϵ are residuals (i.e., model errors; the distances between each data point and the model in the *y*-direction). To determine which model type best explained the general behavior of each response variable statistic throughout the recording interval, we calculated Akaike's Information Criterion (AIC) scores for each model at each station, and selected the one with the lowest AIC score (i.e., the most parsimonious model type) over the majority of stations. By study area, we used the best fitting model for its associated response variable statistic for the remainder of the analysis.

Bootstrapped linear regressions. At this point, we deviated from the statistical methods of Pyatt et al. (2016), and selected an approach that precludes *a priori* assumptions about each response variable's underlying distribution. Once a model type had been selected for a given response variable statistic, we performed a bootstrapped

linear regression of each response variable statistic (y) by time (x, in days) for each microsite type at each study area—that is, we (1) fit a model to each response variable statistic for each microsite type; (2) harvested the predicted values (the *y* predictions by day for each response variable statistic) and residuals (model errors) by microsite type; (3) for each of 5000 iterations, sampled randomly with replacement from the microsite-specific residuals and added them to the predicted values to generate 20,000 bootstrapped samples, 5000 for each microsite type; and (4) fit a model to each bootstrapped sample (n = 5000 models per microsite type).

Parameter estimates. The bootstrap regression resulted in 5000 models per microsite type per response variable statistic, each predicting its corresponding response variable statistic in terms of time (date from Aug. 2 (t_o) to Sept 5 (t_f)). For these models, the total area under the curve (*A*) over the duration of the recording interval is equivalent to the predicted seasonal average ($\bar{F}_{seasonal}$) (Eq. 1).

$$\bar{F}_{seasonal} = \frac{A}{t_f - t_0} \quad (1)$$

To estimate the microclimatic conditions at a given microsite type over the recording interval, we integrated each model with respect to time, and divided the integral by the total change in time (35 days). The calculation for estimating seasonal microclimatic conditions from an intercept model takes the following form:

$$A = \int_{t_o}^{t_f} (\hat{\beta}_o) dt \quad \text{intercept} \quad (2)$$

$$A = [\, \hat{\beta}_o (t_f - t_o) \,] \quad \text{intercept} \quad (3)$$

$$\bar{F}_{seasonal} = \frac{1}{t_f - t_0}\left[\hat{\beta}_o(t_f - t_o)\right] \quad \text{intercept} \quad (4)$$

$$\bar{F}_{seasonal} = \hat{\beta}_o \quad \text{intercept} \quad (5)$$

The calculation for estimating seasonal microclimatic conditions form a linear model takes the following form:

$$A = \int_{t_o}^{t_f} (\hat{\beta}_o + \hat{\beta}_1 t)dt \quad \text{linear} \quad (6)$$

$$A = \left[\hat{\beta}_o(t_f - t_o) + \frac{\hat{\beta}_1({t_f}^2 - {t_o}^2)}{2}\right] \quad \text{linear} \quad (7)$$

$$\bar{F}_{seasonal} = \frac{1}{t_f - t_0}\left[\hat{\beta}_o(t_f - t_o) + \frac{\hat{\beta}_1({t_f}^2 - {t_o}^2)}{2}\right] \quad \text{linear} \quad (8)$$

$$\bar{F}_{seasonal} = \hat{\beta}_o + \frac{\hat{\beta}_1(t_f + t_o)}{2} \quad \text{linear} \quad (9)$$

The calculation for estimating seasonal microclimatic conditions from a quadratic model takes the following form:

$$A = \int_{t_o}^{t_f} (\hat{\beta}_o + \hat{\beta}_1 t + \hat{\beta}_2 t^2)dt \quad \text{quadratic} \quad (10)$$

$$A = \left[\hat{\beta}_o(t_f - t_o) + \frac{\hat{\beta}_1({t_f}^2 - {t_o}^2)}{2} + \frac{\hat{\beta}_2({t_f}^3 - {t_o}^3)}{3}\right] \quad \text{quadratic} \quad (11)$$

$$\bar{F}_{seasonal} = \frac{1}{t_f - t_0}\left[\hat{\beta}_o(t_f - t_o) + \frac{\hat{\beta}_1({t_f}^2 - {t_o}^2)}{2} + \frac{\hat{\beta}_2({t_f}^3 - {t_o}^3)}{3}\right] \quad \text{quadratic} \quad (12)$$

$$\bar{F}_{seasonal} = \hat{\beta}_o + \frac{\hat{\beta}_1(t_f + t_o)}{2} + \frac{\hat{\beta}_2({t_f}^2 + t_f t_o + {t_o}^2)}{3} \quad \text{quadratic} \quad (13)$$

This process generated four sampling distributions for each response variable statistic, one corresponding to each microsite type. Then, we calculated the mean of each sampling distribution to identify the parameter estimate for each microclimatic condition at each

microsite type. Finally, we used the 0.025 and 0.975 quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% high density interval (HDI).

Assessing bias. We employed the model selection, bootstrap regression, and integration to maximize the likelihood of achieving accurate parameter estimates for microclimate in each microsite type. To assess how our estimates differed from simply calculating the crude global mean (i.e., taking the mean of the raw data for each microsite over the entire recording interval), we subtracted the crude mean from our estimated seasonal average ($\bar{F}_{seasonal}$) by microsite during each iteration of the bootstrap regression. This process resulted in a sampling distribution of 5000 *biases* for each microsite type. We calculated the mean of each sampling distribution to identify the parameter estimate for the bias in each microclimatic condition at each microsite type. We used the 0.025 and 0.975 quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% high density interval (HDI).

Parameter estimates for mean differences. We calculated pairwise mean differences in seasonal microclimatic conditions between microsite types by subtracting the bootstrap regression-derived sampling distributions from one-another. For example, we calculated the difference in daily minimum air temperature from August 2nd through September 5th between whitebark pine and Engelmann spruce on Tibbs Butte by subtracting the sampling distribution corresponding to whitebark pine from the sampling distribution of Engelmann spruce. This calculation resulted in a distribution of mean differences between whitebark pine and Engelmann spruce. Once this had been done for each pairwise comparison at each study area, we calculated the mean of each mean-

difference-in-seasonal-microclimatic-condition sampling distribution to identify its corresponding parameter estimate. We made Bonferroni adjustments based on the number of pairwise comparisons to determine which sampling distribution quantiles to use as the HDI lower and upper boundaries. The formula for these adjustments is: $HDI = \alpha/n$, where n is the number of pairwise comparisons; our α for all analyses in this study was 0.05. Comparisons among our four microsite types resulted in six pairwise comparisons, so we estimated the 99.17% HDI by calculating the 0.0042 and 0.9958 quantiles of each sampling distribution as the lower and upper boundary. For all pairwise difference estimates, we concluded that seasonal microclimatic conditions did not differ (i.e., no mean difference) if the estimated HDI included zero.

Parameter estimates for microclimatic variability. To assess variability in each response variable statistic by microsite, we calculated the standard deviation (SD) of each of the 20,000 sets of residuals derived from the bootstrap regression. For this, we followed the following process: We (1) fit a model to each response variable statistic for each microsite type, (2) harvested the residuals (model errors) by microsite type, (3) for each of 5000 iterations, sampled randomly with replacement from the microsite-specific residuals, and (4) calculated the standard deviation of each set of residuals (n = 5000 per microsite type). This process resulted in four sampling distributions corresponding to the *variability* in each response variable statistic, one corresponding to each microsite type. Then, we calculated the mean of each sampling distribution to identify the parameter estimate for the variability of each microclimatic condition at each microsite type. We used the 0.025 and 0.975 quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% high density interval (HDI).

Microclimatic variability mean difference parameter estimates. As we had done mean difference parameter estimates between microsite types, we calculated mean differences in seasonal microclimatic *variability* by subtracting the bootstrap regression-derived sampling distributions of standard deviations from one-another. In doing so, we achieved a sampling distribution of mean differences in variability for each response variable statistic by microsite type. Once this had been done for each pairwise comparison for each study area, we calculated the mean of each mean-difference-in-seasonal-microclimatic-condition-variability sampling distribution to identify its corresponding parameter estimate. As with previous pairwise difference HDIs, we made Bonferroni adjustments based on six pairwise comparisons. We estimated the 99.17% HDI by calculating the 0.0042 and 0.9958 quantiles of each sampling distribution as the lower and upper boundary. For all pairwise difference estimates, we concluded that the variation in seasonal microclimatic conditions did not differ (i.e., no mean difference) if the estimated HDI included zero.

Results

Raw data for all daily response variable statistics are displayed in Figs. 3.3a and 3.3b. Figs 3.4a and 3.4b display model selection results for those data. Additionally, density plots for all raw daily response variable statistics are displayed in Appendix B, Figs. B.2a and B.2b. For stand-alone parameter estimates and 95% HDIs regarding seasonal microclimatic conditions, see Appendix B, Figs. B.3a and B.3b, and Appendix B, Tables B.1 through B.5 for tabulated values. Biases for those parameter estimates are represented in Appendix B, figs. B.4a and B.4b. The primary results of this study, pairwise mean difference parameter estimates for microclimatic conditions (effect sizes),

are displayed in figures 3.5a and 3.5b, and their corresponding values are tabulated in Appendix B, Tables. B.6 through B.10. For parameter estimates and 95% HDIs regarding the variability of seasonal microclimatic conditions, see Appendix B, figures B.5a and B.5b, or Appendix B, Tables. B.11 through B.15 for tabulated values. Finally, pairwise mean difference parameter estimates for microclimatic variability (effect sizes) can be found in figures 3.6a and 3.6b; their corresponding values are also tabulated in Appendix B, Tables. B.16 through B.20.

Air Temperature

The minimum, mean, and maximum daily air temperatures at Tibbs Butte decreased over the course of the growing season, but not linearly; air temperature declines were amplified later in the season following a quadratic curve (Figs. 3.3a and 3.4a). At Mutiny Ridge, the minimum, mean, and maximum daily air temperature were consistent over time following an intercept model (Figs. 3.3b and 3.4b). In general, Mutiny Ridge experienced higher minimum daily air temperatures than Tibbs Butte (Figs 3.3a, 3.3b, 3.5a, 3.5b; Appendix B: B.3a, B.3b, and Tables B.1 and B.6).

We found no differences in mean daily air temperature by microsite at either study area (Figs. 3.5a, 3.5b; Appendix B: Figs. B.3a, B.3b, and Tables B.1 and B.6). At Tibbs Butte, we found that whitebark pine and Engelmann spruce microsites had warmer maximum daily air temperatures than rock microsites. We also found whitebark pine microsites had warmer maximum daily air temperatures than unprotected microsites. For Mutiny Ridge, we found significant differences between rock and unprotected microsites; rocks had a lower minimum and higher maximum daily air temperature than that of unprotected microsites.

Our assessments of variability in seasonal microclimatic conditions revealed that whitebark pine microsites experienced significantly greater variability in maximum daily air temperature than rock microsites at both study areas (Fig. 3.6a and 3.6b; Appendix B: Fig. B.4a and B.4b, and Tables B.11 and B.16).

Percent Relative Humidity

For daily percent relative humidity on Tibbs Butte, the minimum and mean decreased over the course of the growing season following a quadratic curve; maximum daily percent relative humidity held relatively constant (Figs. 3.3a and 3.4a). The general trends for those response variable statistics were identical on Mutiny Ridge (Figs. 3.3b and 3.4b). In general, Tibbs Butte experienced higher minimum and mean daily percent relative humidity than Tibbs Butte (Figs 3.3a, 3.3b, 3.5a, 3.5b; Appendix B: B.3a, B.3b, and Tables B.2 and B.7).

Pairwise differences for minimum, mean, and maximum daily percent relative humidity on Tibbs Butte revealed several significant differences (Fig. 3.5a; Appendix B: Fig. B.3a, and Tables B.2 and B.7). First, we found that whitebark pine microsites had a higher minimum and lower maximum daily percent relative humidity than that of rock microsites and Engelmann spruce microsites. Second, we found unprotected microsites had higher minima and lower maxima for daily percent relative humidity compared to rock and Engelmann spruce microsites. Third, Engelmann spruce microsites had a higher mean daily percent relative humidity than whitebark pine and unprotected microsites. Finally, we found Engelmann spruce microsites had the highest maximum daily percent relative humidity compared to all other microsites.

We found no differences in minimum and mean daily percent relative humidity by microsite on Mutiny Ridge (Fig. 3.5b; Appendix B: Fig. B.3b, and Tables B.2 and B.7). However, whitebark pine microsites had the lowest daily maximum percent relative humidity compared to all other microsite types.

Our assessments at Tibbs Butte revealed that whitebark pine microsites experienced significantly less variability in mean and maximum daily percent relative humidity than rock and Engelmann spruce microsites, which in turn had significantly less variability in maximum daily percent relative humidity compared to unprotected microsites (Fig. 3.6a; Appendix B: Fig. B.4a, and Tables. B.12 and B.17). At Mutiny Ridge, we found that whitebark pine microsites experienced significantly more variability in maximum daily percent relative humidity than rock microsites (Fig. 3.6b; Appendix B: Fig. B.4b, and Tables. B.12 and B.17).

Soil Temperature

Mirroring air temperature trends, the minimum, mean, and maximum daily soil temperature at Tibbs Butte decreased over the course of the growing season, but not linearly; declines were amplified later in the season following a quadratic curve (Figs. 3.3a and 3.4a). For soil temperature on Mutiny Ridge, the minimum and mean were relatively consistent over the course of the growing season, but the maximum daily percent relative humidity decreased following a quadratic curve (Figs. 3.3b and 3.4b). In general, Mutiny Ridge experienced higher minimum daily soil temperatures than Tibbs Butte (Figs 3.3a, 3.3b, 3.5a, 3.5b; Appendix B: B.3a, B.3b, and Tables B.3 and B.8).

At Tibbs Butte, the mean daily soil temperature in whitebark pine microsites was lower than that of Engelmann spruce microsites (Fig. 3.5a; Appendix B: Fig. B.3a, and

Tables B.3 and B.8). We also found that the daily minimum soil temperature in Engelmann spruce and rock microsites was higher than that of unprotected microsites. For daily maximum soil temperature, we found Engelmann spruce microsites to be warmer than rock microsites.

The minimum and mean daily soil temperature at Mutiny Ridge was significantly higher for whitebark pine microsites than for subalpine fir and unprotected microsites (Fig. 3.5b; Appendix B: Fig. B.3b, and Tables B.3 and B.8). We also found that the minimum and mean daily soil temperatures in rock microsites were warmer than that of unprotected microsites. We found the minimum daily soil temperature was greater in rock microsites than that of subalpine fir microsites.

Our assessments of seasonal microclimatic variability at Tibbs Butte revealed no significant differences by microsite type for mean daily soil temperature. However, we found the minimum daily soil temperature in whitebark pine microsites varied more than unprotected microsites. We also found the maximum daily soil temperature in whitebark pine microsites varied more than any other microsite type throughout the season (Fig. 3.6a; Appendix B: Fig. B.4a, and Tables B.13 and B.18). We also found the maximum daily soil temperatures varied more in Engelmann spruce microsites than in rock microsites.

At Mutiny Ridge, unprotected microsites varied significantly more than rock microsites for minimum, mean, and maximum soil temperature (Fig. 3.6b; Appendix B: Fig. B.4b, and Tables B.13 and B.18). For mean and maximum daily soil temperature, we found that whitebark pine microsites experienced greater variability than rock microsites. We also found whitebark pine microsites varied less than subalpine fir and unprotected

microsites for minimum daily soil temperature. Finally, we found that subalpine fir microsites were more variable in minimum daily soil temperature than rock microsites.

Soil Moisture

Throughout the course of the growing season on Tibbs Butte, the minimum and mean daily soil moisture increased following a quadratic curve; the maximum daily soil moisture held constant (Figs. 3.3a and 3.4a). Conversely, on Mutiny Ridge the minimum, mean, and maximum daily soil moisture decreased linearly over the course of the season (Figs. 3.3b and 3.4b).

Every pairwise comparison for minimum, mean, and maximum soil moisture on Tibbs Butte revealed a significant difference, establishing a clear hierarchy (Fig. 3.5a; Appendix B: Fig. B.3a, and Tables B.4 and B.9). Whitebark pine microsites experienced the lowest minimum, mean, and maximum daily soil moisture, followed by rock, unprotected, and Engelmann spruce microsites. At Mutiny Ridge, however, whitebark pine microsites did not experience the driest conditions. In fact, whitebark pine microsites experienced higher soil moisture levels than subalpine fir microsites (Fig. 3.5b; appendix B: Fig. B.3b, and Tables B.4 and B.9). Additionally, whitebark pine microsites experienced higher daily minimum soil moisture than unprotected microsites. We also found rock microsites had higher minimum and mean daily soil moisture than that of subalpine fir microsites.

We found that whitebark pine microsites experienced the most variable maximum daily soil moisture at Tibbs Butte, followed by Engelmann spruce, unprotected, and rock microsites, respectively (Fig. 3.6a; Appendix B: Fig. B.4a, and Tables B.14 and B.19). Results for minimum and mean daily soil moisture showed that whitebark pine and

Engelmann spruce microsites had greater variability than rock and unprotected microsites.

For Mutiny Ridge, results were the same for minimum, mean, and maximum soil moisture variability, with whitebark pine microsites experiencing more variability than any other microsite type assessed (Fig. 3.6b; Appendix B: Fig. B.4b, and Tables B.14 and B.19). Rock microsites experienced more variability than subalpine fir and unprotected microsites.

Wind and Gust Speed

The minimum, mean, and maximum daily wind and gust speeds at Tibbs Butte increased linearly over the course of the growing season (Figs. 3.3a and 3.4a). At Mutiny Ridge, minimum, mean, and maximum wind and gust speeds increased, but the increases were amplified later in the season following a quadratic curve (Figs. 3.3b and 3.4b). In general, Mutiny Ridge experienced greater mean and maximum wind speeds, and greater maximum gust speeds, than Tibbs Butte (Figs 3.3a, 3.3b, 3.5a, 3.5b; Appendix B: B.3a, B.3b, and Tables B.5 and B.10).

On Tibbs Butte, we observed whitebark pine and Engelmann spruce microsites experienced the lowest wind and gust speeds across every statistic assessed (Fig. 3.5a; Appendix B: Fig. B.3a, and Tables B.5 and B.10). Rock microsites experienced lower mean and maximum daily wind speeds compared to unprotected microsites.

At Mutiny Ridge, our analysis revealed no significant differences for daily mean wind speed or maximum daily gust speed (Fig. 3.5b; Appendix B: Fig. B.3b, and Tables B.5 and B.10). Interestingly, we found maximum daily wind speeds were significantly

greater in subalpine fir microsites compared to whitebark pine, rock, and unprotected microsites.

Our assessments of variability of microclimatic conditions at Tibbs Butte revealed that Engelmann spruce experienced the least variability in daily mean and maximum wind speeds relative to any other microsite type (Fig. 3.6a; Appendix B: Fig. B.4a, and Tables B.15 and B.20). For daily maximum gust speed, we found that whitebark pine experienced greater variability than all other microsite types.

At Mutiny Ridge, we found that unprotected microsites had more variable mean daily wind speeds than whitebark pine, subalpine fir, and rocks (Fig. 3.6b; Appendix B: Fig. B.4b, and Tables B.15 and B.20). We also found that microsites protected by subalpine fir experienced greater maximum daily wind speed variability than rock-sheltered microsites. For maximum daily gust speed, we found that subalpine fir microsites had the most variable conditions. Finally, we found whitebark pine microsites had less variable maximum daily gust speeds than unprotected microsites.

Discussion

Our primary objective for this study was to determine whether whitebark pine's prevalence as a tree island initiator in many Rocky Mountain ATEs was attributable to a leeward microclimate that ameliorated the extreme ATE environment. We hypothesized that microsites leeward of whitebark pine would experience (1) higher minimum and lower maximum growing season air and soil temperatures, (2) higher percent relative humidity and soil moisture, and (3) lower wind and gust speeds compared to other conifers and nurse objects.

We found that whitebark pine leeward microsites did not consistently provide the most moderate leeward microclimate. Rather, differences in microclimatic conditions by microsite type depend substantially on general climatic conditions at each study area. At Tibbs Butte, where soil moisture was higher and increased later in the season, we found that whitebark pine microsites experienced the lowest minimum, mean, and maximum daily soil moisture compared to all other microsite types. Conversely, whitebark pine microsites were generally more moist than other microsite types at Mutiny Ridge, where soil moisture conditions were lower and potentially more limiting for tree survival.

We also found an inverse relationship between wind and gust speeds and microclimate amelioration differences by microsite type. At Tibbs Butte, where wind and gust speeds were lower than that on Mutiny Ridge, we found that microsites leeward of conifers experienced lower wind and gust speeds compared to rocks and unprotected sites. At Mutiny Ridge, however, extreme wind and gust speeds precluded microsite ameliorative effects.

When comparing biophysical attributes in microsites leeward of whitebark pine, Engelmann spruce (Picea engelmannii), rocks, and in unprotected (exposed) microsites, Pyatt et al. (2016) found whitebark pine and Engelmann spruce microsites experienced higher daily soil temperature minima, lower daily soil temperature maxima, lower daily photosynthetically active radiation (PAR), and lower daily mean wind speeds than rock or unprotected microsites. Our findings were in line with Pyatt et al. (2016) in that the minimum daily soil temperatures were higher leeward of Engelmann spruce, but did not find evidence for minimum soil temperature moderation by whitebark pine. In fact, we observed generally higher levels of soil temperature variability in whitebark pine

microsites compared to other microsites. For wind/gust speeds, our findings at Tibbs Butte are in line with those observed by Pyatt et al. (2016); conifers significantly ameliorated mean and maximum daily wind speeds, as well as maximum daily wind speeds. However, at Mutiny Ridge, where the ATE experienced significantly greater wind/gust speeds than Tibbs Butte, our results deviated from their general findings. Finally, our results also agree with Pyatt et al. (2016) in that Engelmann spruce may produce a somewhat more favorable microclimate than whitebark pine in regards to mean daily wind speeds.

Tables and Figures

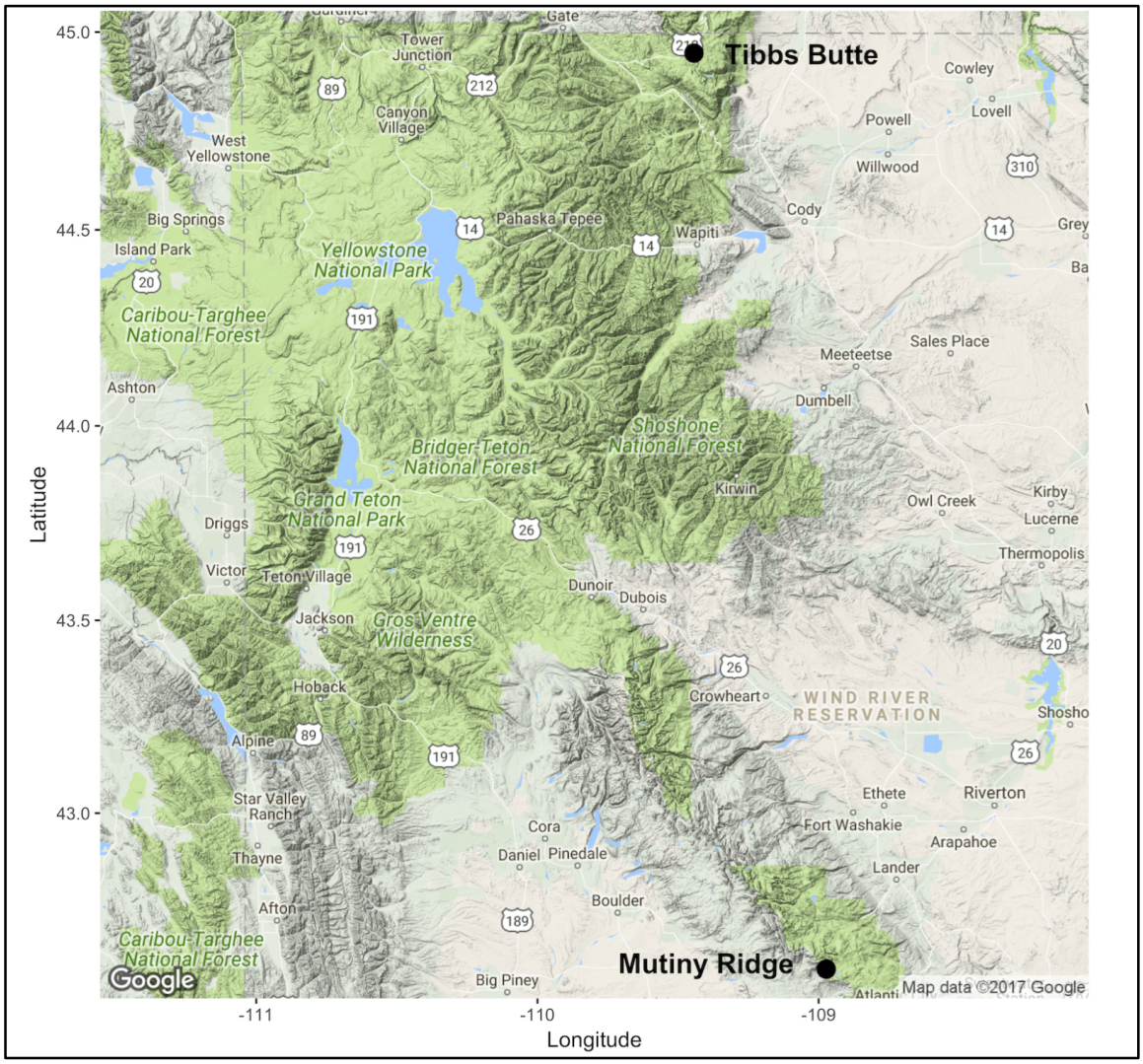


Figure 3.1. Research study areas in the Greater Yellowstone Ecosystem. Study areas include, Tibbs Butte, Shoshone National Forest, WY (44°56'46.48" N, 109°26'39.76" W), and Mutiny Ridge, Shoshone National Forest, WY (42°35'33.56" N, 108°58'07.44" W). Map created using ggmap package in R (Kahle and Wickham 2013).



Figure 3.2. Microclimate weather station. The weather station is established in an unprotected (exposed) microsite on Mutiny Ridge. Photocredit: Elizabeth Pansing.

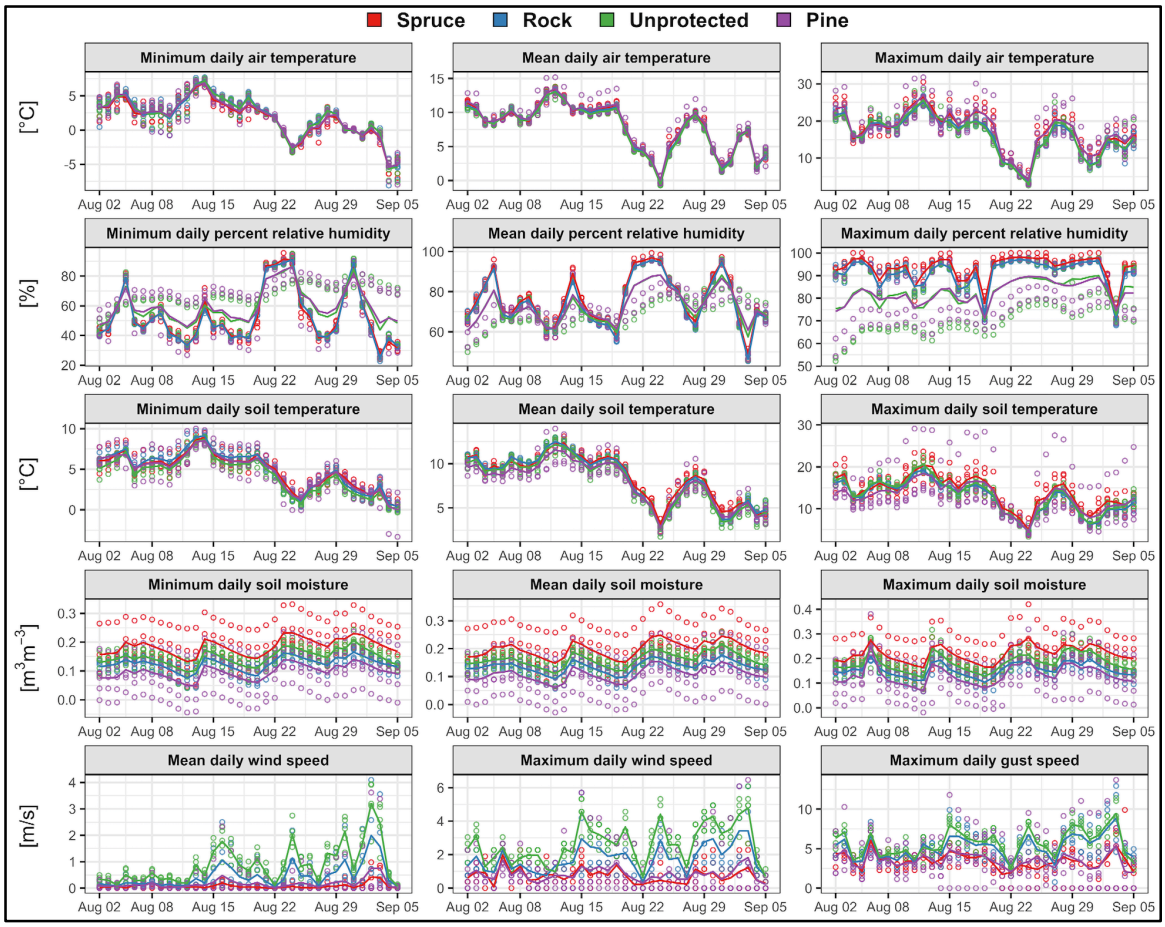


Figure 3.3a. Time series plots for Tibbs Butte. Plots display raw response variable statistics for all biophysical variables at Tibbs Butte. Circles are daily averages for each weather station, and lines are daily averages for each microsite type.

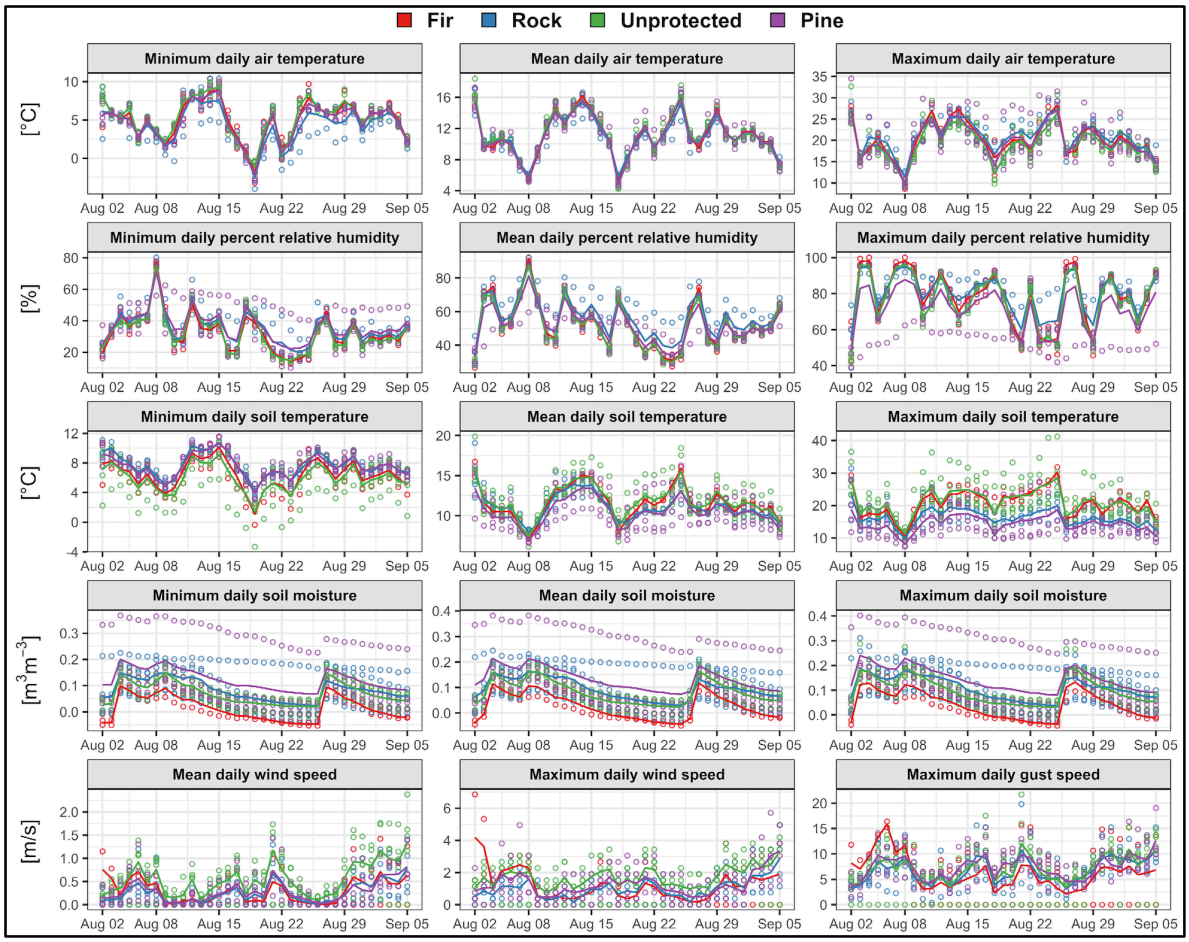


Figure 3.3b. Time series plots for Tibbs Butte. Plots display raw response variable statistics for all biophysical variables at Mutiny Ridge. Circles are daily averages for each weather station, and lines are daily averages for each microsite type.



Figure 3.4a. Best model fits for each response variable statistic at Tibbs Butte.



Figure 3.4b. Best model fits for each response variable statistic at Mutiny Ridge.

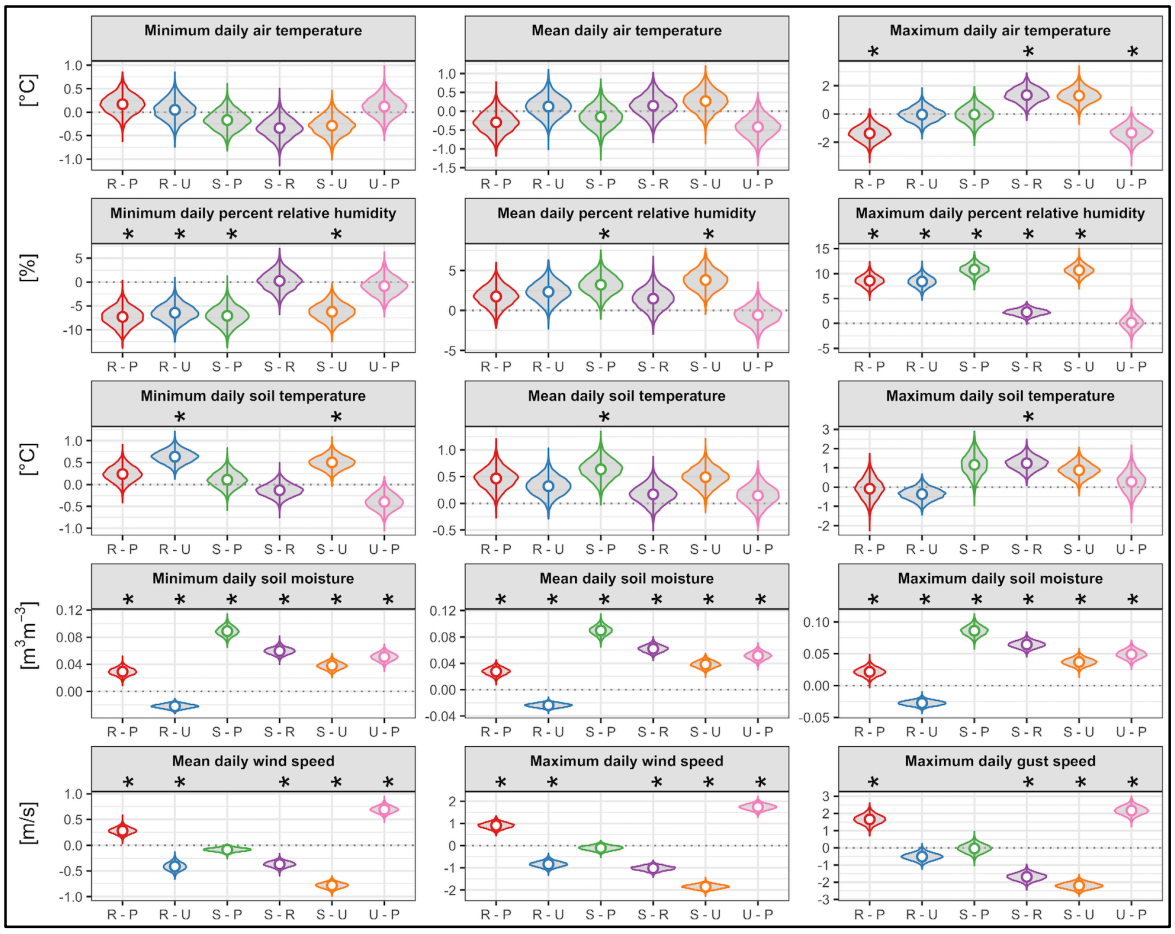


Figure 3.5a. Parameter estimates for mean differences in microclimate at Tibbs Butte. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 99.17% HDIs (lines) for pairwise mean differences in seasonal microclimatic conditions by microsite type at Tibbs Butte. R = Rock, P = Pine, U = Unprotected, and S = Spruce. Asterisks (*) denote significant differences.

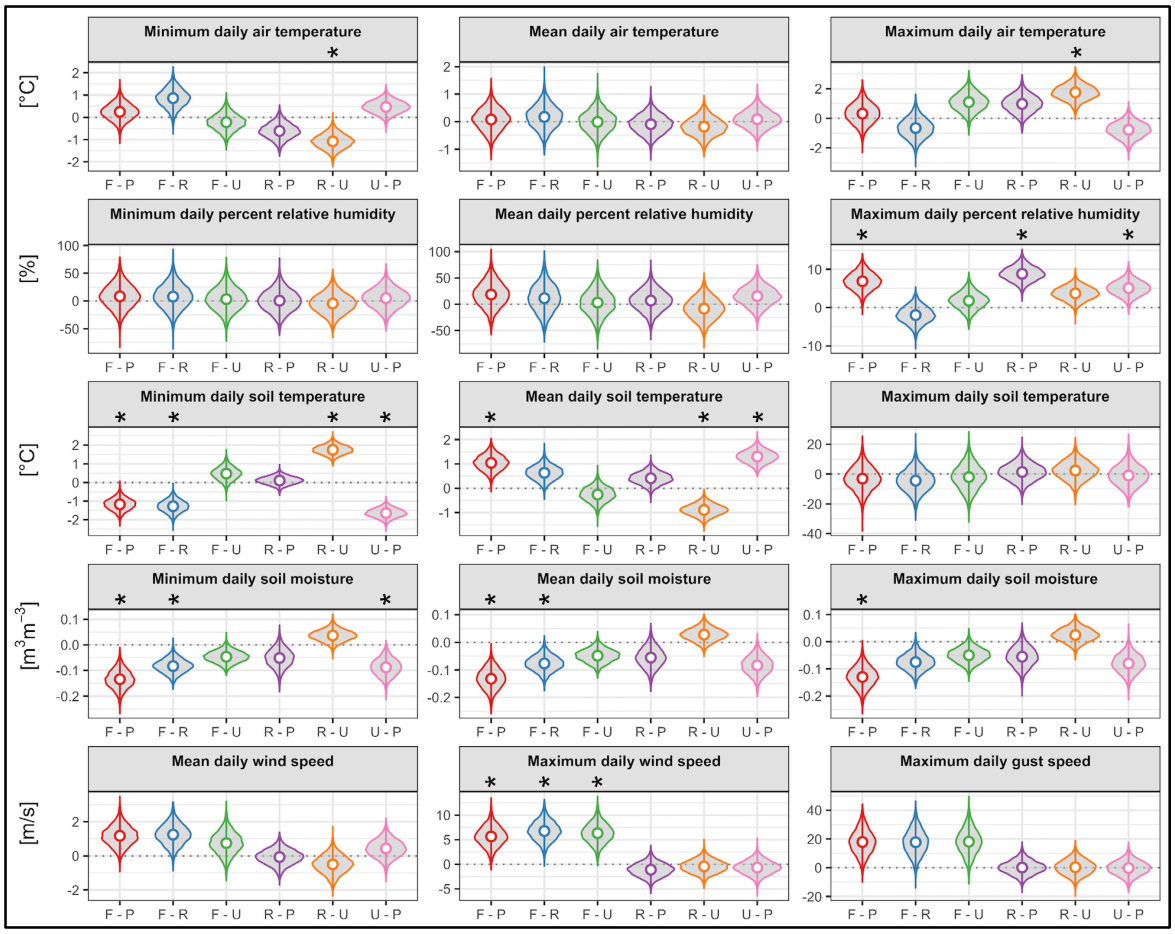


Figure 3.5b. Parameter estimates for mean differences in microclimate at Mutiny Ridge. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 99.17% HDIs (lines) for pairwise mean differences in seasonal microclimatic conditions by microsite type at Mutiny Ridge. R = Rock, P = Pine, U = Unprotected, and F = Fir. Asterisks (*) denote significant differences.

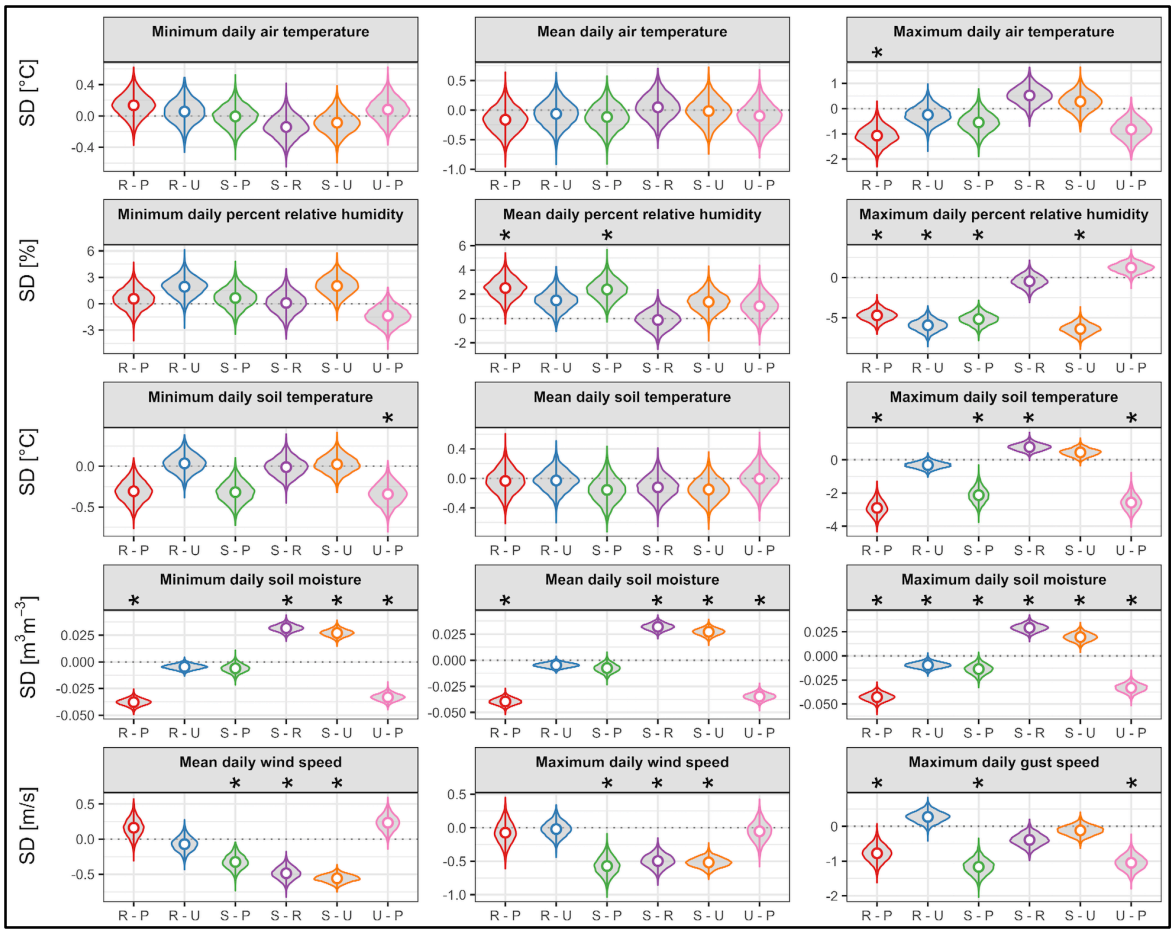


Figure 3.6a. Microclimatic variability mean difference parameter estimates for Tibbs Butte. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 99.17% HDIs (lines) for pairwise mean differences in seasonal microclimatic standard deviations by microsite type at Tibbs Butte. R = Rock, P = Pine, U = Unprotected, and S = Spruce. Asterisks (*) denote significant differences.

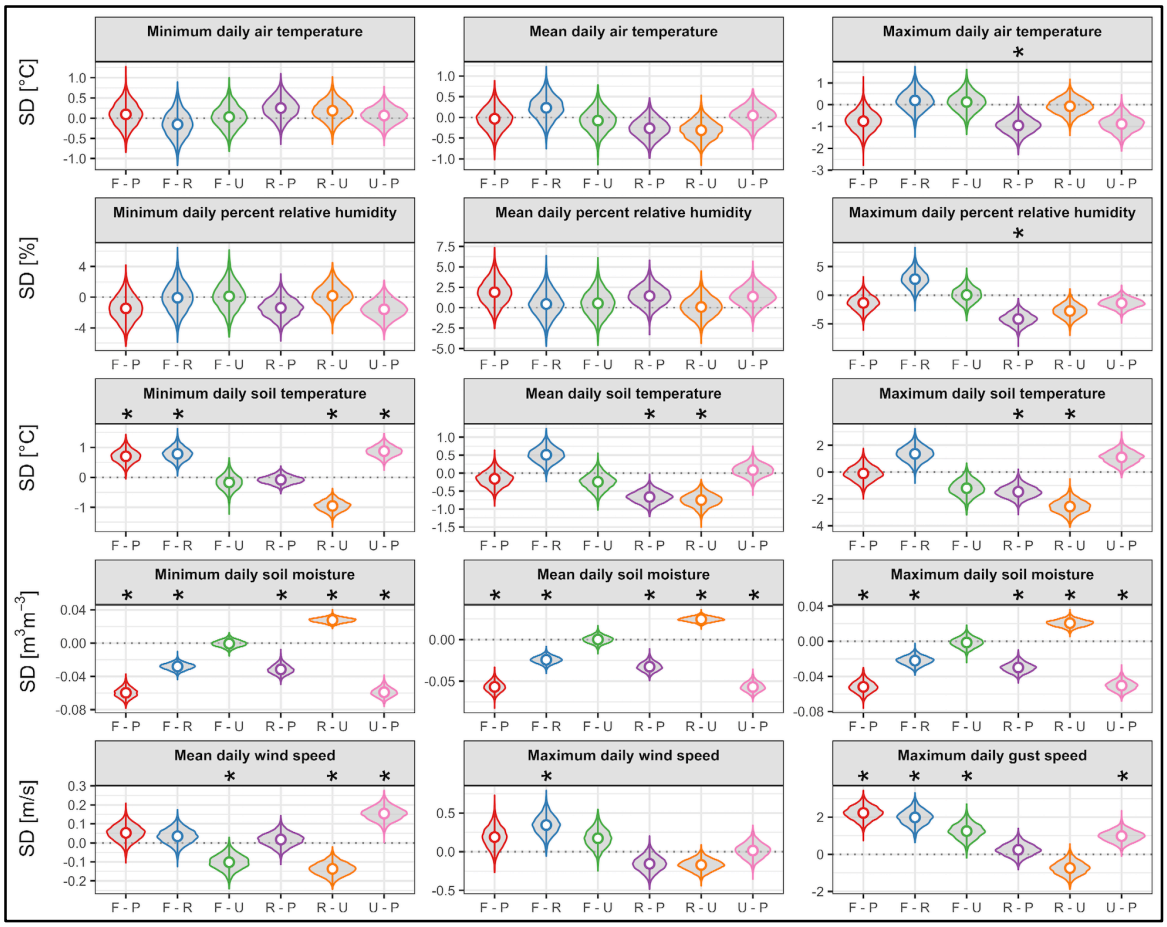


Figure 3.6b. Microclimatic variability mean difference parameter estimates for Mutiny Ridge. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 99.17% HDIs (lines) for pairwise mean differences in seasonal microclimatic standard deviations by microsite type at Mutiny Ridge. R = Rock, P = Pine, U = Unprotected, and F = Fir. Asterisks (*) denote significant differences.

Appendix B

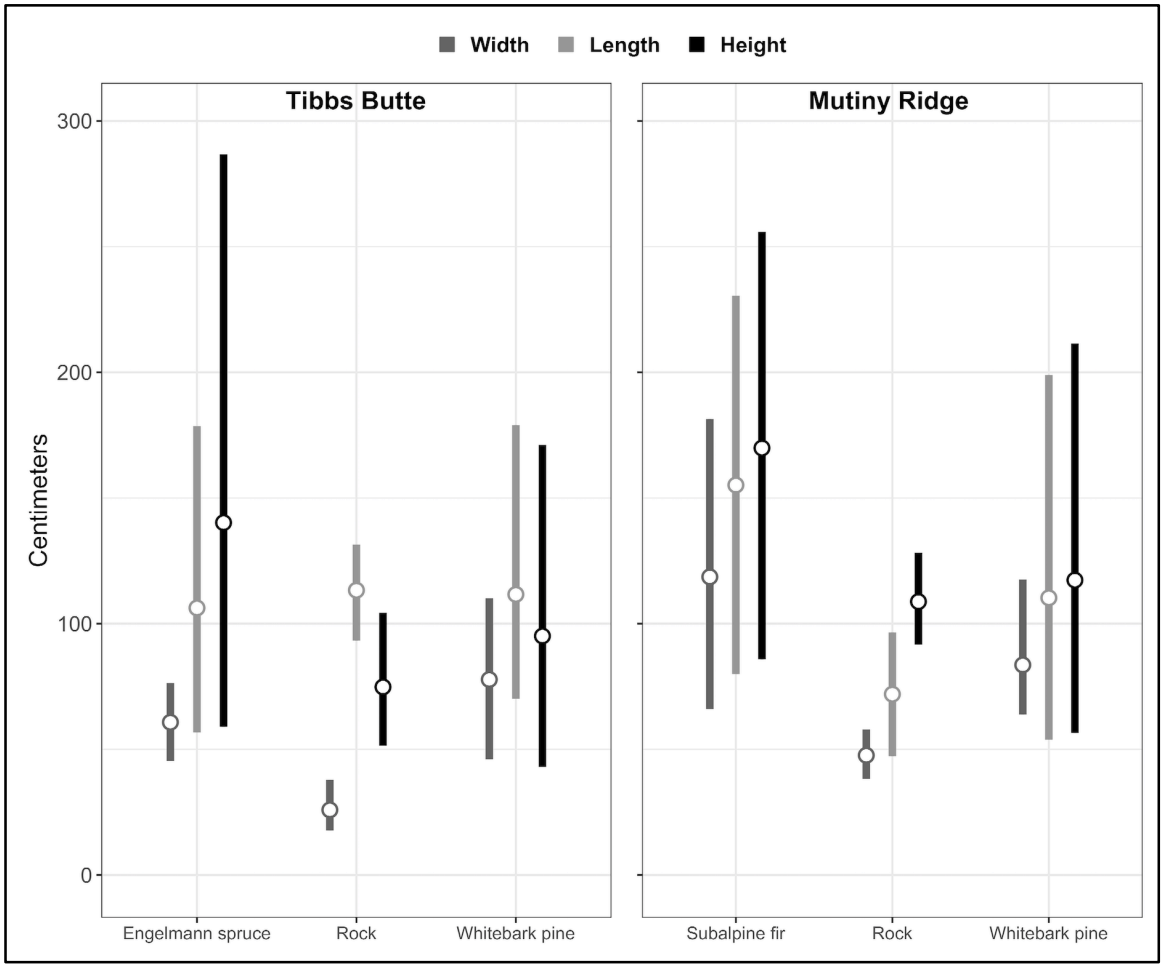


Figure B.1. Nurse object widths, lengths, and heights. To estimate each, we bootstrapped for 5000 iterations to generate a sampling distribution of mean widths, lengths, and heights. We calculated the mean of each sampling distribution to identify its parameter estimate. We used the 0.025 and 0.975 quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% high density interval (HDI). Estimates are indicated by open circles, and lines delineate 95% HDIs.

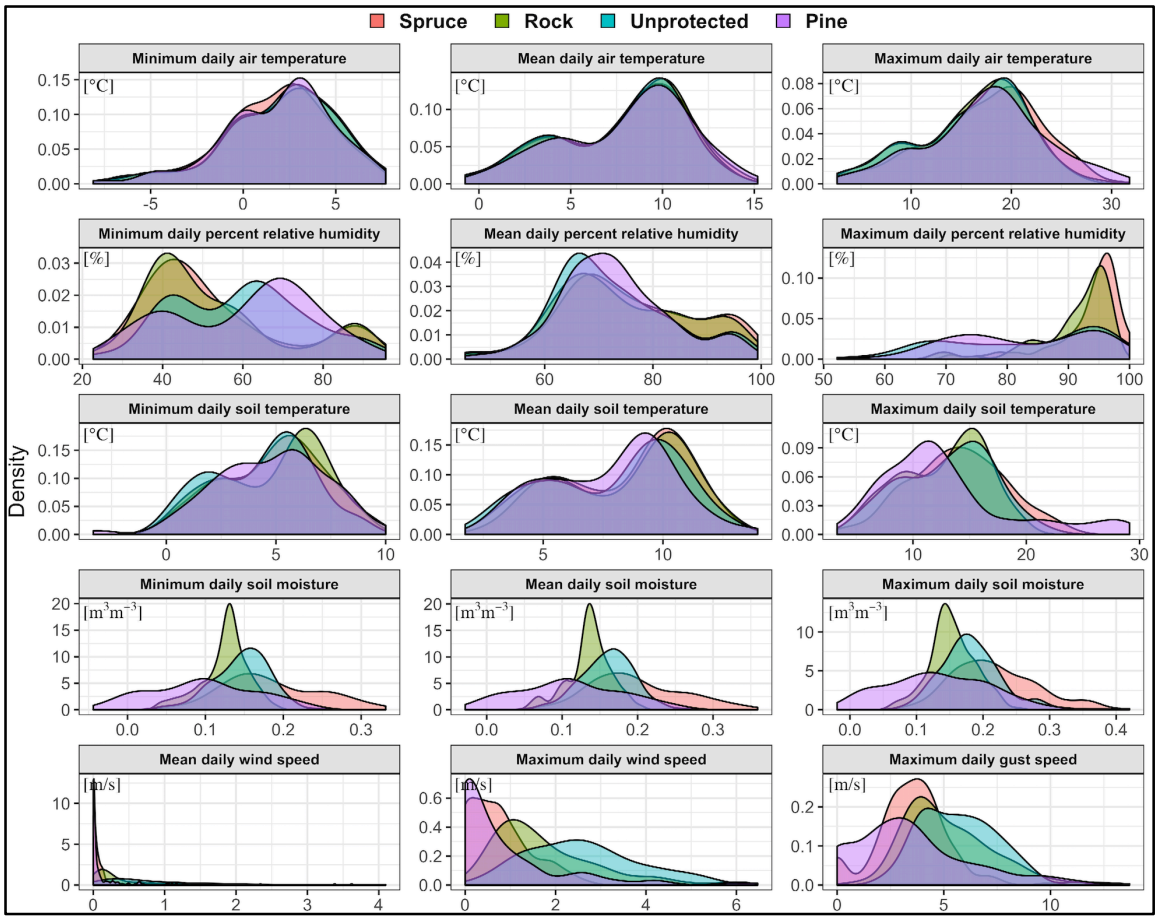


Figure B.2a. Density plots for raw biophysical variables at Tibbs Butte.

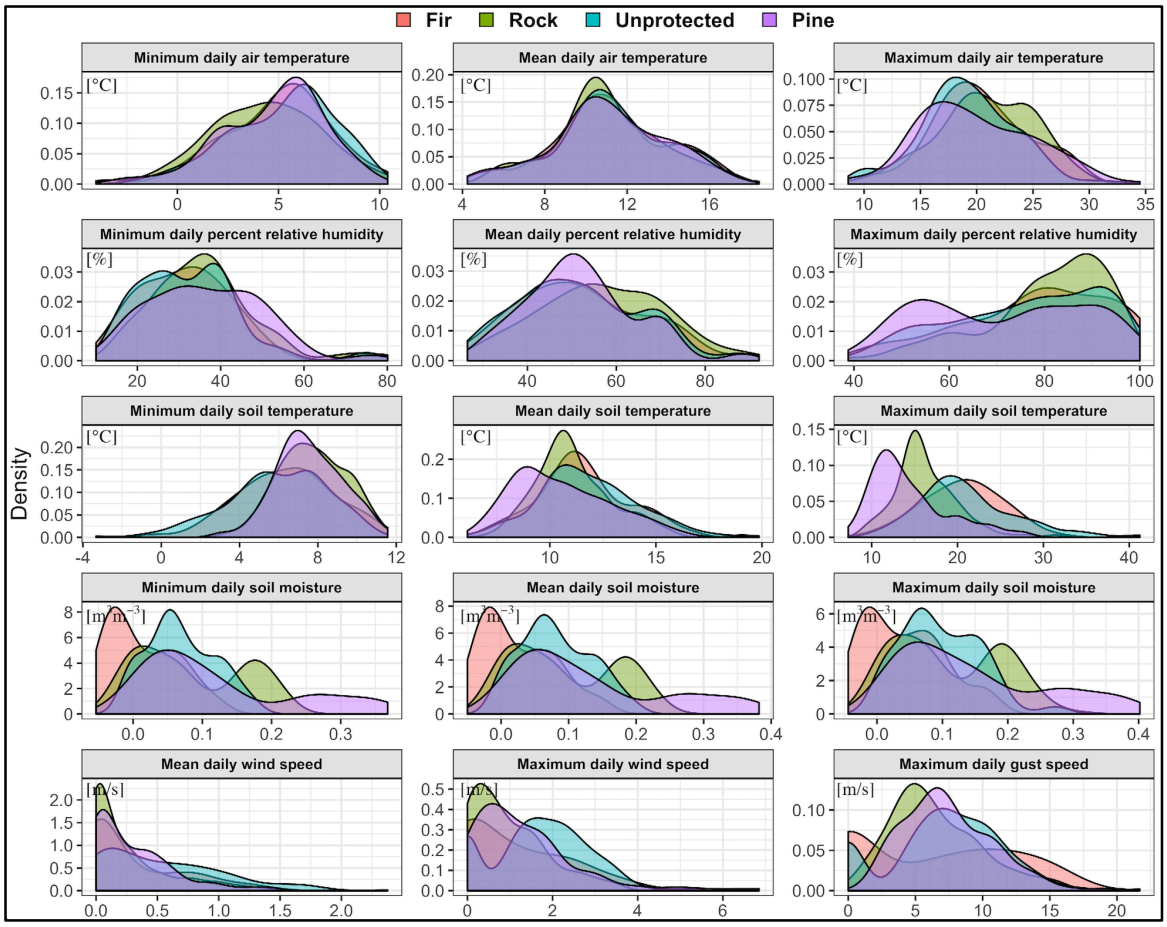


Figure B.2b. Density plots for raw biophysical variables at Mutiny Ridge.

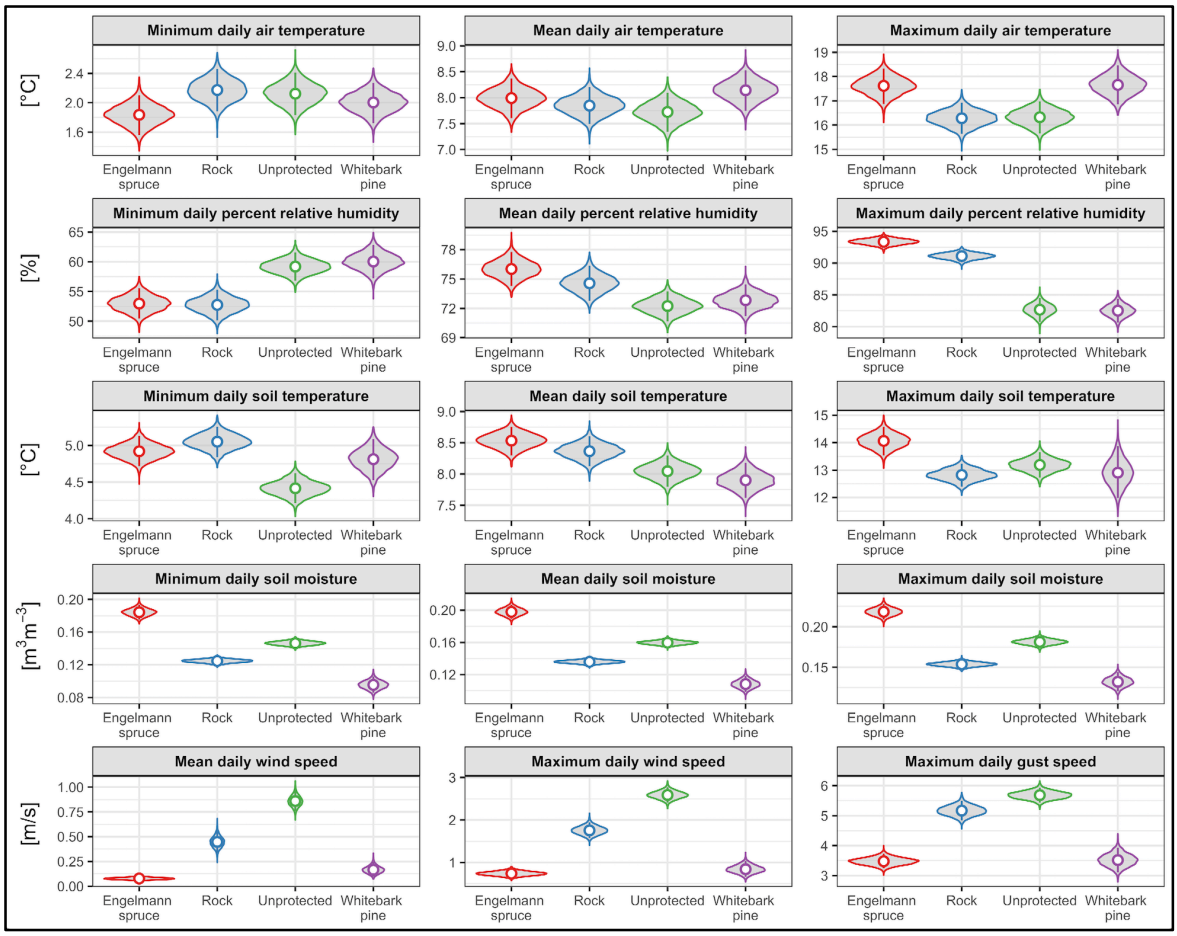


Figure B.3a. Parameter estimates for microclimate at Tibbs Butte. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 95% HDIs (lines) of seasonal microclimatic conditions by microsite type at Tibbs Butte.

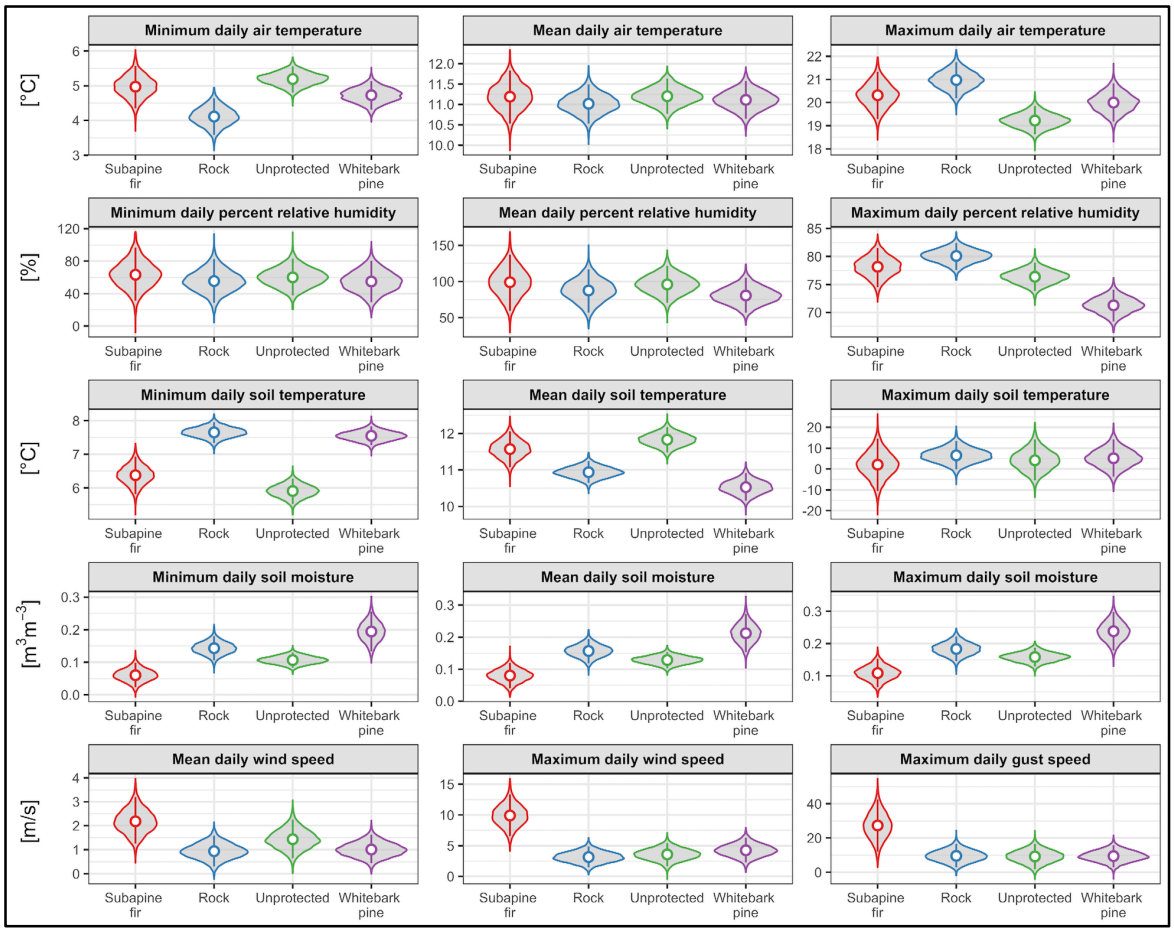


Figure B.3b. Parameter estimates for microclimate at Mutiny Ridge. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 95% HDIs (lines) of seasonal microclimatic conditions by microsite type at Mutiny Ridge.

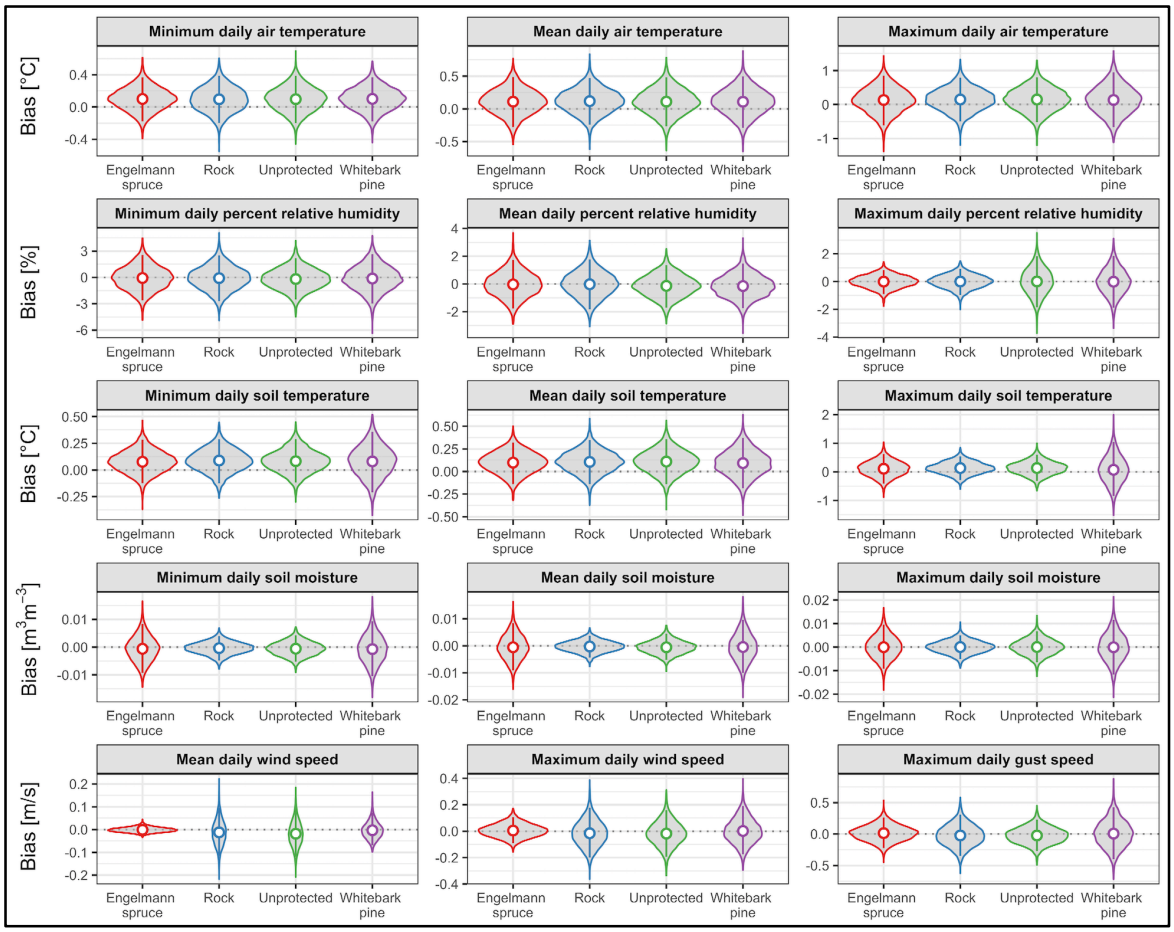


Figure B.4a. Parameter estimates for biases: Tibbs Butte. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 95% HDIs (lines) of bias by microsite type at Tibbs Butte. Bias is the difference between the seasonal climactic estimates derived from modelling and the aggregate temporal mean.

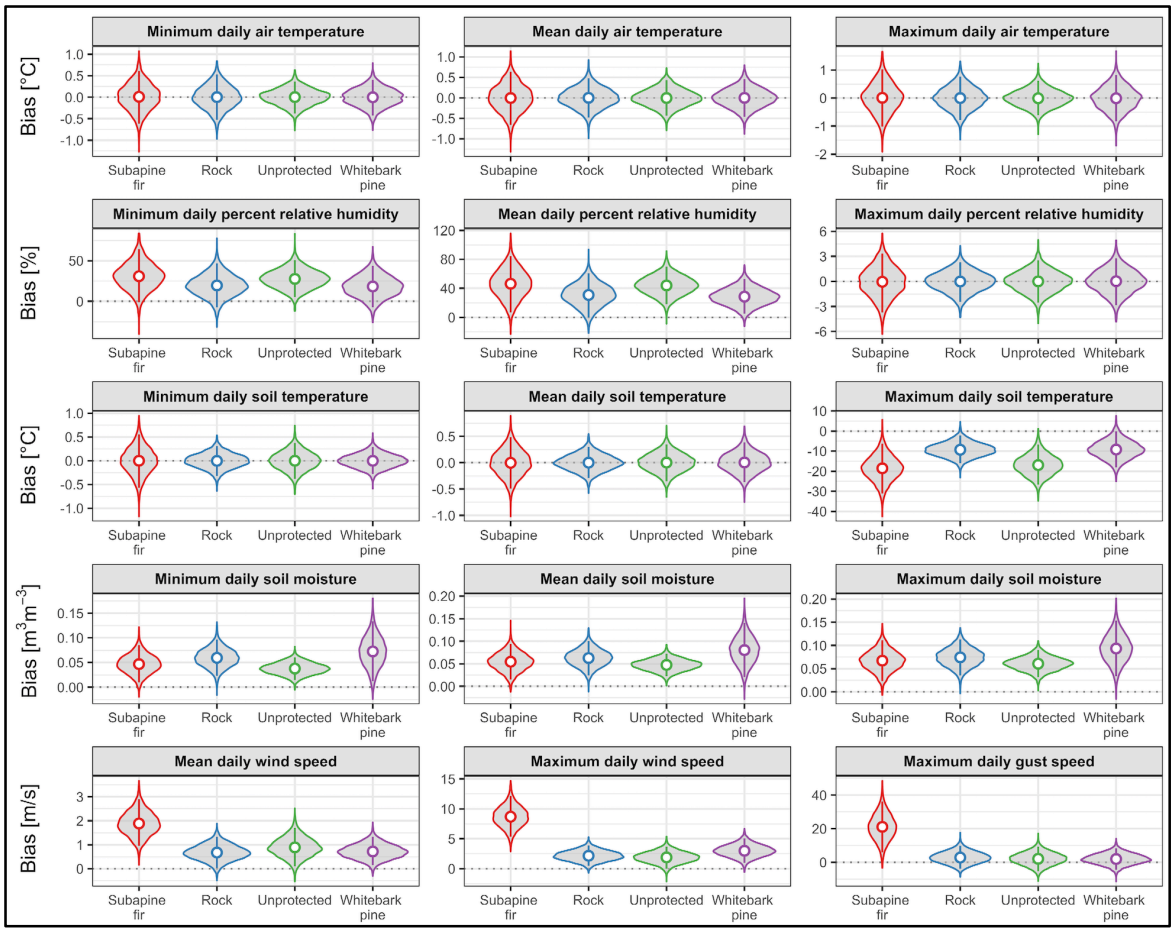


Figure B.4b. Parameter estimates for biases: Mutiny Ridge. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 95% HDIs (lines) of bias by microsite type at Mutiny Ridge. Bias is the difference between the seasonal climactic estimates derived from modelling and the aggregate temporal mean.

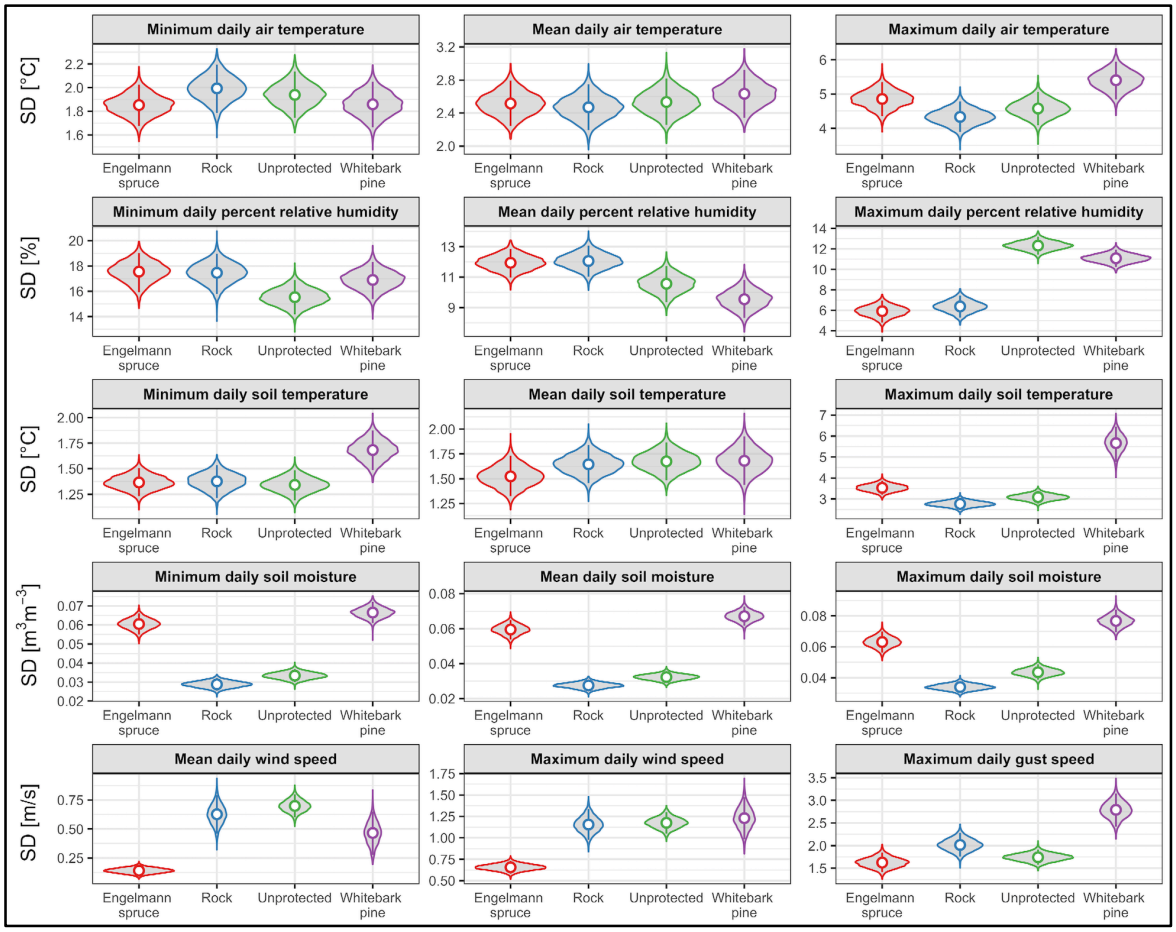


Figure B.5a. Parameter estimates for microclimatic variability at Tibbs Butte. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 99.17% HDIs (lines) of standard deviations in seasonal microclimatic conditions by microsite type at Tibbs Butte.

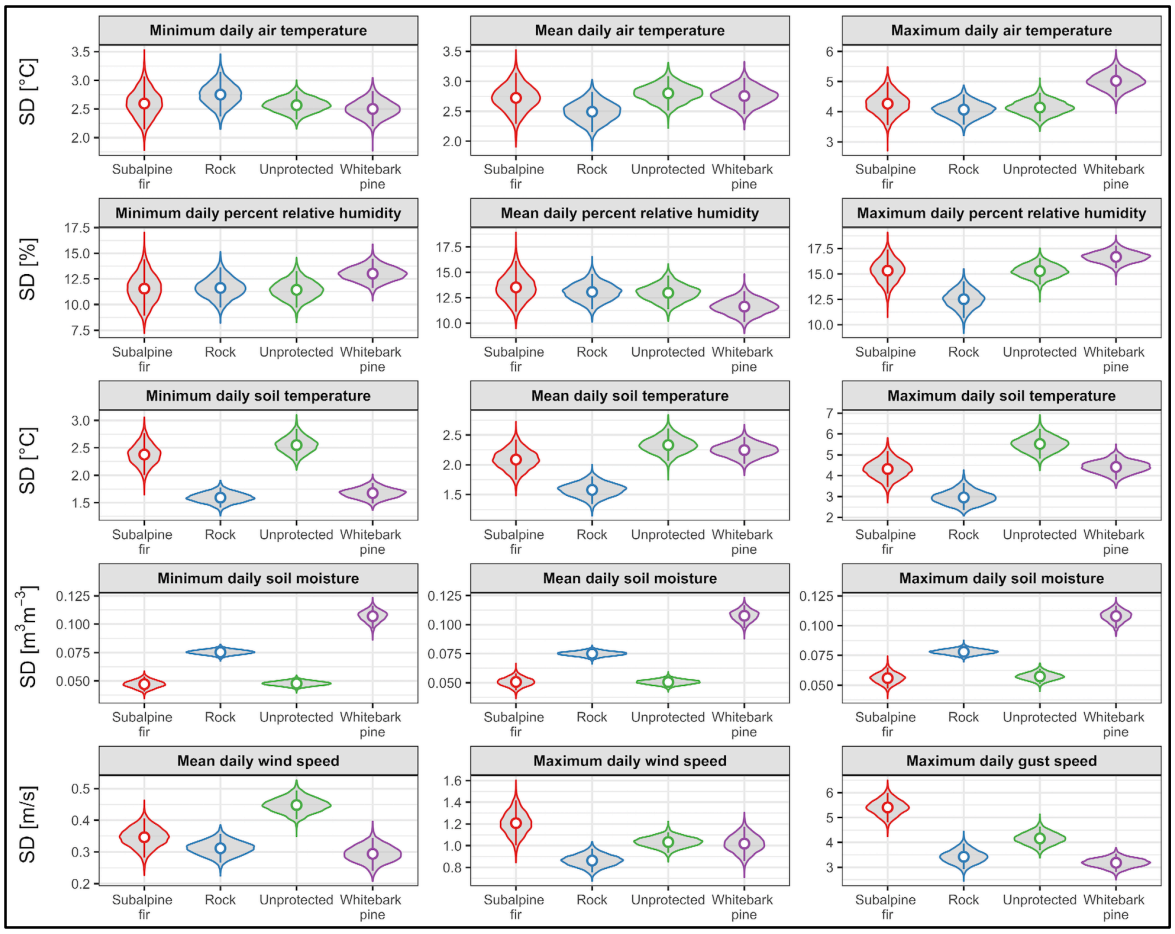


Figure B.5b. Parameter estimates for microclimatic variability at Mutiny Ridge. Violin plot displaying bootstrapped sampling distributions (curves), estimates (open circles), and 99.17% HDIs (lines) of standard deviations in seasonal microclimatic conditions by microsite type at Mutiny Ridge.

Table B.1. Air temperature bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily air temperature	1.56	1.83	2.10
TB	RK	Minimum daily air temperature	1.88	2.17	2.46
TB	UN	Minimum daily air temperature	1.83	2.12	2.41
TB	WB	Minimum daily air temperature	1.73	2.00	2.27
TB	ES	Mean daily air temperature	7.61	7.99	8.37
TB	RK	Mean daily air temperature	7.49	7.85	8.20
TB	UN	Mean daily air temperature	7.34	7.72	8.09
TB	WB	Mean daily air temperature	7.75	8.14	8.53
TB	ES	Maximum daily air temperature	16.87	17.62	18.33
TB	RK	Maximum daily air temperature	15.64	16.28	16.92
TB	UN	Maximum daily air temperature	15.66	16.32	16.97
TB	WB	Maximum daily air temperature	16.86	17.66	18.46
MR	SF	Minimum daily air temperature	4.35	4.97	5.57
MR	RK	Minimum daily air temperature	3.59	4.11	4.64
MR	UN	Minimum daily air temperature	4.81	5.19	5.55
MR	WB	Minimum daily air temperature	4.31	4.73	5.13
MR	SF	Mean daily air temperature	10.54	11.19	11.82
MR	RK	Mean daily air temperature	10.53	11.02	11.49
MR	UN	Mean daily air temperature	10.77	11.20	11.63
MR	WB	Mean daily air temperature	10.65	11.11	11.57
MR	SF	Maximum daily air temperature	19.28	20.31	21.33
MR	RK	Maximum daily air temperature	20.19	20.97	21.74
MR	UN	Maximum daily air temperature	18.62	19.22	19.85
MR	WB	Maximum daily air temperature	19.18	20.00	20.83

Table B.2. Percent relative humidity bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily percent relative humidity	50.43	52.97	55.59
TB	RK	Minimum daily percent relative humidity	50.15	52.75	55.32
TB	UN	Minimum daily percent relative humidity	56.84	59.18	61.56
TB	WB	Minimum daily percent relative humidity	57.22	60.03	62.80
TB	ES	Mean daily percent relative humidity	74.28	76.03	77.79
TB	RK	Mean daily percent relative humidity	72.77	74.56	76.37
TB	UN	Mean daily percent relative humidity	70.67	72.24	73.73
TB	WB	Mean daily percent relative humidity	71.24	72.83	74.45
TB	ES	Maximum daily percent relative humidity	92.45	93.35	94.18
TB	RK	Maximum daily percent relative humidity	90.13	91.10	92.01
TB	UN	Maximum daily percent relative humidity	80.83	82.68	84.50
TB	WB	Maximum daily percent relative humidity	80.67	82.53	84.39
MR	SF	Minimum daily percent relative humidity	31.25	63.31	96.79
MR	RK	Minimum daily percent relative humidity	28.59	55.43	82.54
MR	UN	Minimum daily percent relative humidity	38.03	60.02	83.06
MR	WB	Minimum daily percent relative humidity	29.39	54.95	80.50
MR	SF	Mean daily percent relative humidity	59.76	98.99	137.04
MR	RK	Mean daily percent relative humidity	56.75	87.54	117.12
MR	UN	Mean daily percent relative humidity	70.29	95.87	121.41
MR	WB	Mean daily percent relative humidity	57.18	80.60	105.03
MR	SF	Maximum daily percent relative humidity	74.51	78.16	81.56
MR	RK	Maximum daily percent relative humidity	77.63	80.10	82.40
MR	UN	Maximum daily percent relative humidity	73.86	76.37	78.88
MR	WB	Maximum daily percent relative humidity	68.42	71.27	74.03

Table B.3. Soil temperature bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily soil temperature	4.72	4.92	5.13
TB	RK	Minimum daily soil temperature	4.84	5.05	5.25
TB	UN	Minimum daily soil temperature	4.22	4.42	4.62
TB	WB	Minimum daily soil temperature	4.52	4.81	5.09
TB	ES	Mean daily soil temperature	8.30	8.53	8.76
TB	RK	Mean daily soil temperature	8.12	8.36	8.60
TB	UN	Mean daily soil temperature	7.79	8.04	8.29
TB	WB	Mean daily soil temperature	7.62	7.90	8.18
TB	ES	Maximum daily soil temperature	13.54	14.06	14.58
TB	RK	Maximum daily soil temperature	12.40	12.82	13.23
TB	UN	Maximum daily soil temperature	12.74	13.19	13.66
TB	WB	Maximum daily soil temperature	11.99	12.91	13.87
MR	SF	Minimum daily soil temperature	5.81	6.38	6.94
MR	RK	Minimum daily soil temperature	7.34	7.65	7.96
MR	UN	Minimum daily soil temperature	5.53	5.91	6.28
MR	WB	Minimum daily soil temperature	7.28	7.55	7.84
MR	SF	Mean daily soil temperature	11.08	11.57	12.06
MR	RK	Mean daily soil temperature	10.64	10.94	11.24
MR	UN	Mean daily soil temperature	11.48	11.83	12.17
MR	WB	Mean daily soil temperature	10.15	10.53	10.91
MR	SF	Maximum daily soil temperature	-10.56	2.08	14.48
MR	RK	Maximum daily soil temperature	-0.07	6.54	13.52
MR	UN	Maximum daily soil temperature	-5.45	4.16	14.29
MR	WB	Maximum daily soil temperature	-3.62	5.16	14.23

Table B.4. Soil moisture bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily soil moisture	0.18	0.18	0.19
TB	RK	Minimum daily soil moisture	0.12	0.12	0.13
TB	UN	Minimum daily soil moisture	0.14	0.15	0.15
TB	WB	Minimum daily soil moisture	0.09	0.10	0.11
TB	ES	Mean daily soil moisture	0.19	0.20	0.21
TB	RK	Mean daily soil moisture	0.13	0.14	0.14
TB	UN	Mean daily soil moisture	0.16	0.16	0.16
TB	WB	Mean daily soil moisture	0.10	0.11	0.12
TB	ES	Maximum daily soil moisture	0.21	0.22	0.23
TB	RK	Maximum daily soil moisture	0.15	0.15	0.16
TB	UN	Maximum daily soil moisture	0.17	0.18	0.19
TB	WB	Maximum daily soil moisture	0.12	0.13	0.14
MR	SF	Minimum daily soil moisture	0.02	0.06	0.10
MR	RK	Minimum daily soil moisture	0.11	0.14	0.18
MR	UN	Minimum daily soil moisture	0.08	0.11	0.13
MR	WB	Minimum daily soil moisture	0.13	0.19	0.26
MR	SF	Mean daily soil moisture	0.04	0.08	0.12
MR	RK	Mean daily soil moisture	0.12	0.16	0.19
MR	UN	Mean daily soil moisture	0.10	0.13	0.15
MR	WB	Mean daily soil moisture	0.15	0.21	0.27
MR	SF	Maximum daily soil moisture	0.06	0.11	0.15
MR	RK	Maximum daily soil moisture	0.14	0.18	0.22
MR	UN	Maximum daily soil moisture	0.13	0.16	0.19
MR	WB	Maximum daily soil moisture	0.18	0.24	0.30

Table B.5. Wind and gust speed bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Mean daily wind speed	0.06	0.08	0.10
TB	RK	Mean daily wind speed	0.34	0.45	0.55
TB	UN	Mean daily wind speed	0.76	0.86	0.97
TB	WB	Mean daily wind speed	0.10	0.17	0.24
TB	ES	Maximum daily wind speed	0.65	0.74	0.84
TB	RK	Maximum daily wind speed	1.57	1.76	1.95
TB	UN	Maximum daily wind speed	2.41	2.59	2.77
TB	WB	Maximum daily wind speed	0.67	0.84	1.03
TB	ES	Maximum daily gust speed	3.24	3.48	3.73
TB	RK	Maximum daily gust speed	4.85	5.17	5.50
TB	UN	Maximum daily gust speed	5.44	5.68	5.94
TB	WB	Maximum daily gust speed	3.11	3.52	3.94
MR	SF	Mean daily wind speed	1.25	2.18	3.19
MR	RK	Mean daily wind speed	0.31	0.94	1.58
MR	UN	Mean daily wind speed	0.65	1.43	2.26
MR	WB	Mean daily wind speed	0.44	1.01	1.62
MR	SF	Maximum daily wind speed	6.51	9.91	13.37
MR	RK	Maximum daily wind speed	1.48	3.15	4.86
MR	UN	Maximum daily wind speed	1.69	3.58	5.41
MR	WB	Maximum daily wind speed	2.26	4.25	6.31
MR	SF	Maximum daily gust speed	12.12	27.31	42.48
MR	RK	Maximum daily gust speed	3.01	9.55	16.46
MR	UN	Maximum daily gust speed	1.79	9.19	16.48
MR	WB	Maximum daily gust speed	2.99	9.39	15.69

Table B.6. Air temperature bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily air temperature	-0.361	0.170	0.710
TB	RK-UN	Minimum daily air temperature	-0.516	0.050	0.590
TB	ES-WB	Minimum daily air temperature	-0.673	-0.169	0.344
TB	ES-RK	Minimum daily air temperature	-0.875	-0.339	0.197
TB	ES-UN	Minimum daily air temperature	-0.823	-0.289	0.238
TB	UN-WB	Minimum daily air temperature	-0.420	0.120	0.639
TB	RK-WB	Mean daily air temperature	-1.020	-0.295	0.396
TB	RK-UN	Mean daily air temperature	-0.560	0.123	0.852
TB	ES-WB	Mean daily air temperature	-0.891	-0.151	0.569
TB	ES-RK	Mean daily air temperature	-0.558	0.144	0.834
TB	ES-UN	Mean daily air temperature	-0.465	0.267	0.969
TB	UN-WB	Mean daily air temperature	-1.161	-0.419	0.289
TB	RK-WB	Maximum daily air temperature	-2.725	-1.374	-0.018
TB	RK-UN	Maximum daily air temperature	-1.256	-0.042	1.187
TB	ES-WB	Maximum daily air temperature	-1.570	-0.038	1.408
TB	ES-RK	Maximum daily air temperature	0.028	1.335	2.582
TB	ES-UN	Maximum daily air temperature	-0.088	1.294	2.651
TB	UN-WB	Maximum daily air temperature	-2.759	-1.332	-0.022
MR	SF-WB	Minimum daily air temperature	-0.739	0.244	1.219
MR	SF-RK	Minimum daily air temperature	-0.251	0.860	1.934
MR	SF-UN	Minimum daily air temperature	-1.180	-0.221	0.784
MR	RK-WB	Minimum daily air temperature	-1.503	-0.615	0.275
MR	RK-UN	Minimum daily air temperature	-1.959	-1.081	-0.216
MR	UN-WB	Minimum daily air temperature	-0.296	0.465	1.201
MR	SF-WB	Mean daily air temperature	-1.004	0.078	1.116
MR	SF-RK	Mean daily air temperature	-0.906	0.172	1.264
MR	SF-UN	Mean daily air temperature	-1.091	-0.011	1.043
MR	RK-WB	Mean daily air temperature	-0.975	-0.094	0.822
MR	RK-UN	Mean daily air temperature	-1.041	-0.183	0.655
MR	UN-WB	Mean daily air temperature	-0.704	0.089	0.930
MR	SF-WB	Maximum daily air temperature	-1.463	0.315	2.046
MR	SF-RK	Maximum daily air temperature	-2.319	-0.657	1.099
MR	SF-UN	Maximum daily air temperature	-0.515	1.093	2.697
MR	RK-WB	Maximum daily air temperature	-0.622	0.972	2.510
MR	RK-UN	Maximum daily air temperature	0.400	1.750	3.066
MR	UN-WB	Maximum daily air temperature	-2.146	-0.777	0.591

Table B.7. Percent relative humidity bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily percent relative humidity	-12.056	-7.281	-2.243
TB	RK-UN	Minimum daily percent relative humidity	-11.296	-6.433	-1.686
TB	ES-WB	Minimum daily percent relative humidity	-12.292	-7.063	-1.895
TB	ES-RK	Minimum daily percent relative humidity	-4.832	0.217	5.209
TB	ES-UN	Minimum daily percent relative humidity	-10.695	-6.216	-1.641
TB	UN-WB	Minimum daily percent relative humidity	-5.517	-0.848	3.940
TB	RK-WB	Mean daily percent relative humidity	-1.603	1.738	4.750
TB	RK-UN	Mean daily percent relative humidity	-0.895	2.328	5.681
TB	ES-WB	Mean daily percent relative humidity	0.005	3.204	6.289
TB	ES-RK	Mean daily percent relative humidity	-1.949	1.466	4.976
TB	ES-UN	Mean daily percent relative humidity	0.698	3.795	6.927
TB	UN-WB	Mean daily percent relative humidity	-3.741	-0.591	2.385
TB	RK-WB	Maximum daily percent relative humidity	5.767	8.566	11.380
TB	RK-UN	Maximum daily percent relative humidity	5.645	8.417	11.220
TB	ES-WB	Maximum daily percent relative humidity	8.032	10.817	13.668
TB	ES-RK	Maximum daily percent relative humidity	0.528	2.251	3.983
TB	ES-UN	Maximum daily percent relative humidity	7.959	10.668	13.418
TB	UN-WB	Maximum daily percent relative humidity	-3.326	0.149	3.737
MR	SF-WB	Minimum daily percent relative humidity	-46.538	8.363	65.392
MR	SF-RK	Minimum daily percent relative humidity	-48.694	7.881	65.231
MR	SF-UN	Minimum daily percent relative humidity	-49.467	3.288	58.612
MR	RK-WB	Minimum daily percent relative humidity	-49.002	0.482	51.484
MR	RK-UN	Minimum daily percent relative humidity	-50.793	-4.593	42.605
MR	UN-WB	Minimum daily percent relative humidity	-41.190	5.075	51.247
MR	SF-WB	Mean daily percent relative humidity	-41.709	18.386	79.593
MR	SF-RK	Mean daily percent relative humidity	-52.257	11.449	78.397
MR	SF-UN	Mean daily percent relative humidity	-60.550	3.115	63.105
MR	RK-WB	Mean daily percent relative humidity	-45.590	6.937	58.169
MR	RK-UN	Mean daily percent relative humidity	-60.808	-8.335	41.519
MR	UN-WB	Mean daily percent relative humidity	-31.442	15.272	62.629
MR	SF-WB	Maximum daily percent relative humidity	0.652	6.889	12.518
MR	SF-RK	Maximum daily percent relative humidity	-7.837	-1.938	3.518
MR	SF-UN	Maximum daily percent relative humidity	-4.214	1.786	7.471
MR	RK-WB	Maximum daily percent relative humidity	3.938	8.828	13.724
MR	RK-UN	Maximum daily percent relative humidity	-1.180	3.724	8.349
MR	UN-WB	Maximum daily percent relative humidity	0.256	5.103	10.210

Table B.8. Soil temperature bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily soil temperature	-0.220	0.239	0.699
TB	RK-UN	Minimum daily soil temperature	0.248	0.635	1.016
TB	ES-WB	Minimum daily soil temperature	-0.352	0.108	0.591
TB	ES-RK	Minimum daily soil temperature	-0.525	-0.131	0.239
TB	ES-UN	Minimum daily soil temperature	0.104	0.504	0.880
TB	UN-WB	Minimum daily soil temperature	-0.841	-0.396	0.075
TB	RK-WB	Mean daily soil temperature	-0.033	0.466	0.969
TB	RK-UN	Mean daily soil temperature	-0.174	0.321	0.780
TB	ES-WB	Mean daily soil temperature	0.135	0.635	1.116
TB	ES-RK	Mean daily soil temperature	-0.313	0.169	0.615
TB	ES-UN	Mean daily soil temperature	0.000	0.490	0.938
TB	UN-WB	Mean daily soil temperature	-0.361	0.145	0.630
TB	RK-WB	Maximum daily soil temperature	-1.464	-0.083	1.239
TB	RK-UN	Maximum daily soil temperature	-1.197	-0.366	0.452
TB	ES-WB	Maximum daily soil temperature	-0.319	1.158	2.553
TB	ES-RK	Maximum daily soil temperature	0.335	1.240	2.131
TB	ES-UN	Maximum daily soil temperature	-0.064	0.875	1.795
TB	UN-WB	Maximum daily soil temperature	-1.148	0.283	1.669
MR	SF-WB	Minimum daily soil temperature	-2.028	-1.171	-0.323
MR	SF-RK	Minimum daily soil temperature	-2.125	-1.274	-0.456
MR	SF-UN	Minimum daily soil temperature	-0.460	0.470	1.389
MR	RK-WB	Minimum daily soil temperature	-0.507	0.103	0.651
MR	RK-UN	Minimum daily soil temperature	1.053	1.745	2.386
MR	UN-WB	Minimum daily soil temperature	-2.310	-1.642	-1.017
MR	SF-WB	Mean daily soil temperature	0.202	1.044	1.831
MR	SF-RK	Mean daily soil temperature	-0.148	0.634	1.431
MR	SF-UN	Mean daily soil temperature	-1.065	-0.256	0.548
MR	RK-WB	Mean daily soil temperature	-0.256	0.410	1.042
MR	RK-UN	Mean daily soil temperature	-1.499	-0.890	-0.252
MR	UN-WB	Mean daily soil temperature	0.617	1.300	1.985
MR	SF-WB	Maximum daily soil temperature	-23.973	-3.073	17.615
MR	SF-RK	Maximum daily soil temperature	-23.209	-4.456	14.872
MR	SF-UN	Maximum daily soil temperature	-22.992	-2.076	19.365
MR	RK-WB	Maximum daily soil temperature	-13.813	1.383	16.166
MR	RK-UN	Maximum daily soil temperature	-14.602	2.380	18.192
MR	UN-WB	Maximum daily soil temperature	-18.382	-0.997	17.833

Table B.9. Soil moisture bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily soil moisture	0.014	0.029	0.043
TB	RK-UN	Minimum daily soil moisture	-0.031	-0.022	-0.013
TB	ES-WB	Minimum daily soil moisture	0.071	0.089	0.107
TB	ES-RK	Minimum daily soil moisture	0.047	0.060	0.073
TB	ES-UN	Minimum daily soil moisture	0.025	0.038	0.051
TB	UN-WB	Minimum daily soil moisture	0.036	0.051	0.065
TB	RK-WB	Mean daily soil moisture	0.013	0.028	0.041
TB	RK-UN	Mean daily soil moisture	-0.032	-0.024	-0.015
TB	ES-WB	Mean daily soil moisture	0.071	0.090	0.108
TB	ES-RK	Mean daily soil moisture	0.049	0.062	0.076
TB	ES-UN	Mean daily soil moisture	0.025	0.038	0.052
TB	UN-WB	Mean daily soil moisture	0.037	0.051	0.066
TB	RK-WB	Maximum daily soil moisture	0.006	0.022	0.038
TB	RK-UN	Maximum daily soil moisture	-0.038	-0.027	-0.016
TB	ES-WB	Maximum daily soil moisture	0.067	0.086	0.106
TB	ES-RK	Maximum daily soil moisture	0.050	0.065	0.079
TB	ES-UN	Maximum daily soil moisture	0.022	0.037	0.052
TB	UN-WB	Maximum daily soil moisture	0.031	0.049	0.066
MR	SF-WB	Minimum daily soil moisture	-0.231	-0.134	-0.036
MR	SF-RK	Minimum daily soil moisture	-0.151	-0.083	-0.011
MR	SF-UN	Minimum daily soil moisture	-0.105	-0.046	0.012
MR	RK-WB	Minimum daily soil moisture	-0.152	-0.051	0.042
MR	RK-UN	Minimum daily soil moisture	-0.023	0.036	0.097
MR	UN-WB	Minimum daily soil moisture	-0.182	-0.088	-0.006
MR	SF-WB	Mean daily soil moisture	-0.233	-0.132	-0.040
MR	SF-RK	Mean daily soil moisture	-0.151	-0.077	-0.002
MR	SF-UN	Mean daily soil moisture	-0.111	-0.049	0.016
MR	RK-WB	Mean daily soil moisture	-0.151	-0.055	0.041
MR	RK-UN	Mean daily soil moisture	-0.032	0.028	0.088
MR	UN-WB	Mean daily soil moisture	-0.176	-0.084	0.001
MR	SF-WB	Maximum daily soil moisture	-0.229	-0.130	-0.031
MR	SF-RK	Maximum daily soil moisture	-0.153	-0.075	0.007
MR	SF-UN	Maximum daily soil moisture	-0.118	-0.050	0.021
MR	RK-WB	Maximum daily soil moisture	-0.150	-0.055	0.041
MR	RK-UN	Maximum daily soil moisture	-0.042	0.025	0.092
MR	UN-WB	Maximum daily soil moisture	-0.169	-0.080	0.005

Table B.10. Wind and gust speed bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Mean daily wind speed	0.108	0.281	0.452
TB	RK-UN	Mean daily wind speed	-0.602	-0.412	-0.214
TB	ES-WB	Mean daily wind speed	-0.208	-0.088	0.003
TB	ES-RK	Mean daily wind speed	-0.526	-0.369	-0.228
TB	ES-UN	Mean daily wind speed	-0.936	-0.782	-0.648
TB	UN-WB	Mean daily wind speed	0.524	0.693	0.865
TB	RK-WB	Maximum daily wind speed	0.552	0.913	1.269
TB	RK-UN	Maximum daily wind speed	-1.173	-0.834	-0.471
TB	ES-WB	Maximum daily wind speed	-0.375	-0.102	0.170
TB	ES-RK	Maximum daily wind speed	-1.314	-1.014	-0.733
TB	ES-UN	Maximum daily wind speed	-2.129	-1.848	-1.583
TB	UN-WB	Maximum daily wind speed	1.393	1.746	2.078
TB	RK-WB	Maximum daily gust speed	0.939	1.651	2.336
TB	RK-UN	Maximum daily gust speed	-1.055	-0.516	0.034
TB	ES-WB	Maximum daily gust speed	-0.713	-0.040	0.610
TB	ES-RK	Maximum daily gust speed	-2.260	-1.691	-1.128
TB	ES-UN	Maximum daily gust speed	-2.670	-2.207	-1.733
TB	UN-WB	Maximum daily gust speed	1.491	2.167	2.824
MR	SF-WB	Mean daily wind speed	-0.287	1.175	2.803
MR	SF-RK	Mean daily wind speed	-0.314	1.246	2.834
MR	SF-UN	Mean daily wind speed	-0.976	0.748	2.468
MR	RK-WB	Mean daily wind speed	-1.251	-0.070	1.076
MR	RK-UN	Mean daily wind speed	-1.868	-0.498	0.902
MR	UN-WB	Mean daily wind speed	-0.991	0.428	1.753
MR	SF-WB	Maximum daily wind speed	0.310	5.659	11.319
MR	SF-RK	Maximum daily wind speed	1.674	6.759	11.949
MR	SF-UN	Maximum daily wind speed	1.113	6.326	11.801
MR	RK-WB	Maximum daily wind speed	-4.655	-1.100	2.505
MR	RK-UN	Maximum daily wind speed	-3.788	-0.433	2.970
MR	UN-WB	Maximum daily wind speed	-4.435	-0.666	3.036
MR	SF-WB	Maximum daily gust speed	-3.138	17.915	39.174
MR	SF-RK	Maximum daily gust speed	-3.423	17.756	39.272
MR	SF-UN	Maximum daily gust speed	-4.119	18.115	40.527
MR	RK-WB	Maximum daily gust speed	-11.720	0.158	12.833
MR	RK-UN	Maximum daily gust speed	-12.524	0.358	14.197
MR	UN-WB	Maximum daily gust speed	-13.120	-0.200	12.659

Table B.11. Air temperature standard deviation bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily air temperature	1.68	1.85	2.03
TB	RK	Minimum daily air temperature	1.79	1.99	2.20
TB	UN	Minimum daily air temperature	1.75	1.94	2.14
TB	WB	Minimum daily air temperature	1.67	1.86	2.05
TB	ES	Mean daily air temperature	2.24	2.52	2.79
TB	RK	Mean daily air temperature	2.19	2.47	2.75
TB	UN	Mean daily air temperature	2.26	2.53	2.82
TB	WB	Mean daily air temperature	2.34	2.63	2.92
TB	ES	Maximum daily air temperature	4.35	4.85	5.35
TB	RK	Maximum daily air temperature	3.89	4.33	4.79
TB	UN	Maximum daily air temperature	4.09	4.57	5.06
TB	WB	Maximum daily air temperature	4.84	5.40	5.94
MR	SF	Minimum daily air temperature	2.14	2.59	3.06
MR	RK	Minimum daily air temperature	2.37	2.75	3.15
MR	UN	Minimum daily air temperature	2.32	2.56	2.81
MR	WB	Minimum daily air temperature	2.20	2.50	2.81
MR	SF	Mean daily air temperature	2.29	2.72	3.14
MR	RK	Mean daily air temperature	2.15	2.49	2.82
MR	UN	Mean daily air temperature	2.51	2.80	3.09
MR	WB	Mean daily air temperature	2.45	2.75	3.06
MR	SF	Maximum daily air temperature	3.56	4.27	4.98
MR	RK	Maximum daily air temperature	3.58	4.07	4.57
MR	UN	Maximum daily air temperature	3.68	4.14	4.62
MR	WB	Maximum daily air temperature	4.48	5.02	5.56

Table B.12. Percent relative humidity standard deviation bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily percent relative humidity	15.91	17.55	19.02
TB	RK	Minimum daily percent relative humidity	15.80	17.45	18.95
TB	UN	Minimum daily percent relative humidity	14.18	15.53	16.86
TB	WB	Minimum daily percent relative humidity	15.38	16.89	18.32
TB	ES	Mean daily percent relative humidity	10.97	11.94	12.86
TB	RK	Mean daily percent relative humidity	11.04	12.06	13.07
TB	UN	Mean daily percent relative humidity	9.37	10.57	11.71
TB	WB	Mean daily percent relative humidity	8.32	9.54	10.80
TB	ES	Maximum daily percent relative humidity	4.83	5.92	6.94
TB	RK	Maximum daily percent relative humidity	5.28	6.38	7.46
TB	UN	Maximum daily percent relative humidity	11.47	12.32	13.17
TB	WB	Maximum daily percent relative humidity	10.25	11.08	11.94
MR	SF	Minimum daily percent relative humidity	8.90	11.55	14.39
MR	RK	Minimum daily percent relative humidity	9.70	11.62	13.61
MR	UN	Minimum daily percent relative humidity	9.69	11.44	13.26
MR	WB	Minimum daily percent relative humidity	11.65	13.01	14.46
MR	SF	Mean daily percent relative humidity	11.12	13.53	16.12
MR	RK	Mean daily percent relative humidity	11.38	13.07	14.84
MR	UN	Mean daily percent relative humidity	11.41	12.99	14.67
MR	WB	Mean daily percent relative humidity	10.14	11.64	13.15
MR	SF	Maximum daily percent relative humidity	13.07	15.33	17.40
MR	RK	Maximum daily percent relative humidity	10.68	12.52	14.28
MR	UN	Maximum daily percent relative humidity	13.99	15.29	16.57
MR	WB	Maximum daily percent relative humidity	15.57	16.69	17.79

Table B.13. Soil temperature standard deviation bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily soil temperature	1.23	1.37	1.51
TB	RK	Minimum daily soil temperature	1.21	1.38	1.54
TB	UN	Minimum daily soil temperature	1.19	1.34	1.48
TB	WB	Minimum daily soil temperature	1.49	1.68	1.88
TB	ES	Mean daily soil temperature	1.32	1.52	1.73
TB	RK	Mean daily soil temperature	1.46	1.65	1.84
TB	UN	Mean daily soil temperature	1.48	1.67	1.87
TB	WB	Mean daily soil temperature	1.44	1.68	1.92
TB	ES	Maximum daily soil temperature	3.20	3.53	3.87
TB	RK	Maximum daily soil temperature	2.50	2.77	3.03
TB	UN	Maximum daily soil temperature	2.79	3.09	3.38
TB	WB	Maximum daily soil temperature	4.79	5.66	6.46
MR	SF	Minimum daily soil temperature	2.00	2.38	2.77
MR	RK	Minimum daily soil temperature	1.41	1.59	1.78
MR	UN	Minimum daily soil temperature	2.26	2.55	2.85
MR	WB	Minimum daily soil temperature	1.49	1.67	1.86
MR	SF	Mean daily soil temperature	1.75	2.09	2.42
MR	RK	Mean daily soil temperature	1.34	1.58	1.81
MR	UN	Mean daily soil temperature	2.07	2.33	2.61
MR	WB	Mean daily soil temperature	2.02	2.25	2.47
MR	SF	Maximum daily soil temperature	3.45	4.32	5.18
MR	RK	Maximum daily soil temperature	2.36	2.96	3.65
MR	UN	Maximum daily soil temperature	4.82	5.52	6.25
MR	WB	Maximum daily soil temperature	3.81	4.42	5.02

Table B.14. Soil moisture standard deviation bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Minimum daily soil moisture	0.05	0.06	0.07
TB	RK	Minimum daily soil moisture	0.03	0.03	0.03
TB	UN	Minimum daily soil moisture	0.03	0.03	0.04
TB	WB	Minimum daily soil moisture	0.06	0.07	0.07
TB	ES	Mean daily soil moisture	0.05	0.06	0.06
TB	RK	Mean daily soil moisture	0.02	0.03	0.03
TB	UN	Mean daily soil moisture	0.03	0.03	0.04
TB	WB	Mean daily soil moisture	0.06	0.07	0.07
TB	ES	Maximum daily soil moisture	0.06	0.06	0.07
TB	RK	Maximum daily soil moisture	0.03	0.03	0.04
TB	UN	Maximum daily soil moisture	0.04	0.04	0.05
TB	WB	Maximum daily soil moisture	0.07	0.08	0.08
MR	SF	Minimum daily soil moisture	0.04	0.05	0.05
MR	RK	Minimum daily soil moisture	0.07	0.08	0.08
MR	UN	Minimum daily soil moisture	0.04	0.05	0.05
MR	WB	Minimum daily soil moisture	0.10	0.11	0.12
MR	SF	Mean daily soil moisture	0.04	0.05	0.06
MR	RK	Mean daily soil moisture	0.07	0.07	0.08
MR	UN	Mean daily soil moisture	0.05	0.05	0.05
MR	WB	Mean daily soil moisture	0.10	0.11	0.12
MR	SF	Maximum daily soil moisture	0.05	0.06	0.06
MR	RK	Maximum daily soil moisture	0.07	0.08	0.08
MR	UN	Maximum daily soil moisture	0.05	0.06	0.06
MR	WB	Maximum daily soil moisture	0.10	0.11	0.12

Table B.15. Wind and gust speed standard deviation bootstrapped parameter estimates and 95% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Microsite type	Response variable	2.5% Quantile	Estimate	97.5% Quantile
TB	ES	Mean daily wind speed	0.10	0.14	0.18
TB	RK	Mean daily wind speed	0.46	0.63	0.79
TB	UN	Mean daily wind speed	0.60	0.70	0.80
TB	WB	Mean daily wind speed	0.28	0.47	0.65
TB	ES	Maximum daily wind speed	0.58	0.66	0.73
TB	RK	Maximum daily wind speed	0.98	1.16	1.34
TB	UN	Maximum daily wind speed	1.05	1.18	1.30
TB	WB	Maximum daily wind speed	0.99	1.23	1.47
TB	ES	Maximum daily gust speed	1.41	1.62	1.85
TB	RK	Maximum daily gust speed	1.75	2.01	2.28
TB	UN	Maximum daily gust speed	1.58	1.74	1.91
TB	WB	Maximum daily gust speed	2.42	2.79	3.15
MR	SF	Mean daily wind speed	0.28	0.35	0.41
MR	RK	Mean daily wind speed	0.27	0.31	0.36
MR	UN	Mean daily wind speed	0.40	0.45	0.49
MR	WB	Mean daily wind speed	0.24	0.29	0.34
MR	SF	Maximum daily wind speed	1.00	1.21	1.42
MR	RK	Maximum daily wind speed	0.75	0.86	0.97
MR	UN	Maximum daily wind speed	0.94	1.03	1.12
MR	WB	Maximum daily wind speed	0.86	1.02	1.17
MR	SF	Maximum daily gust speed	4.81	5.41	6.00
MR	RK	Maximum daily gust speed	2.92	3.42	3.96
MR	UN	Maximum daily gust speed	3.69	4.16	4.64
MR	WB	Maximum daily gust speed	2.81	3.18	3.54

Table B.16. Air temperature standard deviation bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily air temperature	-0.254	0.135	0.508
TB	RK-UN	Minimum daily air temperature	-0.340	0.055	0.431
TB	ES-WB	Minimum daily air temperature	-0.364	-0.007	0.355
TB	ES-RK	Minimum daily air temperature	-0.498	-0.142	0.224
TB	ES-UN	Minimum daily air temperature	-0.438	-0.087	0.262
TB	UN-WB	Minimum daily air temperature	-0.273	0.080	0.459
TB	RK-WB	Mean daily air temperature	-0.692	-0.164	0.374
TB	RK-UN	Mean daily air temperature	-0.609	-0.064	0.447
TB	ES-WB	Mean daily air temperature	-0.650	-0.118	0.408
TB	ES-RK	Mean daily air temperature	-0.451	0.046	0.565
TB	ES-UN	Mean daily air temperature	-0.537	-0.018	0.518
TB	UN-WB	Mean daily air temperature	-0.619	-0.099	0.435
TB	RK-WB	Maximum daily air temperature	-2.020	-1.070	-0.097
TB	RK-UN	Maximum daily air temperature	-1.132	-0.245	0.643
TB	ES-WB	Maximum daily air temperature	-1.538	-0.546	0.496
TB	ES-RK	Maximum daily air temperature	-0.404	0.524	1.429
TB	ES-UN	Maximum daily air temperature	-0.696	0.280	1.210
TB	UN-WB	Maximum daily air temperature	-1.832	-0.826	0.189
MR	SF-WB	Minimum daily air temperature	-0.684	0.093	0.856
MR	SF-RK	Minimum daily air temperature	-0.981	-0.156	0.637
MR	SF-UN	Minimum daily air temperature	-0.653	0.028	0.729
MR	RK-WB	Minimum daily air temperature	-0.399	0.249	0.898
MR	RK-UN	Minimum daily air temperature	-0.444	0.184	0.806
MR	UN-WB	Minimum daily air temperature	-0.450	0.065	0.571
MR	SF-WB	Mean daily air temperature	-0.773	-0.032	0.657
MR	SF-RK	Mean daily air temperature	-0.506	0.231	0.923
MR	SF-UN	Mean daily air temperature	-0.821	-0.078	0.611
MR	RK-WB	Mean daily air temperature	-0.865	-0.263	0.328
MR	RK-UN	Mean daily air temperature	-0.886	-0.309	0.289
MR	UN-WB	Mean daily air temperature	-0.510	0.046	0.594
MR	SF-WB	Maximum daily air temperature	-1.918	-0.756	0.441
MR	SF-RK	Maximum daily air temperature	-0.978	0.196	1.319
MR	SF-UN	Maximum daily air temperature	-1.009	0.126	1.286
MR	RK-WB	Maximum daily air temperature	-1.974	-0.953	-0.006
MR	RK-UN	Maximum daily air temperature	-1.003	-0.070	0.789
MR	UN-WB	Maximum daily air temperature	-1.845	-0.883	0.083

Table B.17. Percent relative humidity standard deviation bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily percent relative humidity	-2.298	0.563	3.361
TB	RK-UN	Minimum daily percent relative humidity	-0.903	1.928	4.680
TB	ES-WB	Minimum daily percent relative humidity	-2.232	0.656	3.537
TB	ES-RK	Minimum daily percent relative humidity	-2.994	0.092	3.126
TB	ES-UN	Minimum daily percent relative humidity	-0.740	2.020	4.573
TB	UN-WB	Minimum daily percent relative humidity	-3.906	-1.364	1.256
TB	RK-WB	Mean daily percent relative humidity	0.331	2.517	4.638
TB	RK-UN	Mean daily percent relative humidity	-0.543	1.495	3.657
TB	ES-WB	Mean daily percent relative humidity	0.307	2.397	4.503
TB	ES-RK	Mean daily percent relative humidity	-1.988	-0.120	1.664
TB	ES-UN	Mean daily percent relative humidity	-0.668	1.375	3.409
TB	UN-WB	Mean daily percent relative humidity	-1.307	1.021	3.291
TB	RK-WB	Maximum daily percent relative humidity	-6.490	-4.707	-2.935
TB	RK-UN	Maximum daily percent relative humidity	-7.742	-5.945	-4.046
TB	ES-WB	Maximum daily percent relative humidity	-7.097	-5.168	-3.419
TB	ES-RK	Maximum daily percent relative humidity	-2.548	-0.461	1.461
TB	ES-UN	Maximum daily percent relative humidity	-8.192	-6.406	-4.603
TB	UN-WB	Maximum daily percent relative humidity	-0.405	1.238	2.886
MR	SF-WB	Minimum daily percent relative humidity	-5.482	-1.460	2.627
MR	SF-RK	Minimum daily percent relative humidity	-4.357	-0.066	4.527
MR	SF-UN	Minimum daily percent relative humidity	-4.307	0.117	4.697
MR	RK-WB	Minimum daily percent relative humidity	-4.499	-1.394	1.753
MR	RK-UN	Minimum daily percent relative humidity	-3.186	0.183	3.559
MR	UN-WB	Minimum daily percent relative humidity	-4.543	-1.577	1.381
MR	SF-WB	Mean daily percent relative humidity	-1.760	1.892	5.822
MR	SF-RK	Mean daily percent relative humidity	-3.627	0.455	4.817
MR	SF-UN	Mean daily percent relative humidity	-3.388	0.541	4.570
MR	RK-WB	Mean daily percent relative humidity	-1.562	1.436	4.527
MR	RK-UN	Mean daily percent relative humidity	-3.058	0.086	3.283
MR	UN-WB	Mean daily percent relative humidity	-1.627	1.351	4.347
MR	SF-WB	Maximum daily percent relative humidity	-4.629	-1.359	1.790
MR	SF-RK	Maximum daily percent relative humidity	-0.988	2.809	6.561
MR	SF-UN	Maximum daily percent relative humidity	-3.501	0.036	3.334
MR	RK-WB	Maximum daily percent relative humidity	-6.990	-4.169	-1.358
MR	RK-UN	Maximum daily percent relative humidity	-5.877	-2.773	0.198
MR	UN-WB	Maximum daily percent relative humidity	-3.754	-1.396	0.837

Table B.18. Soil temperature standard deviation bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily soil temperature	-0.630	-0.307	0.028
TB	RK-UN	Minimum daily soil temperature	-0.261	0.035	0.316
TB	ES-WB	Minimum daily soil temperature	-0.635	-0.318	0.003
TB	ES-RK	Minimum daily soil temperature	-0.288	-0.011	0.281
TB	ES-UN	Minimum daily soil temperature	-0.251	0.024	0.288
TB	UN-WB	Minimum daily soil temperature	-0.671	-0.342	-0.013
TB	RK-WB	Mean daily soil temperature	-0.443	-0.035	0.375
TB	RK-UN	Mean daily soil temperature	-0.390	-0.029	0.342
TB	ES-WB	Mean daily soil temperature	-0.574	-0.157	0.284
TB	ES-RK	Mean daily soil temperature	-0.489	-0.122	0.258
TB	ES-UN	Mean daily soil temperature	-0.532	-0.151	0.227
TB	UN-WB	Mean daily soil temperature	-0.423	-0.006	0.397
TB	RK-WB	Maximum daily soil temperature	-4.016	-2.897	-1.667
TB	RK-UN	Maximum daily soil temperature	-0.861	-0.320	0.218
TB	ES-WB	Maximum daily soil temperature	-3.284	-2.129	-0.879
TB	ES-RK	Maximum daily soil temperature	0.218	0.767	1.368
TB	ES-UN	Maximum daily soil temperature	-0.118	0.448	1.046
TB	UN-WB	Maximum daily soil temperature	-3.715	-2.577	-1.341
MR	SF-WB	Minimum daily soil temperature	0.117	0.703	1.276
MR	SF-RK	Minimum daily soil temperature	0.238	0.785	1.364
MR	SF-UN	Minimum daily soil temperature	-0.839	-0.172	0.479
MR	RK-WB	Minimum daily soil temperature	-0.426	-0.082	0.267
MR	RK-UN	Minimum daily soil temperature	-1.429	-0.957	-0.514
MR	UN-WB	Minimum daily soil temperature	0.418	0.875	1.348
MR	SF-WB	Mean daily soil temperature	-0.696	-0.159	0.389
MR	SF-RK	Mean daily soil temperature	-0.037	0.508	1.057
MR	SF-UN	Mean daily soil temperature	-0.832	-0.244	0.304
MR	RK-WB	Mean daily soil temperature	-1.108	-0.667	-0.248
MR	RK-UN	Mean daily soil temperature	-1.259	-0.752	-0.296
MR	UN-WB	Mean daily soil temperature	-0.371	0.085	0.573
MR	SF-WB	Maximum daily soil temperature	-1.473	-0.097	1.338
MR	SF-RK	Maximum daily soil temperature	-0.096	1.365	2.803
MR	SF-UN	Maximum daily soil temperature	-2.795	-1.198	0.248
MR	RK-WB	Maximum daily soil temperature	-2.589	-1.462	-0.259
MR	RK-UN	Maximum daily soil temperature	-3.826	-2.563	-1.219
MR	UN-WB	Maximum daily soil temperature	-0.133	1.101	2.392

Table B.19. Soil moisture standard deviation bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Minimum daily soil moisture	-0.047	-0.038	-0.029
TB	RK-UN	Minimum daily soil moisture	-0.011	-0.005	0.002
TB	ES-WB	Minimum daily soil moisture	-0.017	-0.006	0.004
TB	ES-RK	Minimum daily soil moisture	0.023	0.032	0.041
TB	ES-UN	Minimum daily soil moisture	0.018	0.027	0.036
TB	UN-WB	Minimum daily soil moisture	-0.042	-0.033	-0.024
TB	RK-WB	Mean daily soil moisture	-0.048	-0.039	-0.031
TB	RK-UN	Mean daily soil moisture	-0.011	-0.005	0.001
TB	ES-WB	Mean daily soil moisture	-0.018	-0.008	0.003
TB	ES-RK	Mean daily soil moisture	0.023	0.032	0.040
TB	ES-UN	Mean daily soil moisture	0.019	0.027	0.036
TB	UN-WB	Mean daily soil moisture	-0.044	-0.035	-0.026
TB	RK-WB	Maximum daily soil moisture	-0.054	-0.043	-0.032
TB	RK-UN	Maximum daily soil moisture	-0.018	-0.010	-0.001
TB	ES-WB	Maximum daily soil moisture	-0.028	-0.014	0.000
TB	ES-RK	Maximum daily soil moisture	0.019	0.029	0.039
TB	ES-UN	Maximum daily soil moisture	0.008	0.020	0.030
TB	UN-WB	Maximum daily soil moisture	-0.046	-0.033	-0.022
MR	SF-WB	Minimum daily soil moisture	-0.075	-0.060	-0.043
MR	SF-RK	Minimum daily soil moisture	-0.039	-0.028	-0.018
MR	SF-UN	Minimum daily soil moisture	-0.011	-0.001	0.010
MR	RK-WB	Minimum daily soil moisture	-0.045	-0.032	-0.016
MR	RK-UN	Minimum daily soil moisture	0.020	0.028	0.036
MR	UN-WB	Minimum daily soil moisture	-0.072	-0.059	-0.043
MR	SF-WB	Mean daily soil moisture	-0.072	-0.057	-0.040
MR	SF-RK	Mean daily soil moisture	-0.036	-0.024	-0.013
MR	SF-UN	Mean daily soil moisture	-0.011	0.000	0.012
MR	RK-WB	Mean daily soil moisture	-0.046	-0.033	-0.018
MR	RK-UN	Mean daily soil moisture	0.017	0.024	0.032
MR	UN-WB	Mean daily soil moisture	-0.070	-0.057	-0.042
MR	SF-WB	Maximum daily soil moisture	-0.068	-0.052	-0.033
MR	SF-RK	Maximum daily soil moisture	-0.035	-0.022	-0.009
MR	SF-UN	Maximum daily soil moisture	-0.016	-0.001	0.013
MR	RK-WB	Maximum daily soil moisture	-0.043	-0.030	-0.015
MR	RK-UN	Maximum daily soil moisture	0.010	0.021	0.031
MR	UN-WB	Maximum daily soil moisture	-0.065	-0.051	-0.035

Table B.20. Wind and gust speed standard deviation bootstrapped mean difference parameter estimates and 99.17% HDIs. TB = Tibbs Butte, MR = Mutiny Ridge; WB = Whitebark pine, ES = Engelmann spruce, SF = Subalpine fir, RK = Rock, and UN = Unprotected.

Study area	Comparison	Response variable	0.42% Quantile	Estimate	99.58% Quantile
TB	RK-WB	Mean daily wind speed	-0.161	0.162	0.498
TB	RK-UN	Mean daily wind speed	-0.328	-0.072	0.185
TB	ES-WB	Mean daily wind speed	-0.589	-0.325	-0.078
TB	ES-RK	Mean daily wind speed	-0.715	-0.487	-0.258
TB	ES-UN	Mean daily wind speed	-0.706	-0.559	-0.418
TB	UN-WB	Mean daily wind speed	-0.047	0.234	0.510
TB	RK-WB	Maximum daily wind speed	-0.488	-0.074	0.330
TB	RK-UN	Maximum daily wind speed	-0.306	-0.020	0.263
TB	ES-WB	Maximum daily wind speed	-0.909	-0.573	-0.234
TB	ES-RK	Maximum daily wind speed	-0.760	-0.499	-0.244
TB	ES-UN	Maximum daily wind speed	-0.702	-0.519	-0.317
TB	UN-WB	Maximum daily wind speed	-0.427	-0.054	0.313
TB	RK-WB	Maximum daily gust speed	-1.372	-0.776	-0.164
TB	RK-UN	Maximum daily gust speed	-0.138	0.273	0.671
TB	ES-WB	Maximum daily gust speed	-1.741	-1.165	-0.577
TB	ES-RK	Maximum daily gust speed	-0.868	-0.390	0.058
TB	ES-UN	Maximum daily gust speed	-0.496	-0.117	0.269
TB	UN-WB	Maximum daily gust speed	-1.568	-1.048	-0.513
MR	SF-WB	Mean daily wind speed	-0.062	0.052	0.161
MR	SF-RK	Mean daily wind speed	-0.075	0.035	0.133
MR	SF-UN	Mean daily wind speed	-0.209	-0.102	-0.002
MR	RK-WB	Mean daily wind speed	-0.075	0.018	0.111
MR	RK-UN	Mean daily wind speed	-0.221	-0.137	-0.049
MR	UN-WB	Mean daily wind speed	0.061	0.154	0.249
MR	SF-WB	Maximum daily wind speed	-0.157	0.189	0.539
MR	SF-RK	Maximum daily wind speed	0.015	0.345	0.671
MR	SF-UN	Maximum daily wind speed	-0.132	0.174	0.484
MR	RK-WB	Maximum daily wind speed	-0.407	-0.156	0.094
MR	RK-UN	Maximum daily wind speed	-0.359	-0.171	0.019
MR	UN-WB	Maximum daily wind speed	-0.234	0.015	0.263
MR	SF-WB	Maximum daily gust speed	1.274	2.226	3.145
MR	SF-RK	Maximum daily gust speed	0.896	1.984	2.970
MR	SF-UN	Maximum daily gust speed	0.188	1.246	2.295
MR	RK-WB	Maximum daily gust speed	-0.583	0.242	1.098
MR	RK-UN	Maximum daily gust speed	-1.664	-0.738	0.189
MR	UN-WB	Maximum daily gust speed	0.191	0.980	1.801

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